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## Review and synthesis of knowledge of insular ecology, with emphasis on the islands of Western Australia

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# Review and synthesis of knowledge of insular ecology, with emphasis on the islands of Western Australia

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## ABSTRACT

This paper assesses the legacy of isolation from the mainland and the influence of other factors on biodiversity, biogeography, and faunal and floral change on islands of Western Australia (WA). An empirical perspective from WA reveals numerous neglected insights and overlooked factual information, illustrating the need for improved synthesis of existing knowledge in order to understand the generality of biodiversity patterns and change on islands. A recent loss of direction in the discipline of island biogeography appears to have resulted from over-emphasis of island area, distance from mainland, and absence of competitor species as the key variables in explaining the nature and evolution of insular biodiversity. While these three factors are relevant, they are not always sufficient and should instead be considered as embedded in a more general set of 12 parameters, namely geographic location (including climatic conditions and geomorphological features); history (both geological and human); productivity (soil nutrient status); disturbance (including degree of exposure to salt-laden winds and the presence of Indigenous people); occurrence of breeding marine birds and mammals (particularly significant on small islands); and sampling compatibility. These nine factors are less unequal than is conceded in the literature. Furthermore, most of the 12 factors are interconnected and interdependent, and in combination provide a more satisfactory explanation of insular phenomena. However, the relative influence of these factors differs among species and among higher taxa.

Baselines for the biotas of WA islands date from 1843 (for landbirds and seabirds), much earlier than for mammals (1906), plants (1950), and butterflies (1969). Most WA islands demonstrate no extinctions or immigrations of landbird species, evidence of a static equilibrium. On some other WA islands, immigrations of native landbird species exceed extinctions. Immigrations of seabird species also exceed extinctions. In contrast, the native mammal fauna of WA islands shows few immigrations or extinctions unrelated to human activities. The floras of WA islands show numerous immigrations of species, many of which involve plant species not native to WA. Island floras generally exhibit many extinctions and immigrations, with small islets having the most stable floras. Before Europeans settled WA, it appears that species turnover on islands was either non-existent or infrequent. The concept of punctuated equilibrium appears to provide a better explanation of ongoing biodiversity change on islands than dynamic equilibrium, with the intrusion of humans representing a turning point. Dynamic equilibrium is then a special case applicable to relatively short time scales and islands within the dispersal capabilities of species in a particular taxon.

We are optimistic about the future of biodiversity on the islands of WA if current policies, management and monitoring are maintained and strengthened. Garden and Barrow islands, with their extensive naval or mining infrastructure, demonstrate successful coexistence for at least several decades between humans and biodiversity. The main challenge to protecting biodiversity on the islands of WA is to prevent the establishment of pest species, particularly of ants, rodents, cats (*Felis catus*), house mice (*Mus musculus*) and weeds, and plant and animal diseases. Continual and vigilant monitoring and public education are required. To facilitate this, we recommend that one management plan be prepared to apply to all islands of WA.

Our review concludes with numerous suggestions for future research on the islands of WA, as well as on continental and oceanic islands globally. We advocate a systematic comparative approach, based on a comprehensive global synthesis of information already available on islands in the ecological and natural history literature. Fifteen themes are briefly outlined. Regional syntheses will remain important, but many more are needed in order to achieve effective global synthesis and a more complete and holistic understanding of island ecology. These suggestions should result in improved knowledge about insular biodiversity and more comprehensive protection and management of island life.



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**Key words:** biodiversity, biogeography, explanatory frameworks, insular processes, island, MacArthur and Wilson.

*'24th [June 1865]…Passing islands* [of the Kimberley region of WA] *all day…25th…Still passing islands…26th…There seemed…an unbroken continuity of islands…Still islands, islands, islands. After leaving Cape Bougainville we passed at least 500, of every shape, size, and appearance…Infinitely varied as these islands are – wild and picturesque, grand sometimes almost to sublimity – there is about them all an air of dreariness and gloom…They seem abandoned by nature to complete and everlasting desolation…It was a relief from weariness, anxiety, and danger, when we escaped from this Archipelago.'* JP Stow, Voyage of the Forlorn Hope. *The South Australian Advertiser* 22.8.1865: 3.

*'understanding is not achieved by generality alone, but by a relation between the general and the particular'* (Levins 1966: 430).

*'La verité consiste dans les nuances'* (JR Renan, 1832–1892).

## INTRODUCTION

About 70% of Earth's surface is covered by ocean, comprising an area of c. $3.6 \times 10^8$ km$^2$. Pieces of land completely surrounded by water are a fundamental constituent of Earth's land surface, with perhaps one million islands in existence at present (Fig. 1). Knowledge about islands has contributed significantly to the disciplines of geography, geology, biology, ecology and history, and has provided a rich seam for analyses of pattern and process. The distinction between continents and islands is, however, an arbitrary one based on area (Udvardy 1969; Simberloff 1974; Lack 1976; Mueller-Dombois & Fosberg 1998), whereas the distinction between continental islands (remnants of partially submerged coastal hills) and oceanic islands (land never connected to a continent) is not artificial (Wallace 1881: 230).

There is probably no single reason to account for the attraction of islands to curious and observant minds. Islands provided safe anchorages on long ocean voyages (during the era of wind-powered ships), commercial opportunities (such as sealing and farming), or exotic locations for explorations (as during the voyages of discovery in the Southern Hemisphere in the 1700s and 1800s). Collection of biological specimens for the attention of savants in London and Paris provided a motive for self-advancement. Islands settled by Europeans furnished the means for prolonged visits by naturalists or residency of professionals with personal interest in natural history. Additional enticement included the discrete nature of islands; their utmost simplicity, self-contained nature and sense of exile; the presence of large numbers of breeding seabirds; and the occurrence of unusual species (such as large tortoises).

Visits to, or residence on, islands by scientists have resulted in the collection of information about island biotas, and this has advanced understanding of the origin of species, evolutionary change associated with isolation, and extinction and introduction or unassisted immigration of species. Studies of the natural history of islands have contributed disproportionately to knowledge about the evolution and ecology of species (Mayr 1942). The reason for this is that islands are very numerous; have smaller and simpler biotas than comparably-sized areas on the nearby mainland; demonstrate interesting ecological idiosyncrasies (such as unexpected occurrences of species and unexpected absences of species); and offer opportunities to compare and contrast biotas which, in effect, represent the results of experiments in nature (Wallace 1881: 229; AR Main 1959; 1967; Simberloff 1974). As eloquently expressed by Wollaston (1865: xi), 'islands possess a charm which is peculiarly their own, – each one being in itself a kind of separate, miniature world, in which we may wander at large, observe, and speculate'.

One of the earliest, if not the first, book about islands (apart from Britain) and written in English is that by Sloane (1707, 1725). Based principally on Jamaica as it was in the late 1680s, both volumes provide detailed descriptions of plant and animal species but do not offer any comment about the origin or features of the biota. Overt interest in island biotas by pioneers such as Forster (1778), Lyell (1830, 1832), Darwin (1839, 1859), Hooker (1847, 1853; 1860a, 1860b), Wollaston (1864, 1865, 1867, 1877, 1878), and Wallace (1869, 1881) did not attempt numerical analyses (e.g. numbers of species in relation to areas of islands). Instead their studies provided perceptive generalisations and a plausible narrative based on comparing islands, relating and connecting observations, and carefully sifting factors such as island area, isolation, age, habitat types, fertility, climate, human occupation, collecting effort and interspecific competitors. This multifactorial perspective remained the standard approach up to the 1950s (e.g. K Dammerman 1948 in Thornton 1992; Allee & Schmidt 1951; Darlington 1957). A late example is the detailed appraisal of the avifauna of St Lawrence Island (Alaska) by Fay and Cade (1959). They did not think that isolation completely explained the depauperate nature of the landbird fauna but instead emphasised a combination of three factors – physiography, climate and vegetation.

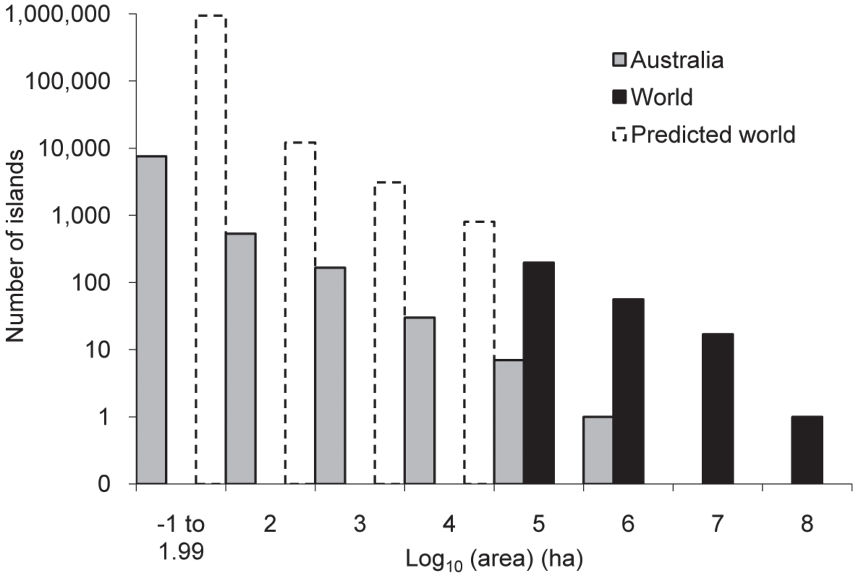



*Figure 1. Number of islands around Australia (grey bars), number of islands in the world with an area >$10^5$ ha (i.e. >$10^3$ km$^2$) (black bars), and predicted number of islands in the world with an area >$10^{-1}$ and <$10^5$ ha (open bars) based on extrapolation from the number of islands >$10^5$ and <$10^8$ ha and assuming an average of regional variation in the Korcak exponent* K *and self-similarity across spatial scales (Mandelbrot 1975). Island area intervals have been rounded down to nearest integer to simplify the x axis. For example, axis label of 2 denotes the interval ≥2 and <3 (or ≥$10^2$ and <$10^3$ ha). Note the change in scale in island area between the first and second columns of the same colour. Number of islands greater than area (A) = 245,988(A)$^{-0.59}$, $R^2$ = 0.999, n = 3.*

This approach was eclipsed by the equilibrium theory proposed by MacArthur and Wilson (1963, 1967). It has since been revived from time to time (e.g. Moreau 1966; Ouellet 1967; Van Balgooy 1969; Salomonsen 1976; Fosberg 1987; Gillespie & Roderick 2002; Lazell 2005; Steadman 2006; Kreft et al. 2008). One potential disadvantage of this approach is that it results in over-complex interpretation, thus raising questions as to what constitutes an appropriate blending of theory and observation. In addition, this approach results in numerous case histories which remain unsynthesised and from which broader generalisations and patterns are not elucidated.

Current perspectives about the causes of species richness on islands provide disproportionate attention to island area and distance from the nearest source area. Both factors have been allowed to obscure the relevance and operation of numerous other factors (Van Balgooy 1969). Area is regarded as predominantly influencing the extinction rate of species (highest on small islands) and distance is held to affect the immigration rate (least on remote islands). An early but informal version of the species richness versus island area relationship was published by Darlington (1957: 483). Since 1963 an equilibrium theory that assumes balance of rates of extinction and immigration of species (MacArthur & Wilson 1963) has resulted in numerous publications showing that species richness and area are correlated (Connor & McCoy 1979). Species richness and distance are inversely correlated (MacArthur & Wilson 1963; Adler & Dudley 1994), but are these correlations cause and effect? Are distance and area most used because they can be easily measured from maps, and if so, are theories based on these factors misconceived? Is this perspective an oversimplification? Has it diverted attention from other important factors? Is a single explanation that is applicable globally possible? What do the data from Western Australian islands indicate?

Part of the attraction of islands is that each is of its own kind (*sui generis*) and the possibility that other physical factors may be relevant and influential is commonly neglected in the scientific literature. Other broad criticisms of the current status of understanding of island ecology can be offered. The first concerns the representativeness of the islands that have been studied (Abbott 1980b). How typical of the world's islands are exotic and remote archipelagoes such as the Canary and Galápagos islands? Since Darwin (1859), oceanic islands have been emphasised over continental islands. In contrast, Wallace (1881) explicitly acknowledged that most of the world's islands are continental in origin. Nor are studies of islands after volcanic eruption (such as Krakatau and Surtsey) representative. Small continental islands (the most common type) have been inadequately studied, and perhaps neglected because of their apparent ordinariness and familiarity. Second, how geographically comprehensive have analyses and syntheses of island ecological and biogeographic data been? Although many WA islands have been investigated, few of the many publications available have been cited by authors of syntheses or textbooks. This is probably because most of these authors live and work in Europe and North America. Third, the islands of southern WA are globally significant as a result of their inaccessibility to Indigenous people for 7–10 ka [tens of thousands of years], an unusual characteristic of continental islands that is also shared in Australia with offshore islands of South Australia and those in Bass Strait (between mainland Australia and Tasmania). Finally, WA islands share with the Australian mainland many species that have evolved when Australia was part of Gondwana (Ericson et al. 2002; Holt et al. 2013). This phylogenetic distinctiveness in itself should attract the attention of Northern Hemisphere researchers interested in achieving a robust global synthesis.

Many studies of island ecology have, however, not focused solely on area, isolation or interspecific competition. These have emphasised other factors, including ecological changes via nutrient enrichment caused by nesting seabirds (Gillham 1956, 1961a,1961b, 1961c, 1962, 1963; Anderson & Polis 1999); extent of suitable habitat (Halkka et al. 1971); cessation of top-down effects following the absence of vertebrate predators (Terborgh et al. 2001); presence of invasive species such as cats (*Felis catus*), snakes, mongooses (*Herpestes* spp.) and weeds introduced inadvertently or deliberately by humans (Elton 1958; Fritts & Rodda 1998); and the likely frequent use of fire on islands occupied or visited by Indigenous people (Abbott 1980c). These and other factors can be accommodated under the traditional multifactorial model but not by the equilibrium model.

Of more practical importance is the significant role that islands now play globally in the conservation of biodiversity. For example, islands comprise 49% of Endemic Bird Areas (Stattersfield et al. 1998). In WA, islands have allowed many species and populations of mammals to persist and thus have conserved such entities (AR Main 1968; AA Burbidge & McKenzie 1989; Maynes 1989; Dickman 1992; Kennedy 1992; AA Burbidge 1999; Woinarski et al. 2014b). This is a consequence of threats that are prevalent on the adjacent mainland not occurring on most WA islands, especially feral cats (AA Burbidge & Manly 2002), red foxes (*Vulpes vulpes*; JE Kinnear et al. 2002), and habitat destruction caused by settlement (Abbott 1997).

Western Australia (WA), with a coastline of one-third of the Australian coastline (Geoscience Australia 2013), is an ideal geographical region for island studies. Nearly all of its islands share the same post-glacial history, representing detached fragments of flooded coastal hills. These continental islands are numerous, occur within a wide range of latitude (13° 30′–35° S) and longitude (113°–129° E) and consequential climatic differences, show great variation in area, distance from the mainland, shape, elevation, and rock type (Abbott & Burbidge 1995), and some have a lengthy history of scientific observation (Table 1).

Before proceeding to a consideration of historical studies of WA islands, it is useful to provide context by examining briefly the development of knowledge about islands elsewhere in Australia. Concerted attempts to document at least the floral and vertebrate faunal components of island biodiversity in Australia began in Tasmania in the 1830s and 1840s with the visits of John Gould, John Gilbert and Joseph Hooker, and the settlement of naturalists such as Thomas Ewing and Ronald Gunn. The establishment of the Field Naturalists' Club of Victoria (1880) and the Australasian Ornithologists Union (1901) in Melbourne gave impetus to the biological exploration of islands in Bass Strait (King Island 1887, 1902; Kent Group 1890; Furneaux Group 1893, 1901, 1912; Albatross Island 1894, 1895) and in Victorian waters (Mud Island 1903–1928; Lawrence Rocks 1907; Lady Julia Percy Island 1935–1936). This interest extended to South Australia in 1905 (Kangaroo Island). Members of naturalist and scientific societies based in Sydney, Brisbane and Adelaide investigated islands in the Capricorn Group (1904–1931), Moreton Bay (1908–1926), Nuyts Archipelago and Investigator Group (1922–1924), Fraser Island (1930), and Sir Joseph Banks Group (1937–1937). The individual papers are too numerous (>80) to cite here, but may be accessed in the state-based naturalist and Royal Society journals and *The Emu*.

In marked contrast, until c. 1950 there were few attempts to list the terrestrial species present on WA islands (Table 1). Rottnest Island, being close to Perth, was given most attention, particularly with respect to invertebrates (Michaelsen & Hartmeyer 1907–1930; J Clark 1929; WH Mathews 1930), frogs (Glauert 1928), reptiles (Glauert 1928), and birds (Lawson 1905; Glauert 1928). There was an expedition to Houtman Abrolhos in 1913 that resulted in several papers, including one by Alexander (1922). Other contributions from this era, varying in their comprehensiveness, are noted in Table 1.

The literature (both published papers and unpublished reports) on WA islands is extensive but remains scattered across many journals and archives (Table 1). It awaits broad synthesis. Nevertheless, some compilations and analyses of data have been published during the past 60 years. Topics studied include:

- Macropodoid (kangaroo, wallaby and bettong) species richness in relation to island area (AR Main 1961a; AR Main & Yadav 1971) and Aboriginal access (Abbott 1980c) [The superfamily Macropodoidea includes the families Macropodidae (with only the genera *Lagorchestes, Lagostrophus, Macropus, Petrogale,* and *Setonix* represented on WA islands) and Potoroidae (with only the genus *Bettongia* recorded on WA islands). The genera *Thylogale* and *Potorous* are represented on other Australian islands].
- Plant communities and species composition (JH Willis 1953; McArthur 1957; Storr et al. 1959; AA Burbidge & Prince 1972; Edmiston & White 1974; AA Burbidge et al. 1978, 1982; Abbott & Black 1980; Pen & Green 1983; Buckley 1983; DCLM 1990; Backhouse 1993; G Keighery 1995; JM Harvey et al. 2001; G Keighery et al. 2002, 2006; Henson et al. 2014; Lyons et al. 2014);
- Vegetation maps of islands (McArthur 1957; Storr 1965a; Garden Island Working Group 1974; Anon.

**Table 1**

Contributors to the enrichment of knowledge about the terrestrial ecology and biodiversity of islands of Western Australia – A chronology since the European settlement of Western Australia**.** WAH = Western Australian Herbarium collection. WAM = Western Australian Museum collection. Islands are listed from north to south, then west to east. Multi-authored studies conducted as part of the same expedition are usually grouped together.

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1830 | C Barker | Seal (King George Sound), Michaelmas, Green (Oyster Harbour) | plants, vegetation, seabirds | Abbott 2001; Mulvaney & Green 1992: 288, 290–291, 295 |
| 1831 | A Collie | Coffin | plants, seabirds, seals | Shoobert 2005: 250 |
| 1839, 1842-1843 | J Gilbert | Houtman Abrolhos (Pelsaert, Mangrove, East & West Wallabi), Rottnest, Garden, St Alouarn | birds, reptiles, mammals, plants | Fisher 1992, *The Inquirer* 19.4.1843, Whittell 1942 |
| 1839 | J Drummond | Rottnest, Carnac, Garden | plants | Drummond 1839 |
| 1839–1842 | JAL Preiss | Rottnest, Carnac, Garden, Penguin, Mistaken | plants, invertebrates?, reptiles?, birds?, mammals? | Lehmann 1844–1847, McGillivray 1975, NG Marchant 1990 |
| 1841–1842 | WN Clark | Rottnest, Garden, Carnac, Penguin, Cape Leeuwin islands, Sandy, Chatham, Goose, Saddle, Eclipse, Bald, Middle (Recherche) | seabirds, seals, wallabies | *The Inquirer* 25.8.1841, 1.9.1841, 6.10.1841 *The Perth Gazette* 20.8.1842, 3.9.1842, 10.9.1842, 1.10.1842, 8.10.1842 |
| 1845?–1866 | G Maxwell | Newdegate, Mistaken, Breaksea, Bald, Doubtful, Middle (Recherche), Gulch | plants | H Henderson pers. comm. 2013, JH Willis 1953 |
| 1856?–1862? | A Oldfield | Rottnest, Garden, Doubtful, Bald | plants | H Henderson pers. comm. 2013 |
| 1889 | AJ Campbell | Houtman Abrolhos (Rat, Pelsaert), Rottnest, Breaksea | birds, plants | AJ Campbell 1890 a,b |
| 1890–1891 | JJ Walker | 'Queen', Parry, Cassini, Condillac, Baudin, (W?) Montalivet, N Maret, Heywood, Adele, Dirk Hartog, East Wallabi | land snails, insects, birds, mammals | Solem 1979, 1981, 1985, 1988; J Walker 1892, JJ Walker 1897 |
| 1894–1910 | HFO Lipfert | Bernier, Dorre, Houtman Abrolhos (Beacon, Rat, Morley, Wooded, Gun, 'an island off' Gun, Middle, Pelsaert), Rottnest | birds, mammals | Alexander 1922, Glauert 1928, Lipfert 1912, *The West Australian* 15.12.1894: 2, WAM, Whittell 1940b |
| 1896–1906 | JT Tunney | Bedout, Barrow, Lewis, Bernier, Dorre, Bald, Archipelago of the Recherche (Boxer, Mondrain, Sandy Hook, Remark, Twin Peak, Station, Goose, Middle) | birds, mammals | Kitchener & Vicker 1981, Tunney 1902, Whittell 1938 |
| 1897, 1903, 1907, 1913?, 1916? | CP Conigrave | Pelsaert, Rottnest | birds | Conigrave 1916, Glauert 1928 |
| 1897 | R Helms | Houtman Abrolhos (including Rat, Pelsaert, Gun, small island near Gun) | plants, birds | Alexander 1922, Helms 1898 |
| 1899 | R Hall | Houtman Abrolhos (West Wallabi, East Wallabi, Pigeon, Rat, Pelsaert [South]) | birds | Hall 1902 |
| 1900 | S Le Souëf | Shoalwater Bay (Seal?, Middle Shag?, West Shag?, Bird) | birds | S Le Souëf 1902 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1903*, 1908, 1918, 1920 | FL Whitlock | Delambre, Bezout, Dampier Archipelago (Legendre, Dolphin, Angel, Gidley, Enderby, Eaglehawk), Fortescue, Passage, Barrow, Round, Double, Osprey, Cormorant, Dirk Hartog, Rat, Rottnest | birds | Lawson 1905; Whitlock 1918, 1919, 1921a; Whittell 1940a |
| 1905 | W Michaelsen & R Hartmeyer | Dirk Hartog, Rottnest | invertebrates, frogs, reptiles | Michaelsen & Hartmeyer 1907–1930 |
| 1905–1906 | GC Shortridge | Bernier, Mistaken | birds, mammals | Ogilvie-Grant 1909, 1910 |
| 1905–1906 | WV Fitzgerald | Sunday | plants | Fitzgerald 1907, 1919 |
| 1907 | CG Gibson, AW Milligan, CP Conigrave | Houtman Abrolhos (E Wallabi, Rat, Wooded, Pelsaert) | birds, mammals | CG Gibson 1908, *The West Australian* 23.11.1907: 4, 6.12.1907: 7, 7.12.1907: 5 |
| 1908 | WD Campbell | Sunday | Aborigines & their names for species | WD Campbell 1916 |
| 1909–1922 | T Carter | Dirk Hartog, Mistaken, Breaksea | birds | Carter 1910, 1917; Whitley 1971 |
| 1909–1910 | GF Hill | Hecla, Augustus, Mary, Bernier | birds | GF Hill 1911, Mees 1962 |
| 1910–1911 | EL Grant Watson | Bernier | reptiles | AM Douglas & Ride 1962 |
| 1911 | R Söderberg | Sunday | mammals | Mjöberg 1913, Söderberg 1918 |
| 1912 | PD Montague | Hermite, Trimouille, SE Long, & other unnamed islands in Montebello Group | centipedes, spiders, insects, reptiles, birds, mammals | HR Hogg 1914; Montague 1913, 1914 |
| 1913, 1919 | WB Alexander | Houtman Abrolhos (North, Pelican, East Wallabi, West Wallaby, Pigeon, Long, Sandy, Rat,, 'an island off Rat Island', Wooded, Pelsaert), Garden | plants, vegetation, reptiles, birds, mammals | Alexander 1921ab, 1922 |
| 1920–1944 | CA Gardner | Cockatoo, Rottnest | plants | WAH |
| 1921 | AFB Hull, HS Grant, JH Wright | Mistaken, Michaelmas, Archipelago of the Recherche (Rabbit, Woody, Lion, Charley, Gunton, Rob, Mondrain) | frogs, reptiles, birds | Hull 1922; Kinghorn 1925, 1927 |
| 1922 | AH Robinson | Parrakeet (Rottnest), Rottnest | birds | A Robinson 1935 |
| 1925, 1927, 1935, 1937–1949, 1958, 1967–1970 | DL Serventy | Browse, Adele, East Lacepede, Bedout, Montebello Group, Lowendal Group, Barrow, North West Cape to Cape Preston islands, Shark Bay, Houtman Abrolhos (Pelsaert, Wooded), Culeenup, Archipelago of the Recherche (Charley, Rabbit, Cliff, Gunton, Sandy Hook, Corbett, Woody, Lion, New, Marts, Station, George, Gulch, Owen, Middle, Wickham [Stanley], Goose, Daw [Christmas], New Year) | land snails, birds, plants | Gardner 1949, Serventy 1938, 1947, 1949, 1970, Serventy & Marshall 1964, Serventy et al. 1971, D Serventy 1952, Storr et al. 1986, WAH, JH Willis 1953 |
| 1927–1928 | L Glauert | Rottnest, Archipelago of the Recherche | frogs, reptiles, birds | Glauert 1928, 1954 |
| 1930, 1936 | PT Sandland | Pelsaert, Sandland | birds | Sandland 1931, 1937 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1931 | Harvard Expedition (including GM Allen, PJ Darlington, WE Schevill) | West Wallabi, Rottnest | reptiles | Loveridge 1934 |
| 1938–1940, 1976 | EH Sedgwick | Barrow, Garden, Shoalwater Bay islands | birds | Sedgwick 1940, 1978 |
| 1940–1942, 1947–1950, 1963 | VN Serventy | Houtman Abrolhos (Pelsaert, Morley, Wooded), Lancelin, Shoalwater Bay, Archipelago of the Recherche (Figure of Eight, Boxer, Sandy Hook, Remark, Long, Pasco, Thomas, Woody, Burton Rock, Cloud, Hastings, MacKenzie [Round], Termination, Mondrain, Nares [Menzies], North Twin Peak, South Twin Peak, Cave, Kermadec [Wedge], Westall [Combe], Middle, Goose, Douglas, Salisbury, Daw [Christmas]) | spiders, opiliones, snails, birds, reptiles, mammals | Glauert 1954, Macpherson 1954, BY Main 1954, Serventy 1943, 1950, 1952, 1953, 1965, Serventy & White 1943, Serventy et al. 1971 |
| 1944–1946 | S Fowler | Lesueur, Jones, Stewart, White, Low Rocks, Bedout, Dirk Hartog, Egg, Pelican, Faure | seabirds (aerial counts) | Fowler 1947, D Serventy 1952 |
| 1945–1980 | GG Smith | Pelsaert, Rottnest, Garden | plants | WAH, GG Smith 1978 |
| 1947 | JM Thomson, B Shipway | Goose | birds, mammals | Thomson & Shipway 1948 |
| 1947 | WR Serventy | Green (near Rottnest) | seabird | Serventy [WR] 1947, WABN No. 5: 15 |
| 1950 | JH Willis | Archipelago of the Recherche (Figure of Eight, Boxer, Woody, Sandy Hook, Remark, Long, Pasco, Mackenzie [Round], Termination, Mondrain, North Twin Peak, South Twin Peak, Cave, Kermadec [Wedge], Westall [Combe], Middle, Goose, Douglas, Salisbury, Daw [Christmas]) | plants, vegetation, fungi, mosses, lichens | JH Willis 1953 |
| 1948 | HE Tarr | Pelsaert | birds | Tarr 1949 |
| 1948 | K Buller | Garden | birds | K Buller 1949 |
| 1948–1949 | D Reid | Dyer, Green (Rottnest) | seabirds | Reid 1949, 1950 |
| 1950–1962 | RD Royce | Depuch, Dampier Archipelago (6), Great Sandy [Beagle], Serrurier [Long], Thevenard, Dorre, Bernier, East Wallabi, Rottnest, Archipelago of the Recherche (7) | plants | Royce 1964, WAH |
| 1950, 1954–1958 | J Warham | Cockatoo, Pelsaert, Lancelin, Eclipse, Dirk Hartog | plants, birds | Dunlop & Mitchell 2001, J Ford 1965, Serventy et al. 1971; WAH, Warham 1956b, 1958 |
| 1951–1952, 1978, 1990–1997 | WM McArthur | Rottnest, Garden, Carnac | plants, vegetation, fire succession | McArthur 1957, 1996a, 1996b, 1998; McArthur & Bartle 1981; Wykes & McArthur 1995 |
| 1952 | FL Hill | Trimouille, South East, Flag, North West, Alpha, North Delta, South Delta, Hermite, East Hermite | plants, vegetation, insects, reptiles, birds | Britton 1955, M Cameron 1955, FL Hill 1955, Kimmins 1955, Pope 1955, Salmon 1955 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1953 | EHM Ealey | Pelsaert | birds | Ealey 1954 |
| 1953 | DN Calderwood | Garden | birds | Calderwood 1953 |
| 1954–1984 | BY Main | Koolan, Cockatoo, Barrow, Dirk Hartog, North (Abrolhos), East Wallabi, Rat, Rottnest, Garden, Bald, Termination, Mondrain, North Twin Peak | spiders | BY Main 1954, 1957, 1984 |
| 1954–1988 | WH Butler | Barrow, Lowendal, North Sandy, Middle Mangrove, Thevenard, Dirk Hartog | plants, frogs, reptiles, birds, mammals | Bannister 1969, Butler 1970, 1975, 1989, Heatwole & Butler 1981, AR Main & Yadav 1971, WAH |
| 1955–1978 | JW Green | Houtman Abrolhos (2), Rottnest, Dyer | plants | WAH |
| 1955–1965 | GM Storr | Depuch, Dampier Archipelago (Legendre, Dolphin, Angel, Gidley, West Lewis, Rosemary, Enderby), Shark Bay (Bernier & 12 small islands), Houtman Abrolhos (North, West Wallabi, East Wallabi, Pigeon, Tattler, Long, Mangrove, Beacon, Pelican), North & South Green, Sandland, Jurien Bay islands (Boullanger [Long], Whitlock, Essex Rocks, Tern), Wedge, Lancelin, Edward, Rottnest, Green & other satellite islets [Rottnest], Carnac, Garden, Shoalwater Bay islands (Gull Rock, Bird, Seal, Shag, Penguin), Bald | plants, vegetation, birds, reptiles | Johnstone & Storr 1988, 1998, 2004; Storr MSab, 1960, 1961, 1962, 1963, 1964abcd, 1965abcd, 1966, 1968, unpubl.; pers. comm. 1971; Storr et al. 1959, 1986, 1999, 2002; WAH |
| 1956 | JAL Watson | Carnac | birds | JAL Watson 1956 |
| 1956–1958 | AM Baird | Garden | plants | Baird 1958 |
| 1957–1964 | JR Ford | Dongara–Lancelin | reptiles, birds | J Ford 1963 |
| 1959 | WDL Ride, RD Royce, GF Mees, AM Douglas, CH Tyndale-Biscoe | Bernier, Dorre | plants, vegetation, reptiles, birds, mammals, historical | AM Douglas & Ride 1962, Mees 1962, Ride 1962ab, Ride & Tyndale-Biscoe 1962, Royce 1962 |
| | JW Shield | Rottnest | *Setonix brachyurus* | Shield 1964, 1967 |
| 1959 | M Gillham | Houtman Abrolhos (North, West Wallabi, East Wallabi), Fisherman, Favourite, Boullanger [Long], Cervantes, Lancelin, Edward, Rottnest, Green [Rottnest], Parakeet, Carnac, Shoalwater Bay islands (Gull Rock, Bird, Shag, Seal, Penguin), Hamelin, Seal (Cape Leeuwin), St Alouarn | plants, vegetation, seabirds, seals | Gillham 1961a, 1963 |
| 1960s–1974 | FC van Ingen | Koolan | butterflies | LE Koch 1975, LE Koch & van Ingen 1969 |
| 1961–1999 | AS George | East Lewis, Dirk Hartog, East Wallabi, Rat, Wooded, Penguin, Garden, High | plants | WAH |
| 1961–1999 | PJ Fuller | Browse, Adele, Lacepede (West, Middle), Bedout, North Turtle, Shark Bay (42), Houtman Abrolhos (146 islands), Sandland, Boullanger, Whitlock, Essex Rocks, Salisbury | birds, mammals | AA Burbidge & Fuller 1996, 1998, 2000; AA Burbidge et al. 1982, 1987, 1996; Fuller & Burbidge 1981, 1987, 1992, 1998; Fuller et al. 1994ab; Storr unpubl. |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1962 | WDL Ride, RD Royce, GM Storr | Depuch | plants, vegetation, reptiles, birds, mammals, historical | Ride 1964ab, Royce 1964, Storr 1964cd |
| 1962?–1965 | JP Kelsall | West Wallabi, Garden | *Macropus eugenii* | Kelsall 1965 |
| 1963 | RD Hughes | Bernier | *Lagostrophus fasciatus* | Hughes 1965 |
| 1964 | DW Goodall | Barrow, Locker, Ashburton, Long | plants | unpubl. list provided to I Abbott, Buckley 1983, WAH |
| 1964 | Aquinas College | Houtman Abrolhos (Pigeon, Seagull, West Wallabi, East Wallabi, Long, Beacon) | plants, reptiles, seabirds, mammals | O'Loughlin 1965 |
| 1964–1987 | JS Beard | Kimberley (3), Barrow, Dirk Hartog | plants | WAH |
| 1965 | Aquinas College | Houtman Abrolhos (West Wallabi, East Wallabi, Mangrove, Pigeon, Tattler, Eastern, Seagull) | vegetation, reptiles, birds, mammals | O'Loughlin 1966 |
| 1966 | Aquinas College | Houtman Abrolhos (Basile, Pelsaert, Middle, Square, Gun, Jubilee) | plants, invertebrates, reptiles, birds | O'Loughlin 1969 |
| 1966–1967 | E Lindgren | Lancelin, Carnac, Lion | plants | Lindgren 1956, 1973 |
| 1967 | LE Sedgwick | Dirk Hartog | birds | LE Sedgwick MS [unpubl. report provided by Wesley College, South Perth], Sedgwick 1968 |
| 1968 | Aquinas College | Houtman Abrolhos (Basile, Gun, Rat, Murray, Pelsaert) | plants, invertebrates, reptiles, birds, mammals | O'Loughlin 1969 |
| 1969 | GI Pearman | Garden | *Callitris preissii* | Pearman 1971 |
| 1969–1979 | RIT Prince | Dampier Archipelago (Legendre, Dolphin, Angel, Gidley, West Lewis, Enderby, Rosemary), Bernier, Dorre, Dirk Hartog | wallabies | AA Burbidge & Prince 1972, Richards et al. 2001, J Short et al. 1992 |
| 1969–1999 | AA Burbidge | Browse, Adele, Lacepede (West, Middle), Bedout, North Turtle, Dampier Archipelago (Legendre, Dolphin, Angel, Gidley, West Lewis, Enderby, Rosemary), Montebello Islands (7+), Barrow, Shark Bay (43), Houtman Abrolhos (146 islands), Boullanger, Salisbury | plants, vegetation, reptiles, birds, mammals | AA Burbidge 1971, 1999; AA Burbidge et al. 1982, 1987, 1996, 1997, 2000; AA Burbidge & Fuller 1996, 2000, 2004; AA Burbidge & Main 1971; AA Burbidge & Prince 1972, Fuller & Burbidge 1981, 1987, 1992, 1998ab; Fuller et al. 1994, Halse et al. 1995 |
| 1969 | DF Dorward | Archipelago of the Recherche (Cull, Rabbit, Charley, Sandy Hook, Remark, Frederick) | *Cereopsis novaehollandiae* | Department of Fisheries and Fauna file 015054F3102 |
| 1970s | BJ Richardson | Barrow | *Macropus robustus* | BJ Richardson & Sharman 1976 |
| 1970 | Aquinas College | Houtman Abrolhos (Newman, Morley, Pelsaert, Hut, Helsinki, Suomi, Rat, Wooded) | plants, reptiles, birds | GA Green 1972 |
| 1971 | AA Burbidge, D Kitchener, NL McKenzie, LA Smith | Kimberley (14) | plants, vegetation, frogs, reptiles, birds, mammals | AA Burbidge & McKenzie 1978, AA Burbidge et al. 1978, NL McKenzie et al. 1978, LA Smith & Johnstone 1978, LA Smith et al. 1978 |
| 1971 | DH Perry | Barrow | termites | DH Perry 1972 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1971–2007 | RE Johnstone | 185 islands: Kimberley (68), Pilbara (6), Gascoyne (2), Houtman Abrolhos (70), south-west (17), Archipelago of the Recherche (22) | birds, reptiles | Johnstone 1990, 1992; Johnstone & Coate 1992; Johnstone & Smith 1987, 1988; Johnstone & Storr 1998, 2004; Johnstone et al. 1990abcd; LA Smith & Johnstone 1987, 1988ab, 1996; WAM |
| 1971–1979, 1991–1992 | GT Smith | Garden, Coffin, Bald | plants, vegetation, reptiles, birds, seals | MG Brooker et al. 1995ab, GT Smith 1977, GT Smith & Kolichis 1980 |
| 1971–1973, 1985–1987, 1990 | LA Smith | Kimberley (28), Barrow, Archipelago of the Recherche (9) | frogs, reptiles | Johnstone & Smith 1987, 1988; Johnstone et al.abcd; LA Smith 1976; LA Smith & Harold 2011, LA Smith & Johnstone 1978, 1987, 1988ab, 1996; LA Smith et al. 1978, 2005 |
| 1971–1973, 1991 | J Dell | Kimberley (27), Archipelago of the Recherche (Daw, New Year, Spindle, Anvil, Six Mile) | vertebrates | LA Smith et al. 1978, 2005 |
| 1972 | AA Burbidge, A Chapman, J Dell, T Evans, RE Johnstone, NG Marchant, NL McKenzie, LA Smith, PG Wilson | Kimberley (14) | plants, vegetation, frogs, reptiles, birds, mammals | AA Burbidge & McKenzie 1978, AA Burbidge et al. 1978, NL McKenzie et al. 1978, LA Smith & Johnstone 1978, LA Smith et al. 1978 |
| 1972–1978 | NG Marchant | Kimberley (11), Barrow, Pascoe, Rottnest, Garden | plants | Abbott et al. 2000, WAH |
| 1972 | P Hussey | Penguin, Culeenup | vegetation succession, plants | Hussey 1973, Hussey et al. 1992 |
| 1972 | TE Bush, GA Lodge | Bedout | birds | TE Bush & Lodge 1977 |
| 1972–1986 | MIH Brooker | Archipelago of the Recherche (5) | plants | WAH |
| 1973 | AA Burbidge, J Dell, RE Johnstone, NL McKenzie, LA Smith, PG Wilson, WK Youngson | Kimberley (10) | plants, vegetation, frogs, reptiles, birds, mammals | AA Burbidge & McKenzie 1978, AA Burbidge et al. 1978, NL McKenzie et al. 1978, LA Smith & Johnstone 1978, LA Smith et al. 1978 |
| 1973 | P Fullagar, G Van Tets | Eclipse | birds | Fullagar & Van Tets 1976 |
| 1973–2004 | KF Kenneally | Kimberley (40), Pilbara (7), Shark Bay (10) | plants, vegetation | Kenneally 1991, 1992, 1993, 2011; Kenneally et al. 1991, 2000; WAH |
| 1973–2000 | AS Weston | Dolphin, Dorre, Bernier, Observatory, Middle (Recherche) | plants, vegetation, fire succession | WAH, Weston 1985 |
| 1973–2005 | RJ Cranfield | Faure, Garden, Carnac, Saddle | plants | Abbott et al. 2000, 2006; WAH |
| 1973–2000 | ME Trudgen | Dolphin, Angel, Gidley, Wilcox, Salutation, Three Bays, Middle (Recherche) | plants | WAH |
| 1973, 1982, 1995, 2000, 2006 | AS Baynes | Barrow, Bernier, Dirk Hartog, Faure | subfossil mammals | Baynes 2008, pers. comm.; AA Burbidge & George 1978 |
| 1974 | A Keast | Culeenup | birds | Keast 1975 |
| 1974–1978, 1982, | I Abbott | 197 islands: Kimberley (11), Pilbara–northwest | plants, vegetation, invertebrates, | Abbott 1977a, 1978, 1979, 1980a, 1980c, 1980d, |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1984, 1995–1996, 2006 | | (11), Shark Bay (3), Houtman Abrolhos (19), Dongara–Lancelin (12), Trigg, Fremantle–Becher Point (121), Hamelin, Sandy, Chatham, Albany (10), Doubtful (2), Archipelago of the Recherche (4) | reptiles, birds, mammals, historical | 1980e, 1981a, 1981b, 1982, 1992, 2000, 2006, unpubl.; Abbott & Black 1978, 1980; Abbott & Burbidge 1995; Abbott et al. 1978, 2000, 2006; AA Burbidge et al. 1997; WAH |
| 1975 | N Kolichis | Bedout, North Turtle | birds | Kolichis 1977 |
| 1975 | J Goodsell, A Tingay, SR Tingay | Woody | plants, vegetation, reptiles, birds, mammals | Goodsell et al. 1976 |
| 1975 | AC Robinson, JF Robinson | Bernier | mammals & ectoparasites of *Pseudomys fieldi* | AC Robinson et al. 1976, JF Robinson et al.1978 |
| 1975–1988 | AJM Hopkins | Kimberley (11), Middle (Recherche), Salisbury | plants, vegetation, fire succession | AA Burbidge et al. 1982, WAH |
| 1975–2013 | JN Dunlop | Walcott, Dampier Archipelago (Haycock, Elphick Nob, Goodwyn), Rat, Lancelin, Carnac, Penguin | seabirds | Dunlop & Mitchell 2001; Dunlop & Storr 1981; Dunlop et al. 1988, 1994abcd; Wooller & Dunlop 1979, 1981 |
| 1976 | JAK Lane | Adele, Lacepede (West, Middle), Bedout, St Alouarn | seabirds, *Cereopsis novaehollandiae* | AA Burbidge et al. 1987, Halse et al. 1995, Lane 1978 |
| 1976 | AN Start | Bald, Wilson, Corbett, North Twin Peak, South Twin Peak | birds | AN Start pers. comm. |
| 1976–1982 | SG Lane | 23 islands: St Alouarn, Flat, Stanley, Archipelago of the Recherche (12) | seabirds | SG Lane 1982abcdefghijk, 1984ab, 1985 |
| 1976–1977 | A & S Tingay | Archipelago of the Recherche (4) | seabirds | Tingay & Tingay 1982abc |
| 1977 | P Coster | Rottnest islets | reptiles | Coster 1977 |
| 1977 | H Heatwole | Barrow | lizards | Heatwole & Butler 1981 |
| 1977 | M Howard | Bernier | birds | Howard 1978 |
| 1979 | SJJF Davies | Garden | birds | SJJF Davies 1980 |
| 1979–1988 | A Solem | Kimberley (18) | land snails | Solem 1979, 1981, 1985, 1988, 1991, Solem & McKenzie 1991 |
| 1980 | S Bunn | Rottnest islets | terrestrial isopods | Bunn 1980 |
| 1980 | RC Buckley | Barrow, adjacent islands, Lowendal | plants, vegetation | Buckley 1982, 1983 |
| 1980–1992, 2007 | DA Saunders, CPS de Rebeira | Rottnest, Garden | birds | MG Brooker et al. 1995a, Saunders & de Rebeira 1983 |
| 1981 | AK Daw | Canning | birds | Daw 1982ab |
| 1981 | D Perry | Elphick Nob | birds | D Perry 1982 |
| 1982 | CN Smithers | Montebello Group (Long, Trimouille, Hermite), Lowendal Group (North, South), Barrow, North Double, South Double, Middle, Boodie | insects | Smithers & Butler 1983, Smithers 1984ab, 1985, 1988 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1982 | JE Kinnear, NL McKenzie | Salisbury | mammals | AA Burbidge et al. 1982 |
| 1982–1986 | R Browne Cooper, D Robinson, B Maryan | Dirk Hartog, Garden, Serpentine–Murray Rivers delta (Jennala, Culeenup, Meeyip, Jeegarnyeejip, Ballee, Worallgarook, Yunderup, Little Yunderup) | frogs, reptiles, mammals | Browne Cooper [sic] et al. 1989, Maryan et al. 1984, D Robinson et al. 1987 |
| 1982–2003 | SD Hopper | Bald, Remark, Sandy Hook, Mondrain | plants | Pearson et al. 2004, WAH |
| 1983 | JC Moredoundt | Garden | plants, *Macropus eugenii* | Bell et al. 1987 |
| 1983 | GW Connell | Dampier Archipelago (10 islands) | plants, reptiles, birds | Connell 1983 |
| 1983–1993 | L Fontanini | Koolan | birds | NL McKenzie et al. 1995 |
| 1984? | RJ Mead | Rottnest, Bald | *Setonix brachyurus* | Mead et al. 1985 |
| 1984, 1987, 1999 | JM Harvey | Houtman Abrolhos (118) | plants | JM Harvey et al. 2001 |
| 1985–1986 | PC Arena, RD Wooller | Penguin | *Egernia kingii* | Arena & Wooller 2003 |
| 1985–1986, 1993 | KD Morris | Barrow, Bernier | birds, mammals, turtles | KD Morris 1987, K Morris et al. 1994 |
| 1985–1989 | JJ Alford | 65 islands: Kimberley (2), Shark Bay (9), Houtman Abrolhos (32), Dongara–Lancelin (20), Carnac, Shoalwater Bay islands (2) | plants | JM Harvey et al. 2001, Keighery et al. 2002, WAH |
| 1985–2007 | G Keighery | 64 islands: Kimberley (3), Shark Bay (2), south-west (30), Albany (2), Archipelago of the Recherche (12), estuarine islands in south-west (15) | plants | G Keighery 1995, 2015; G Keighery et al. 2006; G Keighery & Muir 2008, 2010, WAH |
| 1986, 1992 | B Maryan, D Robinson | King Hall, Woody | reptiles | Maryan & Robinson 1987, 1997 |
| 1986–1988 | CR Dickman, SEJ Daly, GW Connell | Boullanger, Escape, Whitlock | birds | Dickman et al. 1991 |
| 1986–1998 | PG Kendrick | Dampier [Burrup Peninsula] | frogs, reptiles, mammals | Kendrick 2007 |
| 1986–2004 | V Long | Delambre, Dampier Archipelago (9), Varanus, Bridled, Airlie, Thevenard, South Muiron | plants | WAH |
| 1986–2008 | K Coate | Kimberley (15), Dirk Hartog, Houtman Abrolhos (18) | plants, birds | Coate 1989, 1997, 2008ab; Coate et al. 1994, 2011; Harvey et al. 2001, Johnstone & Coate 1992, WAH |
| 1987–1988 | JM Courtenay | Bernier, Dorre | wallabies | Richards et al. 2001 |
| 1987–1989 | AN Andersen, L Belbin, AH Burbidge, GR Dyne, ED Edwards, GR Friend, MS Harvey, GS Hunt, BPM Hyland, RE Johnstone, GJ Keighery, PG Kendrick, KF Kenneally, BY Main, JD Majer, WM | Kimberley (7) | soil properties, earthworms, land snails, pseudoscorpions, scorpions, spiders, opiliones, ants, other insects, plants, vegetation, frogs, reptiles, birds, mammals (not all islands were sampled for each attribute or taxon) | Andersen & Majer 1991, Friend et al. 1991, MS Harvey 1991, Hunt 1991, Johnstone & Burbidge 1991, Kendrick & Rolfe 1991, Kenneally et al. 1991, BY Main 1991, NL McKenzie & Dyne 1991, NL McKenzie et al. 1991, Naumann et al. 1991, GT Smith 1991, Solem 1991, Stoneman et al. 1991 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| | McArthur, NL McKenzie, KD Morris, ID Naumann, JK Rolfe, GT Smith, A Solem, TC Stoneman, FJ Walsh, TA Weir | | | |
| 1987–1992 | NJ Gales, PD Shaughnessy | Houtman Abrolhos to Archipelago of the Recherche | seals | Gales et al. 1994, Shaughnessy et al. 1994 |
| 1988 | T Lebel | Rottnest | introduced snail | Lebel 1991 |
| 1988–1995 | J Short, B Turner, JD Richards | Barrow, Bernier, Dorre | vegetation, mammals | Richards et al. 2001, J Short & Turner 1991, 1992, 1993, 1994, 1999; J Short et al. 1997, 1998 |
| 1988–1990 | AN Start, NL McKenzie | Tent, Burnside, Simpson, Hope Point, Roberts, Doole, Sandalwood | plants, reptiles, birds, mammals | Start & McKenzie 1992 |
| 1988, 1990–1992 | PD Shaughnessy, B Haberley | Eclipse, Coffin, Bald, Bird Rock, Haul Off Rock, Doubtful Islands, Archipelago of the Recherche (98 islands) | *Cereopsis novaehollandiae* | Shaughnessy & Haberley 1994 |
| 1988 | PG Cale | Dorre | birds | Cale 1992 |
| 1990s | EA Sinclair | Rottnest, Bald | *Setonix brachyurus* | Sinclair 1998, 2001 |
| 1990s | MDB Eldridge | Barrow, Wilson, Westall [Combe], Salisbury | *Petrogale lateralis* | Eldridge et al. 1999 |
| 1990, 1998, 2003 | R Powell | Rottnest | butterflies | Powell 1993, 1998; AAE Williams & Powell 2000, 2006 |
| 1991–1992 | MG Brooker | Garden | reptiles, birds | MG Brooker et al. 1995a, 1995b |
| 1991–2006 | C Surman | Houtman Abrolhos (192 islands) | seabirds | Surman 1994ab; Surman & Nicholson 2009, 2015 |
| 1992–1995 | JD Richards, J Short | Bernier | predation of mammals by *Aquila audax* | Richards & Short 1998 |
| 1992–1999 | JA Friend | Dorre | wallabies | Richards et al. 2001 |
| 1992, 2004–2008 | B Maryan, L Reinhold | Koolan, Dirk Hartog | amphibians, reptiles | Maryan 1996, Maryan & Reinhold 2009 |
| <1993 | J Backhouse | Rottnest | pollen | Backhouse 1993 |
| 1993 | SA Halse | Archipelago of the Recherche | *Cereopsis novaehollandiae* | Halse et al. 1995 |
| 1993 | GJ Keighery, N Gibson, KF Kenneally, AA Mitchell | Koolan | vegetation, plants | G Keighery et al. 1995 |
| 1993 | NV Lindus, NL McKenzie, M Williams | Koolan | invertebrates, frogs, reptiles, mammals | NL McKenzie et al. 1995 |
| 1995–1997, 2003 | AAE Williams | Dorre, East Wallabi, West Wallabi, Rottnest, Garden, Middle (Recherche) | butterflies | AAE Williams 1997; AAE Williams & Powell 1998, 2006; AAE Williams et al. 1998 |
| 1995–1998 | DJ Pearson | West Wallabi, Garden, Mondrain | *Morelia spilota* | Pearson et al. 2002ab, 2004, 2005 |
| 1996–1998 | BJ Wykes, D Pearson, J Maher | Garden | Invertebrates, reptiles, birds, mammals | Wykes et al. 1999 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 1996–1998 | PG Kendrick | Dampier [Burrup Peninsula] | frogs, reptiles, mammals | Kendrick 2007 |
| 1996– | B Maryan | Koolan, Montebello Islands, Airlie, Dirk Hartog, Houtman Abrolhos, Woody | reptiles | Maryan 1996, Maryan & Reinhold 2009, Maryan & Robinson 1987; Maryan et al. 1984, 2009, 2013ab |
| 1997–2005? | F Aubret, X Bonnet | Carnac | *Notechis scutatus* | Aubret & Shine 2007; Bonnet et al. 2002, 2005 |
| 1998 | SJ Claymore, AJ Markey | Bernier, Dorre | plants | Claymore & Markey 1999 |
| 1998 | S Pruett-Jones, KA Tarvin | Barrow | *Malurus leucopterus* | Pruett-Jones & Tarvin 2001 |
| 1998, 2000 | J Richardson, FJ Stanley, PG Kendrick, G Kregor | Legendre | plants, birds, mammals | J Richardson et al. 2007 |
| 1998–2012 | E Rippey | Houtman Abrolhos (3), Lancelin, Rottnest, Carnac, Garden, Shoalwater Bay (5), Woody | plants | Rippey 2004, Rippey & Hobbs 2003, Rippey & Rowland 1995, Rippey et al. 1998, 2002ab, 2003, WAH |
| 1999 | NJ Gales. B Haberley, P Collins | 16 (between Cape Leeuwin and Israelite Bay) | *Arctophoca australis forsteri* | Gales et al. 2000 |
| 1999–2011 | S Barrett | Breaksea, Bald, Archipelago of the Recherche (9) | plants | WAH |
| 1999 | V Longman | Houtman Abrolhos (118), Dongara–Lancelin (37) | plants | JM Harvey et al. 2001, G Keighery et al. 2002, Longman et al. 2000, WAH |
| 1999 | AF Longbottom | Woody (Archipelago of the Recherche) | *Atelomastix dendritica* | Edward & Harvey 2010 |
| 2000 | B Wilson | Faure | terrestrial gastropods | B Wilson 2008a |
| 2000 | J Richardson, G Watson, G Kregor | Montebello Islands (13) | reptiles, birds | J Richardson et al. 2006 |
| 2000–2001 | MK Rathburn, R Montgomerie | Dirk Hartog | *Malurus leucopterus* | Rathburn & Montgomerie 2003 |
| 2000, 2002 | A Schmitz, JD Richards | Faure | reptiles | Schmitz & Richards 2008 |
| 2000, 2005 | J Dell, S Cherriman | Faure | birds | Dell & Cherriman 2008 |
| 2000, 2005 | K Aplin, J Dell | Faure | reptiles | Aplin et al. 2008 |
| 2001– | EA Alacs | Rottnest | *Setonix brachyurus* | Alacs et al. 2011 |
| 2002–2005 | RA How, L Schmitt, R Teale, M Cowan | Kimberley (35) | frogs, reptiles, mammals | How et al. 2006 |
| 2002–2005 | S Comer | Bald, Doubtful, Archipelago of the Recherche (Mondrain, Middle, Wickham [Stanley], Glennie, North Twin Peak, Taylor, Cranny, Daw, New Year, Cooper, Salisbury) | plants, fauna | Comer & Adams 2012; Pearson et al. 2004, 2005; WAH |
| 2002–2005 | NK Cooper, RA How | East Wallabi | *Rattus fuscipes* | NK Cooper & How 2006 |
| 2003 | D Nicolle, ME French | Sandy Hook | eucalypts | Nicolle & French 2012 |

| Year(s) | Contributor(s) | Island(s) | Contribution(s) | Reference(s) |
|---|---|---|---|---|
| 2003 | ND Thomas | Dorre | mammals, turtles | ND Thomas 2003 |
| 2003–2008 | RA How, DJ Pearson, B Maryan | Houtman Abrolhos (18) | reptiles | How et al. 2004, Maryan et al. 2009 |
| 2005–2009 | SK Callan, K Edwards, JD Majer | Barrow | invertebrates | Callan et al. 2011 |
| 2005–2012 | JD Majer, SK Callan, K Edwards, NR Gunawardene, CK Taylor | Barrow | invertebrates, survey methodology | Bickel 2013, Car et al. 2013, Framenau & Leung 2013, Gopurenko et al. 2013, Greenslade 2013, Heterick 2013, Humphreys et al. 2013, MS Johnson et al. 2013, DT Jones 2013, Judd & Perina 2013, Majer et al. 2013, Mound 2013, G Smith 2013, Stevens et al. 2013, CK Taylor 2013ab, K Walker 2013, Whittle et al. 2013, Yeates & Oberprieler 2013 |
| 2006 | NR Gunawardene, CK Taylor, JD Majer | Barrow | Psocoptera | Gunawardene et al. 2012 |
| 2006–2007 | M Henson, K Kenneally, E Griffin, R Barrett | North & South Maret, Berthier, East & West Montalivet, Lamarck | vegetation, plants | Henson et al. 2014 |
| 2006–2007 | C Lamont, M Bamford, M Harvey, J Fitzpatrick, MS Johnson | Kimberley (up to 31, including North & South Maret, Berthier, East & West Montalivet, Prudhoe, Lamarck, Walker, Bigge, Albert) | earthworms, arthropods, troglofauna, land snails, herpetofauna, birds | Humphreys 2014, MS Johnson et al. 2010, Köhler & Johnson 2012, Lamont et al. 2014 |
| 2006–2008 | D Waayers | Kimberley (c. 25) | marine turtles | Waayers 2014 |
| 2007 | RL & MD Barrett | Kimberley (9) | plants | WAH |
| 2007–2010 | RD Bullen, W Caton, MA Cowan, P Doughty, LA Gibson, T Handesyde, GJ Keighery, F Köhler, MN Lyons, NL McKenzie, R Palmer, DJ Pearson | Kimberley (22–30) | plants, land snails, frogs, reptiles, birds, mammals (including bats) | Doughty et al. 2012, LA Gibson 2014, LA Gibson & Köhler 2012, LA Gibson & McKenzie 2012ab, Lyons et al. 2014, NL McKenzie & Bullen 2012; R Palmer et al. 2013b, 2013c; Pearson et al. 2013 |
| 2007–2013 | MS Harvey, C Car, KL Edward, R Otto, | Descartes, Barrow | invertebrates (Schizomida, pseudoscorpions, spiders millipedes) | Car & Harvey 2013, Edward & Harvey 2008, MS Harvey et al. 2007, 2008; MS Harvey & Edward |
| 2009 | K Williams, K Onton, A Webb, M Manns, J Edwards, H Smith | Hamelin, Seal, St Alouarn | plants, vegetation, birds, seals | Onton & Webb 2009 |
| 2011 | R Campbell, D Holley, P Collins, S Armstrong | 18 (between Cape Leeuwin & Israelite Bay) | *Arctophoca australis forsteri* | R Campbell et al. 2014 |

* Because Whitlock's paper on Rottnest Island (Lawson 1905) was published in January 1905, his visit cannot have been in 1905 as implied by Saunders & de Rebeira (2009). His visit did not take place in 1904 as stated by Storr (1964a) and Saunders & Rebeira (1985). Whittell (1940a) implies that the visit took place in late 1903. This is confirmed by specimens collected on the island by Whitlock and lodged in the Western Australian Museum. These are dated 7–16 November 1903 (R Johnstone pers. comm.).

1975; Goodsell et al. 1976; Abbott & Black 1978; Abbott 1980d, 1981a; McArthur & Bartle 1981; Hesp et al. 1983; V & C Semeniuk Research Group 1989; Buckley 1983, Mattiske & Associates 1993; G Keighery et al. 1995, 2002, 2006; McArthur 1996a; Apache Energy Pty Ltd 1997; Abbott et al. 2000; JM Harvey et al. 2001; G Keighery & Muir 2008; Henson et al. 2014);

- Zonation of plant species (J Sauer 1965; Hussey 1973; Sedgwick 1973);
- Herpetofaunal composition (LA Smith & Johnstone 1996; R Palmer et al. 2013b);
- Landbirds in relation to environmental factors (Abbott 1978a);
- Avifaunal change (Abbott 1978a; Saunders & de Rebeira 1983);
- Occurrence of seabirds (Serventy et al. 1971; Fullagar & Murray 1973; MD Murray et al. 1989; AA Burbidge et al. 1996; Johnstone & Storr 1998);
- Aboriginal access (DS Davidson 1935);
- Occurrence of seals (Abbott 1979; R Campbell 2005; R Campbell et al. 2014; Gales et al. 1994, 2000; Shaughnessy et al. 1994);
- Impact of seals and seabirds on soil and flora (Gillham 1961a); and
- Presence of weed and pest-animal species and their impact and removal (JM Harvey et al. 2001; G Keighery et al. 2002, 2006; JE Kinnear et al. 2002; AA Burbidge & Manly 2002; MT Lohr & Keighery 2014, 2016; Lyons et al. 2014).

Much of this wealth of information is overlooked in scientific accounts of islands, including textbooks and national and international papers on island ecology (Carlquist 1965, 1974; Sparks 1976; Williamson 1981; Whittaker 1998; Whittaker & Fernández-Palacios 2007; Thornton 2007, Gillespie & Clague 2009). Books of a more general nature have also neglected, to varying degrees, information available at the time about WA islands (Beatty 1965; Berrill & Berrill 1969; Baglin & Mullins 1970; Amos 1980; Dutton 1986; Stevenson & Talbot 1994; Chester & McGregor 1997). Even textbooks about the biology or ecology of Australia make scant reference to island ecology (Attiwill & Wilson 2006; Calver et al. 2009; Ladiges et al. 2010). An important exception is the contribution of HA Ford (2006). A book published in 2008 about environmental policy and management in Australia purported to include all aspects of ecology but failed to examine islands. This omission was rectified by Woinarski et al. (2014a) in the second edition of this book. Another book about the monitoring of biodiversity included no examples from islands, inexplicably excluding from consideration the many long-term studies of seabird populations on Australian islands (Lindenmayer et al. 2014). Finally, an assessment of the conservation value of Australian islands with areas >200 ha neglected to cite relevant papers about the islands of WA (Ecosure 2009).

Unlike other island-rich regions of Australia (WD Williams 1974; T Robinson et al. 1996; Woinarski et al. 1998, 1999a, 1999b, 2000, 2001, 2011; S Harris et al. 2001; Brothers et al. 2001), there has been no overall ecological and biological analysis of WA islands. Indeed, there has been over-emphasis on Rottnest Island, probably because of its convenient proximity to the capital city of WA. A central objective of this paper is to assemble, assess, collate, analyse and interpret all relevant information about WA islands for the benefit of researchers unfamiliar with studies of WA islands. This paper complements a previous review of human impact on the islands of WA (Abbott 2006).

The intent of this review is to synthesise information pertaining to WA islands and gathered from numerous, often disparate, sources into a general theory that accommodates all available data accurately, reconciles any inconsistencies, and offers broad applicability. Our review is organised thematically: Physical description (defining a typical WA island in terms of area, isolation, elevation, landform, topography, geology, climate and habitat structure); biological description (key biodiversity statistics, species composition patterns, vegetation types); European influences (land management practices, introduced species); and conceptual framework (synthesis that distinguishes major factors from subordinate factors without neglecting their potential interplay).

Our underlying motivation in writing this review stems from dissatisfaction with the narrow focus of much of the literature about island ecology and biogeography. For example, the textbook of Whittaker and Fernández-Palacios (2007) pays disproportionate attention to oceanic islands, particularly the Canary Islands and Krakatau, research interests of the authors. It also includes irrelevant information about remnant landscapes on mainlands. Only seven papers relating to the continental islands of Australia are cited, three of which refer to islands of WA. A recent review of island biogeography also indicates increasing focus on volcanic oceanic islands (Santos et al. 2016).

We attempt to demonstrate the necessity of restoring the traditional multifactorial perspective in order to achieve a nuanced understanding of island ecology, to emphasise that area and isolation are not usually or always sufficient to understand island ecology, and to subsume the equilibrium viewpoint as a special case. The importance of adopting both 'microscopic' and 'telescopic' views of island ecology (the 'close' and 'distant' perspectives of Lack 1976) is emphasised. We also consider the following questions:

- Are area and distance adequate proxies for more fundamental factors in explaining the lower species richness on islands (relative to mainland) and differences in species richness between islands?
- Do the differences among islands and between islands and mainland outweigh the similarities?
- How important is history?
- How strong is the evidence for equilibrium?

- How useful is the theory of Huston (1994) for understanding biodiversity patterns on islands?
- Which significant deficits in knowledge remain?

# METHODS

## Data sources

Since 1970, the first author has assembled a collection of scientific papers (>800), unpublished reports ('grey' literature), government documents (such as archival records, current files) and newspaper articles pertaining to the islands of WA. Many of these are descriptive, with some noting new records of species. Few of these papers, however, offer explicit consideration of island ecology per se, particularly in comparison with the nearest mainland or with consideration of all factors responsible for insular characteristics.

All papers were retrieved, aggregated, collated and then reviewed in terms of the assumptions listed below and the questions posed in the introduction. The first author has examined all 165 1: 100,000 scale maps of the coastline of WA, counted all islands, and measured the area of all islands >100 ha. Bathymetric information has been taken from the official Admiralty and Royal Australian Navy charts.

Other research performed on islands elsewhere in Australia and outside Australia is also cited when appropriate. Because of the quantity of material available, only the most relevant papers from outside Australia are cited. The relevance of papers from other regions of Australia is higher, and proportionately more of these are cited. Particularly valuable is the Seabird Island Series Numbers 1–264 (1973–2015), comprising records of seabirds present on >250 Australian islands. Papers that involve physiological or ecological study of a species that could have been undertaken on the mainland and which do not involve comparison with mainland populations (e.g. quokka [*Setonix brachyurus*] and Australian shelduck [*Tadorna tadornoides*] on Rottnest Island, tammar [*Macropus eugenii*] on Garden Island, spectacled hare-wallaby [*Lagorchestes conspicillatus*] on Barrow Island) are usually not considered here. Warburton (2014) provides an entrée to the literature relating to the quokka on Rottnest Island. Also excluded are population ecology studies of seabirds on islands, studies of the littoral environment of islands (marine fauna and flora), and studies of island ecological communities that are not compared with mainland communities.

In order to provide appropriate context in this review, information is usually organized and presented in the following sequence. First, relevant information from a global perspective is provided, then information from an Australian perspective, and finally information about Western Australian islands.

## Personal knowledge

During the past 35 years one of us (IA) visited nearly 200 islands of WA (Table 1) and compiled and published lists of plant species and bird species. In April 1977, IA was flown at a height of 200 ft over all islands between Perth and Duke of Orleans Bay (east of Esperance), and noted details of structural types of vegetation. In September 1998 all inshore islands between Perth and Denham were flown over at low altitude and similar observations were made.

## Assumptions

Few authors outline the assumptions made when compiling species lists for islands. When scrutinising available data sets for numerical analysis, the suitability of each has been assessed with reference to five assumptions:

1. *Reliability.* On each island there has been a thorough search using techniques appropriate to the taxon under study.
2. *Efficiency.* Sufficient time was spent searching the island relative to the surface area.
3. *Equivalence.* If records from several visits to an island are aggregated, the various recorders applied equal search effort.
4. *Validity.* Species that are genuine residents or breeding visitors are distinguished from vagrant, accidental or casual species.
5. *Comprehensiveness.* All relevant factors have been adequately considered and assessed, not only those that are easily measured or readily available.

## Nomenclatural conventions

The following nomenclatural conventions are used in this review. When a species of mammal, bird, reptile or frog is first identified in the text, its vernacular name and Latin binomial are provided. Thereafter only the vernacular name is used in the text. Names generally follow those recommended by Johnstone and Darnell (2015) and Western Australian Museum (2015), except for several Aboriginal names of mammal species in use by the Department of Parks and Wildlife. However, not all reptile species have been assigned a vernacular name (Western Australian Museum 2015), and those used in S Wilson and Swan (2013) and Cogger (2014) do not always agree. This implies that a standard list of vernacular names for Australian reptiles does not yet exist. In tables only Latin binomials are used. For plant species, Latin binomials are used (Western Australian Herbarium 1998–), and only in a few instances are vernacular names provided in addition. A few binomials differ from these official sources as a result of recent information. When a lengthy series of species names is provided in the same paragraph, Latin binomials have been used in preference to vernacular names.

# PRELIMINARY

## Concepts and definitions

Although an island is a piece of land with a clear boundary beyond which water occurs, ecologists have tended to overlook small islands (uncovered at high water mark) and aits (islands situated in rivers). The reasons for this neglect are probably that the former have few plant species present and generally lack landbirds and land mammals, taxa that dominate the scientific and natural history literature about islands. Nevertheless, cays (small sand islands) have proved more attractive to ecologists than stacks (small rocky islands). Islands in rivers, at the mouths of rivers, and bounded by two rivers (interamnium) are insufficiently studied probably because they appear very similar to the riparian and adjacent zone of the nearby mainland, e.g. deltaic islands of Deep and Frankland rivers, WA (Semeniuk et al. 2011); Thomas and Molloy islands, Blackwood River WA (Western Australian Herbarium 1998-); Culeenup and other deltaic islands at the mouth of the Murray River (Serventy 1970; Hussey et al. 1992; Western Australian Herbarium 1998-). Being sheltered from wave action results in similar vegetation, and their proximity to the mainland lies within the dispersal capability of most mammal and bird species.

There is inconsistency in the common nouns applied to groups of islands. In WA there are four named archipelagoes (Bonaparte, Buccaneer, Dampier, Recherche). Each of these includes many islands in a relatively compact area. Yet, similar large numbers of islands elsewhere in WA have not been named as archipelagoes, including islands between Exmouth Gulf and Cape Preston, islands in Shark Bay, Houtman Abrolhos, islands between Dongara and Lancelin, and islands between West Cape Howe and Mermaid Point (Fig. 2). Indeed, 55 archipelagoes/groups have been recognised by AA Burbidge (2004a). The concept of what constitutes an archipelago is thus ill-defined and seems arbitrary in its application.

Some small groups of islands, even within archipelagoes, have been given the appellation Group, Islands or Isles. Examples include Eastern Group, West Group, South East Isles and Marts Islands within the Archipelago of the Recherche. There are >20 other clusters in WA that are so named. Some of the named clusters have evidently been retained for their heritage value because they perpetuate names bestowed by navigators such as Vancouver, d'Entrecasteaux, Flinders and Baudin (e.g. Doubtful Islands, South West Group, East Islands, Eastern Group, Institut Islands).

Apart from Rowley Shoals and rocky islets on Scott and Seringapatam reefs, all WA islands are continental, occurring on land that is part of the continental shelf (<200 m depth). Most, but not all, continental islands are relicts of coastal high ground. The exceptions are depositional islands formed by accretion of sand at river mouths (deltaic islands such as Babbage Island), from sediments derived from nearby rivers (e.g. Ashburton, Robe and Fortescue rivers), or deposited on reefs of rocks offshore (including Adele, Browse, Bedout, Lacepede, Thevenard and Pelsaert islands, and some others in Houtman Abrolhos). Many sandy islands are too high to be described as cays (e.g. Great Sandy Island, 16 m; North Sandy Island, 13 m), suggestive of aeolian processes forming dunes and dominating depositional processes. Lesueur, Adele, Browse, Lacepede, Bedout and North Turtle islands range in elevation from 2–9 m and appear to be true cays. Most of Pelsaert Island appears to be a cay. Radiocarbon dating analysis indicates that Thevenard Island is only c. 3 ka old (WAPET 1987). No WA island is of volcanic origin.

Some islands have become naturally joined permanently to the mainland by a tombolo, apparently since the last glacial. The only radiocarbon-dated example is that of Cape Peron (near Rockingham) at c. 3ka BP (before the present) (PJ Woods & Searle 1983). Other examples on the northern and western coasts of WA include Buckle Head, Cape Thouin, Cape Preston, Peron Peninsula (joined by Taillifer Isthmus to Nanga Peninsula, Shark Bay), Petit Point (joined to Nanga Peninsula), Cape Bellefin-Steep Point, North Head and Sandy Point (between Green Head and Jurien Bay), and Arthur Head (Fremantle). Tombolos are prominent along the southern coast of WA between Albany and Israelite Bay, for example Mt Gardner, Butty Head, Hammer Head and Tagon Point. Several tombolos are wide and elevated, which may indicate that they are not of recent origin. Tombolos are particularly numerous inshore of the Archipelago of the Recherche.

Some islands (e.g. Wedge Island) are joined intermittently to the mainland by a cuspate spit. A few islands consist of two or more islands that have been connected by sand, e.g. Malus Islands, West Intercourse Island, Barrow Island (south-west), Varanus Island, Boullanger (Long) and North Boullanger islands, and Rottnest Island (Playford et al. 1977: 38; Playford 1983).

The range of spring tides varies extensively around the WA coast, being least (<1 m) along the south-western coast and greatest (5–6 m) between Dampier and the northern Kimberley region, and in some places reaching 10 m (AD Short & Woodroffe 2009). On macrotidal coasts some islands are regularly, although only temporarily, connected with the mainland.

## Island nomenclature

The names of WA islands represent an important part of their cultural history. It would not be surprising if all nearshore islands visible from mainland WA had been named by Aborigines. However, few of their names have survived the colonisation by Europeans, probably because islands received Dutch, French or English names well before any familiarity with Aboriginal languages was gained. This is a result of European navigators bestowing names many years before settlement of the adjacent mainland occurred. The earliest of these European names are Dutch: Dorre (1616), Rottnest (1696) and Dirk Hartog (1697). Most

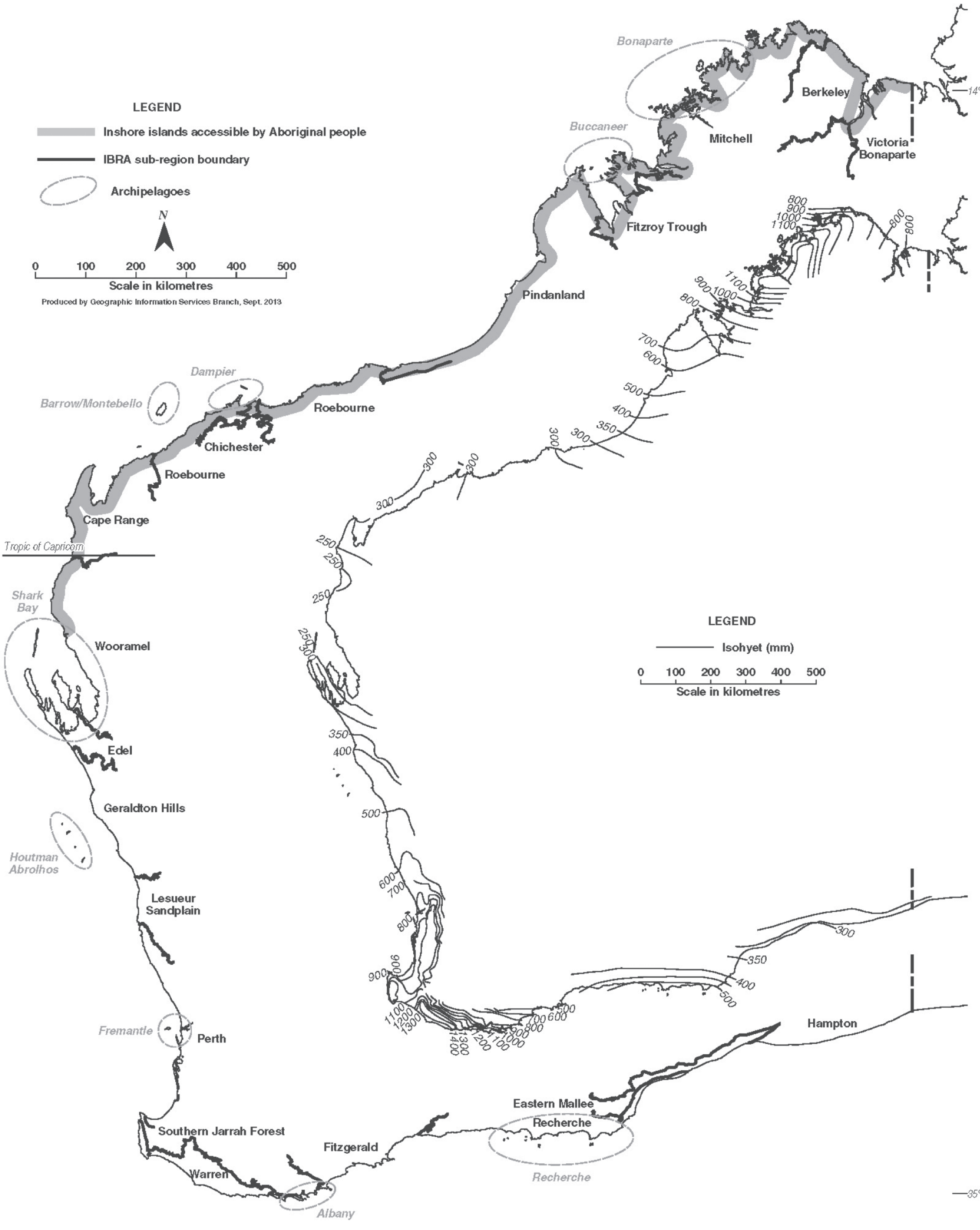



*Figure 2. Maps of the coastline of Western Australia, showing where Aboriginal people visited offshore islands, boundaries of coastal bioregions (after Thackway & Cresswell 1995), and location of major archipelagoes; and (inset) mean annual rainfall along the coastline.*

names are English, dating from Vancouver's visit in 1791. Many WA islands, however, have French names resulting from visits in 1792, 1801 and 1803 by d'Entrecasteaux, Baudin, Hamelin and Freycinet. Aborigines of the Kimberley region have retained use of their island names (Aklif 1999). As these islands become better known, we expect that Aboriginal names will eventually supersede the European ones.

Names bestowed by Europeans are either descriptive or honour a patron, royalty, professional associate (including illustrious scientists such as Laplace, Lavoisier and Babbage), bureaucrat, family member, a significant event connected with the island, or a theme (e.g. botanical names – Montebello Islands). This fascinating topic has been examined in detail by Yarrow (1980), LR Marchant (1982), I Murray & Hercock (2008) and Elliot (2011). Some islands were named more than once, for example wadjemup/Rottnest, meeandip/Buache/Garden, and ngooloomayup/Bertholet/Carnac. This is unusual, as the first European name was generally respected (although sometimes translated into English, the diacritical marks of the original were omitted, or the name was altered in spelling). Descriptive names (referring to colour, length, height, shape, substrate, direction or presence of a seabird) have frequently been bestowed in ignorance of previous use (I Murray & Hercock 2008). In recent times, many of these duplicated names have been replaced with unique toponyms. I Murray and Hercock (2008) provide explanations of the names of >930 WA islands.

A remarkable feature of WA island nomenclature is that many naturalists and scientists who visited and reported on these islands in the past 150 years have been commemorated. This initiative resulted from the need of scientists (particularly JR Ford, RE Johnstone and unnamed malacologists of the WA Museum) to name islands so that they could be referenced unambiguously in publications (I Murray & Hercock 2008). The (then) Department of Lands and Surveys and its Geographic Names Committee were very co-operative. Aboriginal names of islands in the Kimberley region recorded by Andrew Burbidge have also been accepted for islands lacking an English name (I Murray & Hercock 2008).

## Scope

This paper considers all relevant information that has been published about the islands of WA. It is not our purpose, however, to review each island and itemise its physical and biological features. Instead we have attempted to determine the minimal set of factors that best explain the similarities and differences among islands. Unlike many contemporary reviews that narrowly focus only on recently published papers or on papers published in the international and highly cited journals, we have been comprehensive and have not intentionally disregarded the views of 19th century scientists and naturalists.

# INSULAR FEATURES AND THE ISLAND SYNDROME

According to LR Walker and Bellingham (2011), the mystique of islands is in part due to two physical features, isolation and finiteness (sharply defined boundary). Beginning with one of the earliest works in western literature (The Odyssey), and continuing with Shakespeare (The Tempest), island settings have been used often in fiction (Bowman 1971) and many organising themes have been recognised (Divine 1972). Isolation, mystery, unexpected circumstances, strange creatures and unusual human behaviour have all been employed to generate dramatic events and gripping narrative. Biogeographically-impossible assemblages of species have often been deployed, with Wyss (1812) providing one of the worst examples of such errors.

Islands are not to be regarded merely as miniaturised parts of the mainland, as the following points about geography and biology demonstrate.

## Physical description

A recent attempt to characterise the climate of the world's islands focused on those >100 ha and concluded that islands are cooler, wetter or less seasonal than the mainland (Weigelt et al. 2013). Compared to the nearly 18,000 islands studied, WA islands are comparatively small, close to the mainland, of low elevation, warm and dry.

Western Australia has a mainland coastline and an island coastline, determined at a scale of 1:100,000, of 12,900 km and 7,900 km respectively (Geoscience Australia 2013). It is not, however, straightforward to identify some islands. Although we seldom refer to islands in rivers, some islands occur at river mouths in a broad bay and it is difficult to decide which deltaic islands should be counted. In addition, in the Kimberley region some rivers debouche into gulfs (e.g. Ord River), basins (Glenelg, Calder and Charnley rivers) or sounds (Fitzroy River), and some islands occur in arms of the sea that are nearly enclosed, blurring the distinction between islands in rivers and those inshore. Some islands (particularly those with mangal forest) that are very close to the mainland coast are difficult to distinguish from the mainland, as in Exmouth Gulf.

The scale of map also predetermines if all very small islets are actually included. For example, 1: $10^5$ scale maps indicate the presence of only 39 islands between Mullaloo and Becher Point, whereas there are actually 123 (Abbott 1977a). The comparable numbers in Houtman Abrolhos are 94 and 192 (Surman & Nicholson 2009) and in Montebello Group 48, 180 (AA Burbidge & Fuller 1998), and 265 (DEC 2006a).

Finally, very small areas of land surrounded by water are easily misclassified, either as small low rocks (land covered at high water and thus unsuitable for terrestrial life) or small rocky islands (land uncovered at high water). These distinctions are neither trivial nor insignificant. The discovery in 2014 of several previously unsuspected small islets on North Scott Reef and Seringapatam Reef enlarges the territorial extent of WA. By doing so, royalties on natural gas produced from surrounding leases are payable to the WA government and not to the Australian government.

The first listing of WA islands evidently ignored most small islands; it included only 332 islands (Commonwealth of Australia 1912). Mindful of all of the distinctions outlined above, we reckon the number of WA islands to be 3576. This is fewer than recent determinations (3678, Abbott & Burbidge 1995; 3747, Geoscience Australia 2013) but more than one other (2562, Conservation Commission of Western Australia 2009). According to Geoscience Australia (2013), WA has 46% of Australia's islands.

The islands of WA are not distributed uniformly along this mainland coastline (Table 2). Most occur within nine archipelagoes, collectively more than in any other state or territory of Australia. Each archipelago is clearly demarcated, except for the ill-defined northern and southern limits of the Bonaparte Archipelago. About 70% of islands with an area ≥100 ha occur along the Kimberley coastline (Table 2).

The two physical characteristics of islands emphasised in biogeographic literature are area (planar) and distance offshore, features that are readily measured on an appropriately scaled map. This may explain their prominence in this literature. Globally, large islands occur infrequently (Fig. 1). Greenland is conventionally regarded as the largest island in the world. Most (91%) of the islands of Australia (N = 8290) have an area <100 ha (Fig. 1). Most WA islands are <100 ha (Table 2), with the majority probably <10 ha in area. This conforms with islands elsewhere (Fig. 1; Fréchet 1941). Almost all WA islands are close to the mainland (<50 km), with most <20 km.

WA islands are not particularly large in comparison with other Australian islands (Table 3). The four largest

**Table 2**

Number and geographical distribution of the islands and archipelagoes of Western Australia, based on 1: 100,000 scale maps.

| Segment of coastline | No. islands | No. islands with area ≥100 ha | Occurrence of archipelagoes (see Fig. 2) | Comments |
|---|---|---|---|---|
| Northern Territory border to Gantheaume Point | 2358 | 209 | Bonaparte Archipelago, Buccaneer Archipelago | Very few islands between: Cape Talbot and the Northern Territory border; Cape Leveque and Gantheaume Point |
| Gantheaume Point to Cape Lambert | 58 | 2 | | No islands off Eighty Mile Beach |
| Cape Lambert to Cape Preston | 155 | 18 | Dampier Archipelago | |
| Cape Preston to Point Quobba | 195 | 18 | Montebello Islands, Lowendal Islands | Very few islands between: North West Cape and Point Quobba |
| Point Quobba to Zuytdorp Point | 98 | 6 | Shark Bay archipelago | No islands between: Steep Point and Zuytdorp Point |
| Zuytdorp Point to Lynton | 2 | 0 | | |
| Lynton to Dongara | 94 | 4 | Houtman Abrolhos | |
| Dongara to City Beach | 39 | 0 | | Very few islands between: Lancelin and City Beach |
| City Beach to Becher Point | 38 | 2 | Fremantle–Warnbro Sound archipelago | |
| Becher Point to Cape Leeuwin | 54 | 1 | | No islands between: Becher Point and Cape Naturaliste. Very few islands between: Cape Naturaliste and Cape Leeuwin |
| Cape Leeuwin to Torbay Head | 74 | 0 | | |
| Torbay Head to Lookout Point | 66 | 4 | Albany archipelago | |
| Lookout Point to Butty Head | 24 | 0 | | |
| Butty Head to Israelite Bay | 313 | 11 | Archipelago of the Recherche | |
| Israelite Bay to South Australian border | 0 | 0 | | |
| **Total** | 3568 | 101 | 9 | |

**Table 3**

Australian islands with an area ≥100 km$^2$ (accurate to three significant figures), listed in order of decreasing area. Abbreviations: NSW – New South Wales; NT – Northern Territory; Q – Queensland; SA – South Australia; T – Tasmania; V – Victoria); WA – Western Australia. Islands in Western Australia are indicated in **bold**.

| Rank | Name | Area (km$^2$) | Rank | Name | Area (km$^2$) |
|---|---|---|---|---|---|
| 1 | Tasmania *sensu stricto* (T) | 62,000 | 20 | North Stradbroke (Q) | 260 |
| 2 | Melville (NT) | 5730 | 21 | **Barrow** (WA) | 240 |
| 3 | Kangaroo (SA) | 4350 | 22 | Bickerton (NT) | 230 |
| 4 | Groote Eylandt (NT) | 2260 | 23 | Marchinbar (NT) | 210 |
| 5 | Fraser (Q) | 1650 | 24 | Prince of Wales (Q) | 200 |
| 6 | Bathurst (NT) | 1650 | 25 | **Augustus** (WA) | 190 |
| 7 | Flinders (T) | 1350 | 26 | **Bigge** (WA) | 180 |
| 8 | King (T) | 1120 | 27 | Moa (Q) | 170 |
| 9 | Mornington (Q) | 970 | 28 | French (V) | 170 |
| 10 | 'Flinders-Bynoe Rivers' (Q) | 680 | 29 | Moreton (Q) | 170 |
| 11 | **Dirk Hartog** (WA) | 590 | 30 | 'Mitchell River' (Q) | 170 |
| 12 | Curtis (Q) | 560 | 31 | Bentinck (Q) | 140 |
| 13 | Cape Barren (T) | 460 | 32 | West [Pellew] (NT) | 130 |
| 14 | Hinchinbrook (Q) | 390 | 33 | Endyalgout (NT) | 120 |
| 15 | Bruny (T) | 370 | 34 | Casuarina (NT) | 110 |
| 16 | Croker (NT) | 330 | 35 | Badu (Q) | 110 |
| 17 | Elcho (NT) | 300 | 36 | Whitsunday (Q) | 110 |
| 18 | Howard (NT) | 280 | 37 | Maria (NT) | 100 |
| 19 | Vanderlin (NT) | 280 | 38 | Daru (Q) | 100 |
| | | | 39 | Phillip (V) | 100 |

WA islands are 11th, 21st, 25th and 26th in the list of the 39 largest. From a global perspective, no WA island can be considered large. In the world list the three largest Australian islands rank only 25th (Tasmania), 101st (Melville Island), and 131st (Kangaroo Island).

The altitudinal range of WA islands is low (<100 m, with most <20 m). Only nine islands exceed 200 m in elevation. Australia Pilot (1972, 1973) itemises all islands and usually provides their maximum elevation and other relevant information.

The type of rocks (and hence soil) present matches the geology of the adjacent mainland, with basalts and sandstones found in the Kimberley region, basalts and limestones in the Pilbara, granites along the south coast, and aeolianite from the Pilbara to Esperance (although usually overlaying granites along the southern coast; Geological Survey of Western Australia 1975). Detailed geological descriptions of WA islands are limited (Teichert & Fairbridge 1948; Fairbridge & Serventy 1954; Playford 1983; Playford et al. 1977, 2013; Collins et al. 1997).

On the basis of geological structure, dominant processes and landforms, PJ Woods et al. (1985) delineated eight coastal regions for WA: Kimberley coast (Northern Territory border to Cape Leveque); Canning coast (Cape Leveque to Port Hedland); Pilbara coast (Port Hedland to Cape Preston); Carnarvon coast (Cape Preston to Kalbarri); west coast (Kalbarri to Cape Naturaliste); Leeuwin coast (Cape Naturaliste to Cape Leeuwin); south coast (Cape Leeuwin to Cape Arid); and Eucla coast (Cape Arid to South Australian border).

Soils derived from granite are coarse-textured sands and acid, whereas soils derived from aeolianite are alkaline (Anon. 1975). Soil chemistry is also affected by nesting or roosting seabirds, as their excreta (guano) contain high levels of phosphates, which in dry periods are particularly toxic to vegetation.

The topography of WA islands tends to vary with island area and the topographical configuration of the adjacent mainland, with highly dissected landscapes best exemplified in the Archipelago of the Recherche and in the Bonaparte Archipelago. The coastline at Yampi Sound is a true ria, with the geological strike transverse to the coastline, and shows clearly the derivation of the islands from the configuration of the landscape on the mainland (Bird 1964).

Rainfall also matches that prevailing on the adjacent mainland. Islands receiving >1000 mm per annum occur adjacent to the Kimberley coast and the lower south-western coast (Fig. 2). However, the former is most humid during the hottest period (late spring to late summer), whereas the latter receive most rain during the coldest part of the year (late autumn to spring). The most arid islands (<250 mm per annum) are found in Shark Bay. High islands should receive more rainfall than low ones. An island could therefore receive more or less rainfall than does the adjacent mainland coast. Because of the high specific heat of water, islands have a smaller range of daily temperature than does the mainland coast—minima are higher and maxima are lower (Bureau of Meteorology 1975).

Twelve of the 26 bioregions in WA include the coastline (Fig. 2). The congruence of bioregions with the eight coastal regions defined by PJ Woods et al. (1985) is not strong, which is not unexpected given that bioregions include much land that is not coastal. The classifications of the continental climatic and continental environmental domains by Mackey et al. (2008) may provide a more nuanced framework.

Habitat structure (comprising the height, density and stratification of vegetation), while formed by dominant biological organisms (plant species), is a key determinant of shelter, particularly for birds. The emphasis in this section is on habitat structure as living space, not on the plant species that form habitats.This factor obviously includes a biotic component (plant species) and thus links with the biological description of islands discussed in the next section.

Some bird species, discussed below in 'Habitat changes', require rainforest, eucalypt forest, mangrove forest or eucalypt woodland to satisfy their need for shelter. Obviously if the requisite preferred habitat structure is lacking, these species will be absent commensurate with their ecological flexibility. Beard (1990) published a map that shows the regional variation in vegetation types along the entire mainland coastline of WA.

## Biological description

The island syndrome comprises a number of features (Darwin 1859; Adler & Levins 1994; Blondel 2000; Withers 2015), although not all need to be present:

- Reduced species richness relative to a similar-sized source area (mainland or nearby large island);
- Presence of endemic species or subspecies, dependent on the vagility of taxa;
- Disharmonic biota (e.g. lack of large predatory mammals, frogs);
- Hyperabundance of some species (resulting in high levels of intraspecific competition);
- Changes in habitat;
- Behavioural changes (tameness) of bird and mammal species;
- Obvious or subtle changes in the morphology or body size of some species, e.g. seed size, leaf size, beak length, varying degrees of loss of flight (through aptery or brachyptery), gigantism, nanism, arborescent growth of plant species that elsewhere are shrubs;
- Changed reproductive effort (smaller clutch size of birds and litter size of mammals); and
- Reduced genetic diversity (Lennon et al. 2011; Neaves et al. 2012) as alleles become fixed through genetic drift.

All of these features are united by the general question of 'which processes are effective in structuring insular communities?' (Haila et al. 1982).

All species on oceanic islands must have dispersed over water (Paulay 1994). Hence species with low vagility are absent and the species that colonised first are likely to have pre-emptive advantage over later colonists. Islands formed by volcanic eruption are usually millions of years old and have developed a biota dominated by endemic species. Cays are much younger (a few thousand years old) and lack endemic species. Founder effects lead to genetic impoverishment. In contrast, the biota of continental islands (the dominant type of island in WA waters) is largely relictual, representing the outcome of several thousand years of differential extinction of species, with limited colonisation by mainland species. Species that were rare on the soon-to-be-isolated island are likely to become extinct first, leading to under-representation of species in higher trophic levels. Animal species of small body size are more likely to persist relative to those of large body size because of the inverse relationship between home range and body size.

### *Reduced species richness*

Species impoverishment is the most noticeable characteristic of islands, and is well documented. Explaining the absence of species has proven challenging, however, with interspecific competition, habitat availability and habitat structure most often invoked (e.g. MacArthur et al. 1972; Haila et al. 1983). Species present on small islands are usually those species that are widely distributed on the adjacent mainland (J-L Martin 1983; J-L Martin & Lepart 1989).

The biologically depauperate nature of WA islands was noted as early as 1802: 'The botanical gentlemen employed the day in going round Middle Island, but they found very little to reward their labour' (Flinders 1814: 88). Some 3,241 taxa of vascular plants have been recorded on WA islands (A Chapman pers. comm.). This is c. 25% of all such taxa recorded for WA. More specific comparisons, based only on those plant and animal species recorded on islands, the mainland coast, or both, reveal the extent of species impoverishment on islands (10–67%, Table 4). Detailed analysis, based on the WA coastline being subdivided into 15 segments, shows some remarkable regional differences in the reduction in richness of plant species in large genera (Tables 5–7). The major exceptions to species impoverishment on islands are seabirds and seals (Table 4).

### *Occurrence of endemic species or subspecies*

The proportion of endemic plant species on oceanic islands increases with the shortest distance from the nearest continent (usually >100 km) and for ferns, grasses, sedges, composites and vertebrates, the proportion of endemic species increases with length of the diaspore (Adsersen 1995). As previously noted, most

**Table 4**

Comparative species richness for various taxa occurring on the mainland coast and islands of Western Australia. Casual occurrences of bird species are excluded.

| Taxon | No. of species recorded on Coastal mainland | Islands (%) | Reference |
|---|---|---|---|
| *Acacia* | 299 | 66 (22) | Western Australian Herbarium 1998– |
| *Eucalyptus* | 118 | 13 (11) | MIH Brooker & Kleinig 2001 |
| *Grevillea* | 98 | 10 (10) | Western Australian Herbarium 1998– |
| *Drosera* | 66 | 10 (15) | Western Australian Herbarium 1998– |
| *Corymbia* | 18 | 10 (56) | MIH Brooker & Kleinig 2004 |
| Frogs | 72 | 30 (42) | Tyler & Doughty 2009; Western Australian Museum 2015 |
| Skinks | 147 | 75 (51) | Cogger 2014; Storr et al. 1999; Western Australian Museum 2013 |
| Agamid lizards | 41 | 16 (39) | Cogger 2014, Western Australian Museum 2013 |
| Varanid lizards | 16 | 8 (50) | Cogger 2014; Western Australian Museum 2013 |
| Geckoes | 54 | 36 (67) | Cogger 2014; Western Australian Museum 2013 |
| Pygopod lizards | 24 | 13 (54) | Cogger 2014; Western Australian Museum 2013 |
| Snakes (non-marine) | 86 | 32 (37) | Cogger 2014; Storr et al. 2002; Western Australian Museum 1998– |
| Birds (land, non-passerine) | 99 | 52 (53) | Johnstone & Storr 1998 |
| Birds (land, passerine) | 161 | 95 (59) | Johnstone & Storr 2004 |
| Seabirds | 1 | 25 | Johnstone & Storr 1998 |
| Mammals (non-volant) | 91 | 32 (35) | Abbott & Burbidge 1995; Van Dyck & Strahan 2008 |
| Seals | | 2 | Abbott 1979 |
| Turtles | 4 | 4 | R Prince pers. comm. |

WA islands are situated close to the mainland (<20 km), and as with most continental islands (Wallace 1881: 307), few instances of endemic species are to be expected.

It does not seem that any plant species are endemic to WA islands. The few examples of apparent endemism (at the species level), including *Brachyscome eyrensis, Commicarpus chinensis, Dysoxylum acutangulum, Eucalyptus kenneallyi, Heliotropum microsalsoloides, Lepidium desvauxii, Muellerargia timoriensis, Salacia chinensis, Sida pusilla, Stuartina muelleri,* and undescribed species of *Carpobrotus, Cucumis, Gomphrena, Olearia, Polycarpaea, Solanum, Spermacoce, Tribulopsis* and *Triumfetta* (A Chapman, pers. comm.) should arguably (but prudently) be regarded as yet to be collected on mainland WA. This point is well illustrated by the rare fern *Asplenium obtusatum*. Discovered on Breaksea and Chatham islands in 1866 and 1975 respectively, this species was not known to occur on the coastal mainland until 1990. Since then it has been discovered at two other mainland sites. This will probably apply also to the six putative Kimberley island-endemic species identified by Lyons et al. (2014).

Endemism at the level of subspecies has been documented for few plant species. The islands of the Archipelago of the Recherche have been well explored by botanists and *Eucalyptus insularis* has been found on only one of these islands (Nicolle et al. 2014). A few plant species are not strictly island endemics but have been collected rarely on mainland WA, e.g. *Lepidium foliosum,* (NG Marchant et al. 1987; G Keighery et al. 2002), *Lepidium puberulum* (JM Harvey et al. 2001), and *Malva preissiana* (Western Australian Herbarium 1998-).

In contrast, land snails that occur in rainforest on islands in the Kimberley region exhibit a high degree of endemism as they do in mainland rainforest patches, no doubt caused by limited capability for dispersal (LA Gibson & Köhler 2012). Most of the 89 species of camaenids recorded are each restricted to a single island. These species were already present before these islands became separated from the mainland, as the short period (c. 7 ka) seems too brief for in situ speciation to have taken place (MS Johnson et al. 2010; Köhler & Johnson 2012). Other less mobile invertebrates, such as earthworms, are also prime candidates for the evolution of endemic populations on some WA islands. At present, knowledge is insufficient and unreliable for most invertebrate taxa, except for land snails found in rainforest vegetation and for butterflies. No island-endemic butterfly species is known for WA islands (M Williams pers. comm.), although three subspecies have been described (Table 8).

The invertebrate fauna of Barrow Island has recently been studied more thoroughly than any other WA island. Most of the subterranean fauna is endemic (Humphreys et al. 2013). The three camaenid land-snail species present are not endemic but are shared with nearby islands (MS Johnson et al. 2013), and none of the lycosid spiders and termites is endemic (Framenau & Leung 2013, DT Jones 2013). However, three of the six millipede species are endemic (Car et al. 2013). For other taxa (e.g. Thysanoptera, Dolichopodidae) it is premature to deduce island endemism because the mainland fauna is poorly known (Mound 2013; Bickel 2013). Very few ant species appear to be endemic

**Table 5**

Comparative species richness of some speciose plant genera on the mainland coast and adjacent islands of Western Australia. **M** = number of species present in a 1-km-wide coastal strip between the localities nominated (P. Gioia pers. comm. 2007). **I** = number of species present on at least one island between the localities nominated (Western Australian Herbarium 1998–). *The presence of fewer species on this mainland segment is presumably a result of inadequate collecting.

| Segment of coastline | ***Banksia*; sensu George 2014** | ***Banksia*; sensu George 2014** | ***Leucopogon*** | ***Leucopogon*** | ***Grevillea*** | ***Grevillea*** | ***Eremophila*** | ***Eremophila*** | ***Melaleuca*** | ***Melaleuca*** |
|---|---|---|---|---|---|---|---|---|---|---|
| | **M** | **I** | **M** | **I** | **M** | **I** | **M** | **I** | **M** | **I** |
| Northern Territory border to Gantheaume Point | 1 | | | 9 | 8 | | | 5* | 7 | |
| Gantheaume Point to Cape Lambert | | | | | 2 | 1 | 1 | | 3 | |
| Cape Lambert to Cape Preston | | | | | 1 | | 2 | | | |
| Cape Preston to Point Quobba | 1 | | | | 3 | | 6 | 1 | 1 | 1 |
| Point Quobba to Zuytdorp Point | 1 | | | | 3 | 1 | 11 | 5 | 3* | 5 |
| Zuytdorp Point to Lynton | 6 | | 3 | | 12 | | 5 | | 16 | |
| Lynton to Dongara | 4 | | | 1 | 11 | 1 | 2 | 1 | 13 | |
| Dongara to City Beach | 8 | | 7 | | 5 | | 1 | 1 | 7 | |
| City Beach to Becher Point | 5 | | 5 | 2 | 10 | | 1 | 1 | 12 | 2 |
| Becher Point to Cape Leeuwin | 5 | | 16 | 1 | 12 | | 1 | | 12 | |
| Cape Leeuwin to Torbay Head | 10 | | 18 | | 3 | | | | 16 | 1 |
| Torbay Head to Lookout Point | 16 | 1 | 30 | 4 | 6 | | | | 16 | 1 |
| Lookout Point to Butty Head | 19 | | 30 | 1 | 10 | | 1 | | 23 | 2 |
| Butty Head to Israelite Bay | 7 | | 17 | 6 | 2 | | 11 | | 16 | 6 |
| Israelite Bay to South Australian border | 2 | | 2 | | 2 | | 1 | | 5 | |

**Table 6**

Comparative species richness of some speciose plant genera on the mainland coast and adjacent islands of WA. **M** = number of species present in a 1-km-wide coastal strip between the localities nominated (P. Gioia pers. comm. 2007). **I** = number of species present on at least one island between the localities nominated (Western Australian Herbarium 1998–). Subspecies, records of exotic species and plantings of native species are excluded. *The presence of fewer species on this mainland segment is presumably a result of inadequate collecting.

| **Segment of coastline** | ***Acacia* M** | ***Acacia* I** | ***Eucalyptus* M** | ***Eucalyptus* I** | ***Corymbia* M** | ***Corymbia* I** |
|---|---|---|---|---|---|---|
| Northern Territory border to Gantheaume Point | 30* | 35 | 5* | 9 | 12* | 14 |
| Gantheaume Point to Cape Lambert | 19 | 16 | 1 | 1 | 7 | 1 |
| Cape Lambert to Cape Preston | 16 | 13 | 1 | 1 | 1 | 2 |
| Cape Preston to Point Quobba | 13 | 18 | 6 | 4 | 1 | 1 |
| Point Quobba to Zuytdorp Point | 19 | 12 | 5 | | | |
| Zuytdorp Point to Lynton | 16 | 8 | 6 | 1 | | |
| Lynton to Dongara | 13 | 7 | 9 | | | |
| Dongara to City Beach | 13 | 6 | 15 | | | |
| City Beach to Becher Point | 23 | 7 | 8 | | | |
| Becher Point to Cape Leeuwin | 28 | 6 | 11 | | 1 | |
| Cape Leeuwin to Torbay Head | 16 | 5 | 9 | | 2 | |
| Torbay Head to Lookout Point | 20 | 8 | 16 | 3 | 2 | |
| Lookout Point to Butty Head | 33 | 12 | 44 | | | |
| Butty Head to Israelite Bay | 20 | 13 | 32 | 9 | | |
| Israelite Bay to South Australian border | 4 | 6 | 13 | | | |

**Table 7**

Comparative species richness of some speciose plant genera on the mainland coast and adjacent islands of Western Australia. **M** = number of species present in a 1-km-wide coastal strip between the localities nominated (P. Gioia pers. comm. 2007). **I** = number of species present on at least one island between the localities nominated (Western Australian Herbarium 1998–). *The presence of fewer species on this mainland segment is presumably a result of inadequate collecting.

| **Segment of coastline** | ***Dryandra*; *sensu* George 2014 M** | ***Dryandra*; *sensu* George 2014 I** | ***Hakea* M** | ***Hakea* I** | ***Calandrinia* M** | ***Calandrinia* I** | ***Stylidium* M** | ***Stylidium* I** |
|---|---|---|---|---|---|---|---|---|
| Northern Territory border to Gantheaume Point | | | 2 | 1 | | | 5* | 12 |
| Gantheaume Point to Cape Lambert | | | 2 | | | | 1 | |
| Cape Lambert to Cape Preston | | | 1 | 1 | | | 1 | |
| Cape Preston to Point Quobba | | | 1 | 1 | | | | |
| Point Quobba to Zuytdorp Point | | | 1* | 2 | | | | |
| Zuytdorp Point to Lynton | 2 | | | | 5 | | 6 | |
| Lynton to Dongara | 2 | | 2 | | 4 | | 5 | |
| Dongara to City Beach | 5 | | 6 | | 5 | | 7 | |
| City Beach to Becher Point | 4 | | 5 | | 10 | 1 | 13 | |
| Becher Point to Cape Leeuwin | 3 | | 14 | | 36 | | 36 | |
| Cape Leeuwin to Torbay Head | 3 | | 9 | | 25 | | 19 | |
| Torbay Head to Lookout Point | 8 | | 15 | 3 | 23 | 2 | 31 | 2 |
| Lookout Point to Butty Head | 13 | | 21 | | 9 | | 17 | |
| Butty Head to Israelite Bay | 7 | 1 | 8 | 2 | 6 | 3 | 14 | 7 |
| Israelite Bay to South Australian border | | | 2 | | 1 | | 1 | |

(Heterick 2013). That some species of spiders and pseudoscorpions are at present known only from a single island (Edward 2007; Edward & Harvey 2008; Otto & Harvey 2008) should not be taken to indicate endemism.

Many insular species and subspecies of birds have been described as endemic to WA islands (Table 8). None of the endemic species is currently recognised, and only eight endemic subspecies are accepted. The current situation with endemic mammalian species and subspecies is similar, with no species and three subspecies currently recognised as endemic to WA islands. No insular endemic species or subspecies of frogs have been described. Although four species and six subspecies of reptiles are currently recognised as endemic to WA islands, more intensive collecting on other islands and on the mainland is likely to reduce the number of taxa so recognised (e.g. Maryan & Browne-Cooper 1994). Molecular-based comparisons may result in further revision of the endemic status of these taxa and the other taxa listed in Table 8.

Some 17 reptile species are at present known only from islands in the Kimberley region (R Palmer et al. 2013b). It appears that none is truly endemic, as much of the adjacent coastal mainland has not yet been adequately sampled. In one case a new skink species was described from King Hall Island (Kimberley region) based on an aberrant specimen of *Lerista griffini* (Maryan & Robinson 1997).

Currently it is not possible to establish definitively if any fungal species are endemic to islands of WA (N Bougher & M Brundrett pers. comm.).

## *Occurrence of unique ecosystems*

Seabirds and pinnipeds breeding on islands have helped to shape the structure and floristic composition of some vegetation. This has resulted from trampling of vegetation, defaecation of toxic chemicals, and nutrient enrichment of soil. On some islands the absence of humans for millennia has resulted in ecosystems that have escaped anthropogenic fire. All of these features are extremely rare on mainland WA. These characteristics are examined in detail in 'Presence of Indigenous People' below.

## *Species characteristic of WA islands*

The impression evident upon landing on an island is that the vegetation structure, floristics and dominant plant species differ from those of the mainland coast (Seddon 1972; GG Smith 1973; Rippey & Rowland 1995). Plant taxa that predominate or are conspicuous in coastal mainland south-west WA, such as Fabaceae (including *Acacia, Jacksonia*), Myrtaceae (including *Eucalyptus, Corymbia, Melaleuca*), Proteaceae (including *Banksia, Dryandra, Grevillea, Hakea*), Ericaceae (apart from *Leucopogon*), Dilleniaceae, *Anigozanthos, Macrozamia, Xanthorrhoea, Kingia* and *Allocasuarina* are either absent from, or restricted in occurrence on, these islands (Tables 4, 5, 6; Abbott 1977a, 1980a, 1980d,1981b; Abbott & Black 1978, 1980; AA Burbidge & George 1978; JM Harvey et al. 2001; G Keighery et al. 2002, 2006; McArthur 1957; Storr 1960, 1961, 1965a, 1965b, 1965c; JH Willis 1953). Evidence from fossils and pollen deposits on Rottnest Island indicates that some plant species were present at the time of isolation but subsequently became extinct (Churchill 1960).

Like all islands, WA islands are comprised of a nested set of vegetation types and species assemblages. Those on small depauperate islands represent nonrandom subsets of those on species-rich islands nearby (J-L Martin 1983; Lomolino 1996). On continental islands, this hierarchy is presumed to be the consequence of differential extinction of species and elimination of some of the vegetation types present when the island became isolated from the mainland or nearest large island. Through this process of progressive restriction of population size, culminating in selective extinction, smaller islands are expected to converge in their species composition (Patterson & Atmar 1986).

Sometimes there are plant species present on larger islands that are inexplicably absent from adjacent smaller islands (Abbott 1980d). Usually, however, species present on the smallest islands occur also on larger islands nearby (Järvinen & Ranta 1987). Species occurring in simple, ubiquitous habitats are found on more islands than those species with more specialised habitat preferences (Reed 1980). There is no evidence from WA islands of supertramp species (sensu JM Diamond 1975), i.e. species occurring on small islands at high density but absent from larger islands.

A recently updated map of the vegetation of WA is at too large a scale to show the vegetation types present on all but the largest islands (Beard et al. 2013). Nonetheless it usefully demonstrates the vegetation types occurring along the mainland coastline adjacent to islands. Small exposed islands between Shark Bay and the South Australian border support herbland (<50 cm tall) and low open shrubland (<1 m tall) comprised of halophytic or salt-tolerant species (*Carpobrotus virescens, Dispyhma crassifolium, Threlkeldia diffusa*), with *Cotula australis, Enchylaena tomentosa, Frankenia pauciflora, F. tetrapetala, Leucophyta brownii, Lobelia anceps, Samolus repens, Sarcocornia blackiana, S. quinqueflora, Senecio pinnatifolius, Sporobolus virginicus, Tetragonia implexicoma, Zygophyllum billardierei* and *Z. simile* as less dominant or less frequent (Abbott 1980a, 1980e; Abbott & Black 1978, 1980; Abbott et al. 2006; G Keighery 1995; G Keighery et al. 2002, 2006; Storr MSa; JH Willis 1953).

Islands that are larger in area or less exposed to wave action retain low shrubland (1.5–2 m tall) dominated by *Nitraria billardierei, Rhagodia baccata, R. crassifolia, R. latifolia, R. preissii, Scaevola crassifolia, Atriplex cinerea, A. isatidea, A. paludosa, Spinifex longifolius, Tecticornia halocnemoides* and *Malva preissiana*. Some islands are dominated by *Poa poiformis* tussock grassland, whereas the larger islands in Shark Bay are dominated by open hummock grassland of *Triodia plurinervata*.

Less-exposed sites on islands retain tall shrubland (<5 m) dominated by *Myoporum insulare*, *Olearia axillaris*

**Table 8**

Bird, mammal, reptile, and butterfly species and subspecies either described as taxa endemic to one or more WA islands or based on a type specimen collected on a WA island.

| Species/subspecies/circumscriber/year | Island(s) | Current status |
|---|---|---|
| **Birds** | | |
| *Cereopsis novaehollandiae georgi* Mathews 1912 | 'Islands south-east of West Australia' [Archipelago of the Recherche] = 'Twin Peak' (GM Mathews 1920: 56), which is North Twin Peak *fide* V Serventy 1952: 19 | *C. n. grisea* (applies to entire WA population: islands & adjacent mainland of southern WA) |
| *Eudyptula minor woodwardi* Mathews 1912 | Sandy Hook | suppressed |
| *Pterodroma macroptera albani* Mathews 1912 | Mistaken | suppressed |
| *Puffinus sphenurus* Gould 1844 | Houtman Abrolhos | suppressed |
| *Puffinus assimilis tunneyi* Mathews 1912 | Boxer | suppressed |
| *Pelagodroma marina dulciae* Mathews 1912 | Breaksea | current |
| *Phaëthon rubricaudus westralis* Mathews 1912 | Houtman Abrolhos | suppressed |
| *Sula dactylatra bedouti* Mathews 1913 | Bedout | suppressed |
| *Sula leucogaster rogersi* Mathews 1913 | Bedout | suppressed |
| *Fregata ariel tunnyi* [sic] Mathews 1914 | Bedout | suppressed |
| *Phalacrocorax varius nitidus* Serventy 1940 | Houtman Abrolhos | suppressed |
| *Carbo fuscescens tunneyi* Mathews 1912 | Peak = island near North Twin Peak (V Serventy 1952) | suppressed |
| *Eulabeornis philippensis mellori* Mathews 1912 | Sandy Hook | *Gallirallus philippensis mellori* |
| *Hemipodius scintillans* Gould 1845 | Houtman Abrolhos | *Turnix varius scintillans* (North, East Wallabi, West Wallabi Islands) |
| *Arenaria interpres nova* Mathews 1917 | Rottnest | suppressed |
| *Esacus magnirostris neglectus* Mathews 1912 | Lewes [Lewis] | suppressed |
| *Haematopus unicolor bernieri* Mathews 1912 | Bernier | suppressed |
| *Cladorhynchus leucocephalus rottnesti* Mathews 1912 | Rottnest | suppressed |
| *Sterna gracilis* Gould 1845 | Houtman Abrolhos | suppressed |
| *Anous stolidus gilberti* Mathews 1912 | Bedout | suppressed |
| *Anous melanops* Gould 1845 | Houtman Abrolhos | *A. tenuirostris melanops* |
| *Malurus leucopterus* Dumont 1824 | Dirk Hartog | *M. l. leucopterus* (but possibly also on adjacent mainland) |
| *Malurus edouardi* Campbell 1901 | Barrow | *M. leucopterus edouardi* |
| *Malurus bernieri* Ogilvie-Grant 1909 | Bernier | suppressed |
| *Leggornis lamberti hartogi* Mathews 1918 | Dirk Hartog | suppressed |
| *Stipiturus malachurus hartogi* Carter 1916 | Dirk Hartog | current |
| *Diaphorillas textilis carteri* Mathews 1917 | Dirk Hartog | suppressed |
| *Sericornis balstoni* Ogilvie-Grant 1909 | Bernier | *S. frontalis balstoni* |
| *Sericornis maculatus hartogi* Carter 1916 | Dirk Hartog | suppressed |
| *Sericornis maculatus houtmanensis* Zietz 1921 | Houtman Abrolhos | suppressed |
| *Sericornis maculatus fuscipes* Alexander 1922 | Wallabi Islands | suppressed |
| *Sericornis maculata mondraini* Mathews1942 | Mondrain | suppressed |
| *Calamanthus campestris hartogi* Carter 1916 | Dirk Hartog | suppressed |
| *Calamanthus campestris dorrie* Mathews 1912 | Dorre | suppressed |
| *Ptilotis insularis* Milligan 1911 | Rottnest | suppressed |
| *Meliphaga virescens hartogi* Mathews 1920 | Dirk Hartog | suppressed |
| *Meliphaga virescens lewisi* Mathews 1942 | Lewis | suppressed |

| Species/subspecies/circumscriber/year | Island(s) | Current status |
|---|---|---|
| *Oreoica gutturalis lloydi* Mathews 1917 | Dirk Hartog | suppressed |
| *Corvus cecilae hartogi* Mathews 1920 | Dirk Hartog | suppressed |
| *Eremiornis carteri assimilis* Montague 1913 | Hermite | suppressed |
| *Zosterops shortridgei* Ogilvie-Grant 1909 | Mistaken | suppressed |
| *Zosterops lutea hecla* Mathews 1912 | Hecla | suppressed |
| *Zosterops lutea montebelloensis* Ashby 1925 | Montebello Islands | suppressed |
| *Taeniopygia castanotis hartogi* Mathews 1920 | Dirk Hartog | suppressed |
| *Anthus australis montebelli* Montague 1913 | Montebello Islands | suppressed |
| *Anthus australis hartogi* Mathews 1917 | Dirk Hartog | suppressed |
| **Mammals** | | |
| *Sminthopsis griseoventer boullangerensis* Crowther, Dickman & Lynam 1999 | Boullanger | untenable (Start et al. 2006); suppressed |
| *Isoodon barrowensis* Thomas 1901 | Barrow | suppressed |
| *Lagorchestes conspicillatus* Gould 1842 | Barrow | *L. c. conspicillatus* |
| *Lagorchestes hirsutus bernieri* Thomas 1907 | Bernier | current |
| *Lagorchestes hirsutus dorreae* Thomas 1907 | Dorre | suppressed |
| *Lagostrophus fasciatus* Péron & Lesueur 1807 | Bernier | suppressed |
| *Halmaturus binoë* Gould 1842 | Houtman Abrolhos | suppressed |
| *Osphranter isabellinus* Gould 1842 | Barrow | suppressed |
| *Petrogale hacketti* Thomas1905 | Mondrain, Wilson, & Combe [Westall] | *P. lateralis hacketti* |
| *Macroglossus lagochilus nanus* Matschie 1913 | Sunday | suppressed |
| *Rattus fuscipes glauerti* Thomas 1926 | East Wallabi | suppressed |
| *Rattus mondraneus* Thomas 1921 | Mondrain | suppressed |
| *Thetomys ferculinus* Thomas 1902 | Barrow | suppressed |
| *Gymomys albocinereus squalorum* Thomas 1907 | Bernier | suppressed |
| **Reptiles** | | |
| *Aprasia rostrata* Parker 1956 | Hermite | current |
| *Pogona minor minima* Loveridge 1933 | Houtman Abrolhos | current |
| *Ctenotus lancelini* Ford 1969 | Lancelin | not restricted to this island |
| *Ctenotus pantherinus acripes* Storr 1975 | Barrow | current |
| *Egernia s. stokesii* Gray 1845 | Houtman Abrolhos | current |
| *Egernia s. aethiops* Storr 1978 | Baudin | suppressed |
| *Lerista praefrontalis* Greer 1986 | King Hall | current |
| *Tiliqua rugosa konowi* Mertens 1958 | Rottnest | current |
| *Ramphotyphlops longissimus* Aplin 1998 | Barrow | *Anilios longissimus* |
| *Ramphotyphlops yampiensis* Storr 1981 | Koolan | *Anilios yampiensis* |
| *Pseudonaja affinis exilis* Storr 1989 | Rottnest | current |
| *Pseudonaja affinis tanneri* Worrell 1961 | Boxer, Figure of Eight | current |
| **Butterflies** | | |
| *Geitoneura klugii insula* Burns 1951 | Rottnest | suppressed |
| *Motasingha atralba nila* Waterhouse 1932 | Dirk Hartog | *Antipodia dactyliota nila* |
| *Trapezites argenteoornatus insula* Waterhouse 1932 | Hermite, Bernier, Dorre, East Wallabi, Rottnest | suppressed |

Sources: Braby 2000; How et al. 2001; Iredale and Troughton 1934; Johnstone and Storr 1998, 2004; RAOU 1926; Storr et al. 1999; WAM 2013; Whittell & Serventy 1948. Current status based on Department of Terrestrial Zoology, Western Australian Museum (2015) and Johnstone & Darnell (2015).

and *Acacia coriacea, A. ligulata* or *A. rostellifera.* Woodland dominated by *Eucalyptus*, *Callitris* or *Melaleuca* occur only on sheltered parts of larger islands. Mangrove (*Avicennia marina*) occurs only on some islands in Houtman Abrolhos (JM Harvey et al. 2001).

Vegetation of the larger islands in Shark Bay comprises 4–5 structural types, dominated by *Triodia* grassland (with occasional patches of shrubs and stunted eucalypts), tall scrub, low heath, shrubs on coastal sand dunes, and low open heath (AA Burbidge & George 1978; Cale 1992; Royce 1962). Most of the vegetation is of no great height (<1-1.5 m), except where species of *Acacia*, *Pittosporum*, *Diplolaena* and *Alectryon oleifolius* occur as tall shrubs.

Islands between Exmouth Gulf and Port Hedland are dominated by *Acacia* (*A. bivenosa, A. coriacea*) and *Triodia* hummock grassland (Butler 1970; AA Burbidge 1971; Ride 1964a; Royce 1964; Start & McKenzie 1992; WAPET 1987, 1988). Even on the largest, Barrow Island, trees of *Ficus* species, *Eucalyptus* (c. 3 m tall) and *Erythrina vespertilio* (c. 2 m tall) have very limited occurrence (Buckley 1983; *The Perth Gazette* 27.1.1865: 2). The main vegetation of the smaller islands comprises *Spinifex longifolius* and *Acacia* species (F Stanley pers. comm.).

Islands of the Kimberley region are generally larger than elsewhere in WA (Table 2). Many support extensive areas of woodland (dominated by *Eucalyptus* and *Corymbia* over *Triodia* hummock grassland) and limited occurrence of patches of mangrove and closed forest (vine thicket/rainforest) dominated by *Albizia lebbek*, *Canarium australianum*, *Eugenia*, *Ficus*, *Tinospora* and *Toona* species (Beard et al. 1984; AA Burbidge et al. 1978; Coate 2008a; Henson et al. 2014; G Keighery et al. 1995; Kenneally et al. 1991).

Exotic plant species are over-represented on some WA islands, as high as 20-40% of the flora (see 'Activities of Europeans' below). In comparison, the entire area of WA has c. 10% of the entire flora of 12 347 species exotic (Western Australian Herbarium 1998-).

The landbird fauna of islands reflects the structural vegetation types present (Abbott 1977c, 1977d, 1978a,1980e; Abbott & Watson 1978; Abbott et al. 2006; AA Burbidge & Fuller 2000; AA Burbidge & George 1978; Cale 1992; Garstone 1978; GA Green 1972; SG Lane 1982l; Mees 1962; Onton & Webb 2009; Serventy VN 1943, 1952; LA Smith et al. 2005; Storr 1966, MSb; Storr et al. 1986; Surman & Nicholson 2015; Tarr 1949). Small islands between Shark Bay and the South Australian border often have only the welcome swallow (*Hirundo neoxena*), singing honeyeater (*Gavicalis virescens*), rock parrot (*Neophema petrophila*), grey-breasted white-eye (*Zosterops lateralis*), and sometimes the Australian kestrel (*Falco cenchroides*) and Australian pipit (*Anthus australis*), as breeding species. Once taller vegetation is represented the western golden whistler (*Pacycephala occidentalis*) and New Holland honeyeater (*Phylidonyris novaehollandiae*) are able to persist. On larger islands, the western raven (*Corvus perplexus*), brush bronzewing (*Phaps elegans*) and brown quail (*Coturnix ypsilophora*) also occur.

Small islands between Exmouth Gulf and Port Hedland often have the white-breasted woodswallow (*Artamus leucorhynchus*), yellow white-eye (*Zosterops luteus*), bar-shouldered dove (*Geopelia humeralis*), Australian kestrel, brown quail, Australian pipit, welcome swallow, and zebra finch (*Taeniopygia guttata*) present (Abbott 1982; Kenneally et al. 2000; C Williams pers. comm.; WABN 1943-2016, No. 97: 3-4). Large islands of the Pilbara and Kimberley coasts have many additional bird species present (Johnstone & Storr 1998, 2004; Storr MSb). This is because some of these species are associated with mangroves, rainforest, eucalypt woodland and hummock grassland, habitats absent from small islands.

Herpetologists have visited most of the smaller WA islands. Islands between Shark Bay and Israelite Bay usually have present one (occasionally two) gecko species, sometimes an agamid species, and up to four skink species (Kitchener & How 1982; Western Australian Museum 2013). In the well-studied Archipelago of the Recherche, LA Smith & Johnstone (1996) recognised a core group of six reptile species (two geckoes, four skinks) that are widely distributed on 19–32 of the 47 islands studied. The marbled gecko *Christinus marmoratus* and the skinks *Ctenotus labillardieri*, *Hemiergis peronii*, King's skink (*Egernia kingii*) and *E. napoleonis* occur on many islands along the southern coast of WA, whereas on islands of the western coast (between Shark Bay and Perth), the skinks *Ctenotus alleni*, *E. kingii*, *H. quadrilineata*, *Lerista elegans*, *L. lineopunctulata, L. praepedita*, *Menetia greyii* and *Morethia obscura* are well represented.

Little of interest can be disclosed about the characteristic invertebrate and fungal species present on WA islands. Either too few islands have been studied (invertebrates) or studies have not yet commenced (fungi).

## *Hyperabundance*

Some species occur more abundantly on islands than on the mainland, or on small islands relative to larger islands (Crowell 1962; Tompa 1964; Grant 1966a, 1966b; MacArthur et al. 1972; GB Cox & Ricklefs 1977; SG Nilsson 1977; Emlen 1979; Haila et al. 1983; Niemelä et al. 1985; Terborgh et al. 1997; Kotze et al. 2000; Rodda & Dean-Bradley 2002). Reptiles on islands near Arnhem Land, Northern Territory provide some striking examples (Woinarski et al. 1999b). In places without predators, prey species should be more abundant than in places where predators are present. Competitive release, resulting from the absence of close competitors, may also lead to increased density (Gause 1934; Morse 1977).

WA islands (particularly those in the south-west) are without Aborigines, dingoes (*Canis dingo*), and *Dasyurus* species, and typically without raptors (excluding the species feeding on marine food), owls, varanids, and snakes. Many of these islands support (or once supported) large populations of wallabies, breeding turtles, seals, and seabirds. In 1840 more than 400 tammars (*Macropus eugenii*) were shot on West Wallabi Island by two sportsmen in two days (Stokes 1846 Vol. 2: 155). On East Wallabi Island in 1890, 35 of these wallabies were shot in a short period and 'any number could have been obtained if wanted' (JJ Walker 1897: 297). Upon leaving this island the whaleboat was 'almost filled with game'. In 1897 this species was recorded as 'so abundant' on the Wallabi Islands (Helms 1898: 428). In 1913, Dakin (1919: 159) saw 'far more individuals' of this species in one afternoon on East and West Wallabi islands 'than of all species of marsupials seen on the mainland in three years'. This same species on Kangaroo Island (South Australia) is very fecund and females can produce young when less than one year of age (Andrewartha & Barker 1969). The spectacled hare-wallaby (*Lagorchestes conspicillatus*) was 'very numerous' on Trimouille Island in 1840 and afforded excellent sport 'quite equal to any rabbit shooting' (Stokes 1846 Vol. 2: 213). The quokka was recorded as 'rather numerous' in the western portion of Rottnest Island (Stokes 1846 Vol. 2: 128).

There is little doubt that the reason for the great abundance of seabirds that breed on WA islands (particularly those between Shark Bay and Israelite Bay) is the absence of any Aboriginal presence on these islands, presumably during the past 6–14 ka, and certainly when they were first visited by Europeans. Moreover, the major seabird breeding islands in the Kimberley region, to which Aborigines had access, lie well offshore.

The large (220 g) King's skink occurs on Penguin Island at very high densities of c. 100 animals $ha^{-1}$ (Serventy & White 1943; Wooller & Dunlop 1990). On the adjacent mainland it is difficult to find this species. This difference seems attributable to the abundant eggs of seabirds on the island. Similarly, the Lancelin Island ctenotus (*Ctenotus lancelini*) occurs abundantly on Lancelin Island but only one individual has so far been discovered on the adjacent mainland (Pearson & Jones 2000).

Serventy (1951) noted anecdotal examples of great abundance of lizards on Pelsaert and Eclipse islands and of snakes on some islands in the Archipelago of the Recherche. J Ford (1963) reported a similar situation on some islands between Dongara and Lancelin. The tiger snake (*Notechis scutatus*) occurs at very high density (>20 $ha^{-1}$), and with a total biomass of 100 kg, on Carnac Island relative to the mainland. On this island (with an area of 16 ha), the snake population is supported by a very high density (3000–4000) of silver gulls (*Larus novaehollandiae*; Bonnet et al. 2002). Dakin (1919) recorded the occurrence of the carpet python (*Morelia spilota*) in 'very large numbers' on West Wallabi Island, Houtman Abrolhos.

The dibbler (*Parantechinus apicalis*) occurs at higher density on Whitlock Island compared to adjacent Boullanger Island (Wolfe et al. 2004). This seems attributable to the fertiliser effect resulting from the presence of dense populations of breeding seabirds on Whitlock Island. Dibblers on this island have greater longevity and better body condition, and the males do not die off each year.

According to a review of many studies of rodents, reproduction in island populations is lower than in mainland populations (Gliwicz 1980). This is brought about by a shortened breeding season, later maturation of females, and smaller litters. Island bird populations also have smaller territories and clutch sizes (Crowell & Rothstein 1981; Blondel 2000). Comparative studies are yet to be undertaken on WA islands.

It is not known if plant species on WA islands show any change in reproductive biology. Floras of oceanic islands usually have a greater proportion of dioecious species than on continental areas (Eliasson 1995). It is doubtful, however, whether floras of continental islands would demonstrate this trait.

## Habitat changes

Habitat distributions of bird species on islands are often broader than on the mainland (Lack & Southern 1949; Svärdson 1949; Bourne 1955; Benson 1960; GB Cox & Ricklefs 1977). Early accounts of change in habitat usage on islands (e.g. Lack 1942) vaguely attributed this to a psychological factor. Since the late 1940s it is usually presumed that competitive release on islands explains the expanded usage by some species of habitats or even occupation of a habitat that differs from that on the mainland (MacArthur 1965; Lack 1969; JM Diamond 1970). However, the roles of decreased interspecific competition and increased intraspecific competition in causing expanded occupation of habitats are seldom distinguished (Svärdson 1949). Not all differences or anomalies seem attributable to competition (Benson 1960; Vassallo & Rice 1982; J-L Martin 1992), nor is expanded habitat use following reduction in presumptive competitors universal. On Tobago and Granada in the West Indies, the 16 bird species shared between these islands exhibit no ecological release (Wunderle 1985). On Corsica, the number of bird species is not much less than on the mainland (Provence, France), yet forest birds spill over from optimal habitat (forest) to shrubby habitats (Blondel et al. 1988).

Habitat plasticity by some bird species has been documented for islands in Torres Strait (Queensland) and near north-eastern Arnhem Land, Northern Territory (Draffan et al. 1983; Woinarski et al. 2001). Examples from WA islands are also known. For example, the little grassbird (*Megalurus gramineus*) lives in dense *Nitraria* shrubs on Sandland Island, whereas on the mainland it lives in dense bulrushes, sedges and long grass in swamps and around lakes (Johnstone & Storr 2004). The tawny grassbird (*M. timoriensis*) on Adele Island lives in *Spinifex longifolius* (I Abbott pers. obs.), but not in this habitat on the adjacent mainland (Kimberley region). There its habitat is long grass, mainly in swamps (Johnstone & Storr 2004).The willie wagtail (*Rhipidura leucophrys*) and grey butcherbird (*Cracticus torquatus*) were reported in unusual habitats on Garden Island (Abbott 1980f). Alexander (1922: 464) mistakenly queried the occurrence of the spotless crake (*Porzana tabuensis*) on islands in Houtman Abrolhos, based on its habitat on mainland WA: 'this is one of the most unlikely birds one could think of to be found on these dry islands'. Yet, on Pelsaert Island it is a 'common bird in the scrubs' (Garstone 1978, I Abbott pers. obs.).

Examples of habitat expansion shown by reptiles are sparse. The lizard *Ctenotus angusticeps* occurs on Airlie Island in most of the habitats present there, especially tussock grassland (Browne-Cooper & Maryan 1990), whereas on the mainland it is restricted to salt marsh adjacent to mangal (Maryan et al. 2013a).

Many of the landbird species that live in vine thickets (rainforest) on mainland Kimberley show no indication of spreading to more open habitats present on adjacent islands (LA Smith et al. 1978). Examples of these species include orange-footed scrubfowl (*Megapodius reinwardt*), emerald dove (*Chalcophaps indica*), rose-crowned fruit-dove (*Ptilinopus regina*), rainbow pitta (*Pitta iris*), silver-crowned friarbird (*Philemon argenticeps*), little shrike-thrush (*Colluricincla megarhyncha*), Australasian figbird (*Sphecotheres vieilloti*), wood fantail (*Rhipidura dryas*) and shining flycatcher (*Myiagra alecto*). Examples of species also occurring in open woodland include pied imperial-pigeon (*Ducula bicolor*), green-backed gerygone (*Gerygone chloronota*), white-gaped honeyeater (*Stomiopera unicolor*), varied triller (*Lalage leucomela*), yellow oriole (*Oriolus flavocinctus*), spangled drongo (*Dicrurus bracteatus*), northern fantail (*Rhipidura rufiventris*) and leaden flycatcher (*Myiagra rubecula*).

Little evidence was found of habitat change for mammal species occurring on islands of the Kimberley region (NL McKenzie et al. 1978), relative to the adjacent high-rainfall mainland that still retains an almost intact mammalian fauna available for comparison (which is no longer the case in the Pilbara and Shark Bay regions).

### *Behavioural changes*

Many species on islands are renowned for their great tameness, fearlessness of humans, and ease of capture. Examples include the dodo (*Raphus cucullatus*; Strickland & Melville 1848), the white-tailed laurel pigeon (*Columba junoniae*) of the Canary Islands (Bannerman 1963: 127), landbirds in the Galápagos Archipelago (Darwin 1839; I. Abbott pers. obs.), birds on Norfolk Island (K Mills 2012: 30; I. Abbott pers. obs.), the Falkland Islands (Darwin 1839), Cape Verde Islands (Bourne 1955), and Aldabra (Ridgway 1895; Benson & Penny 1971), and mammals on Australian islands (Wood Jones 1924; Andrewartha & Barker 1969). As a group, rails on oceanic islands are often flightless (Livezey 2003).

It is thus not surprising that species on some WA islands unfrequented by Aboriginal people also show lack of wariness. Several Cape Barren geese (*Cereopsis novaehollandiae*) 'allowed themselves to be taken by the hand' on Observatory Island in 1792 (Labillardiere 1800: 258) and some were killed on Goose Island 'mostly with sticks' in 1801 (Flinders 1814: 87). Most seabird species nest only on islands and can be walked up to without eliciting a reaction. The common noddy (*Anous stolidus*) is aptly named, as nesting birds act in a stolid (foolish) manner by not fleeing when approached by a human.

The spotless crake (*Porzana tabuensis*) on Pelsaert Island forages indifferently around an intruder's feet (I Abbott pers. obs. 1975). This foraging behaviour is never seen on mainland WA, where the species is 'very unobtrusive and shy' and 'not venturing much out of the shelter of dense rushes or grass' (Carter 1920: 690). In 1948 some lived around a camp on this island and foraged there, and when chased could not be made to fly (Tarr 1949). On Beacon Island, this species would enter huts and accept oatmeal as food (WABN 1943–2016 No. 35: 7), as well as drinking freshwater provided (WABN 1943–2016 No. 46: 8). Buff-banded rails (*Gallirallus philippensis*) forage on Penguin Island under picnic tables and are less secretive than on the mainland (M Chambers 2005; WABN 1943–2016 No. 78: 21, 94: 23-24,149: 37, 153: 36); similar behaviour has been observed on other islands (J Walter & Walter 1999).

The singing honeyeater on Rottnest Island 'often came to the camp to pick up scraps' (Kilpatrick 1932: 31). Grey-breasted white-eyes on Pelsaert Island ate sugar and jam in a camp mess (Tarr 1949) and ate discarded fruit at huts on West Wallabi Island (Storr 1965d). On Bald Island the red-eared firetail (*Stagonopleura oculata*) has been observed feeding on the ground close to a camping tent, a behaviour that is unusual on the mainland (I Abbott pers. obs.), even though this species will frequent gardens (Pate 2009).

The tammar on East Wallabi Island in 1843 evinced 'very little fear, for instead of running off at their full speed…they merely hop about four or five yards and stop, erecting themselves to their full height, s[t]aring round them with evident surprise' (J Gilbert, *The Inquirer* 19 April 1843). On West Wallabi Island they could be taken alive or easily knocked down with a stick or stone, without the need for using a gun (Pasco 1897; Helms 1898; Dakin 1919). This tameness was confirmed by Kelsall (1965), who found that animals from this population were easily managed in pens and tamed for feeding. In contrast, animals on Garden Island were very shy, difficult to handle and more subject to visible signs of stress—qualities shared with the mainland population studied. This difference was not, however, confirmed by studies of captive animals: Tammars from Garden Island have a lower flight initiation distance relative to animals from the mainland (Blumstein 2002).

On Bernier and Dorre islands, wallabies were so fearless that the chaff-house and another room were floored so as to be secure from them (Chief Protector 1909b). On Hermite Island, the spectacled hare-wallaby, while still nocturnal, was regarded as 'one of the most defenceless animals that can well be imagined', easily dislodged from its seat, and not difficult to catch by running it down (Montague 1914: 631). The grassland melomys (*Melomys burtoni*), a rodent on Sunday Island (Kimberley), is a pest and even allows its tail to be held

(R Palmer et al. 2013c). On Barrow Island the golden bandicoot (*Isoodon auratusi*) is a nuisance around camp (Whitlock 1918), and being inquisitive it has learned to access liquid contained in discarded cans (Butler 1970). The brushtail possum (*Trichosurus vulpecula*) frequents camps and rubbish dumps and damages stores and supplies on Barrow Island and uses rubbish bins as 'pseudo hollows' (K Morris & Burbidge 2002). This island lacks hollow-bearing trees (forcing possums to forage on the ground for most of the time) and exotic predators such as cats and foxes.

On Carnac, Pelsaert, East Wallabi, Sandy and Eclipse islands, King's skink is so aggressive that individuals will eat any bird unfortunate to be captured in the lowest shelf of a mist net set too close to the ground (I Abbott pers. obs. 1974–76). In contrast, Tiger snakes on Carnac Island remain docile when provoked (B Bush et al. 2010), whereas on the mainland they readily exhibit the flat-neck warning signal and strike at the aggressive observer (Bonnet et al. 2005). This difference was attributed to the absence of predators on the island.

Many of the reptile species present on Dirk Hartog Island have been recorded sheltering under discarded corrugated iron and other rubbish (Maryan 1996). However, this trait is shared with the mainland. Some species also occupied the crevices in the limestone walls of the homestead. This demonstrates that some species are not always adversely affected by the presence of humans on islands.

Dietary change has been demonstrated for the tammar on Garden Island. Since the establishment in 1972 of a naval base, tammars have invaded irrigated and fertilised lawns and ovals where introduced couch grass (*Cynodon dactylon*) is an important and seasonally unlimited food source for populations near the southern end of the island (McMillan et al. 2010). Populations at the northern end of the island prefer to eat onion weed (*Asphodelus fistulosus*). On Pelsaert Island (Houtman Abrolhos), King's skinks visited the kitchen of a holiday resort and ate food (Pollard 1949; WABN 1943–2016 No. 32: 1).

There is also evidence of habituation. On frequently visited Penguin Island, bridled terns (*Sterna anaethetus*) allow closer approach by humans (1–2 m) than on a less visited island (5–6 m; Dunlop 1996).

Changes in nest site selection are also known. On Rottnest Island, the Australian kestrel probably originally nested in holes in sea cliffs and the welcome swallow originally nested in 'deep caverns of the Rocks' (Gilbert n.d. – 1840?). In recent times buildings are also used (Lawson 1905; Storr 1965c). The welcome swallow nested under eaves of buildings, in a hut and beneath jetties in Houtman Abrolhos (Serventy 1943; Storr 1960; Storr et al. 1986; Tarr 1949) and under verandahs and in huts on Dirk Hartog Island (Ashby 1929; Carter 1917; Whitlock 1921a). On Dirk Hartog Island the little crow (*Corvus bennetti*) nests on windmills, as trees are absent (Ashby 1929; Whitlock 1921a). All of these uses of human infrastructure are shared with the mainland, and thus do not strictly represent insular adaptation.

Differentiation between mainland and Rottnest Island populations in songs of the singing honeyeater (MC Baker 1994, 1996; MC Baker et al. 2001), red-capped robin (*Petroica goodenovii*; MC Baker et al. 2003a), and western gerygone (*Gerygone fusca*; MC Baker et al. 2003b) demonstrate cultural evolution, either involving loss of vocal variety in the island populations of the singing honeyeater and red-capped robin, or increased vocal complexity in the case of the western gerygone (MC Baker et al. 2006).The western gerygone is particularly interesting because it colonised the island only in c.1950 (Storr 1965c).

The population of the white-winged fairy-wren (*Malurus leucopterus*) on Dirk Hartog Island lays smaller clutches, fledges fewer offspring, and has fewer helpers at the nest compared with the same species on the mainland (Rathburn & Montgomerie 2003).

Populations of the quokka on Rottnest Island differ in reproductive biology from the nearest mainland population (Shield 1964). On the island the breeding season is restricted to six months, whereas on the mainland breeding takes place in all months. The difference is attributed to food shortages caused by the annual long dry period on Rottnest Island.

## Morphological changes

Small-bodied animal species predominate on islands, exemplified by a detailed study of Marion Island (Gaston et al. 2001). Vertebrates on islands often, but not always, exhibit differences in body size relative to source areas, with small species becoming larger and large species becoming smaller (Lomolino 2005; Meiri et al. 2005, 2011). Fewer resources, reduced predation, and lessened competition from other species have been invoked to explain such differences. Variation in some species is, however, irregular—well illustrated by size differences in the sulphur-crested cockatoo (*Cacatua galerita*) on New Guinea (source area) and surrounding islands (Mayr 1942). Body size of terrestrial vertebrate species high in the food web increases with island area and in a way that is suggestive of maximum body size being determined by the number of home ranges that can fit into the area of the island (Burness et al. 2001). Populations of black tiger snakes (*Notechis ater*) on 10 South Australian islands exhibit marked differentiation in body size and mass, apparently linked to the size of prey species present (Schwaner 1985).

Geographical variation in sexual dimorphism of the Pacific robin (*Petroica multicolor*) between Australia and islands of the south-western Pacific Ocean is equally remarkable (Mayr 1942). There is often a tendency for island bird populations to have drab plumage (Bourne 1955; Grant 1965b; NK Johnson 1972; J-L Martin 1991).

Some bird species on islands exhibit changes in body size, bill length, variability in bill length, and sexual dimorphism in bill length relative to the mainland (Grant 1965a, 1965c, 1967, 1968; Keast 1968, 1970; J-L Martin 1991). Although some marked phenotypic differences in avian populations between Tasmania and

Victoria and between Kangaroo Island and the adjacent South Australian mainland have been documented (Abbott 1974c, 1977b; Schlotfeldt & Kleindorfer 2006), few remarkable differences in body size or bill dimensions of mainland and insular populations of bird species are evident on WA islands. The singing honeyeater is heavier on islands than on mainland sites at the same latitude (Wooller et al. 1985), and is c. 20% heavier on Garden and Rottnest islands relative to the adjacent coastal mainland (S McKenzie 1996). This species shows, however, no variation in body mass between Bernier Island, Dirk Hartog Island and the adjacent mainland (Wooller et al. 1985). The painted button-quail (*Turnix varius*) is smaller on Houtman Abrolhos than on the mainland (Johnstone & Storr 1998).

An example of change in morphology for plant species is *Atriplex cinerea* on North Fisherman Island, where it exhibits a thick woody stem (G Keighery pers. comm.). Nanism shown by plant species on islands, such as *Paraserianthes lophantha* on Termination Island in the Archipelago of the Recherche (JH Willis 1953) and *Agonis flexuosa* on Breaksea Island and *Agonis marginata* on Chatham Island (I Abbott pers. obs.) has probably resulted from exposure to strong salt-bearing winds. The tree *Pittosporum ligustrifolium* on Garden Island reaches a height of 8 m in sheltered parts but only forms a shrub 1–2 m tall where exposed to wind action (McArthur & Bartle 1981). Seeds need to be collected from such individuals of these and other species and examined under glasshouse conditions in order to determine if the basis for this is genetic or environmental. Halophytic species also exhibit dwarfing (Gillham 1963).

With mammals, the most striking example is the euro (*Macropus robustus*) on Barrow Island. This population, endemic at the subspecific level, is considerably smaller than on the mainland, with a maximum mass on the island of 20 kg (males) and 8 kg (females) versus 35 and 16 kg on the mainland (BJ Richardson & Sharman 1976; J Short & Turner 1991). Mayne (1989) reported that Rothschild's rock-wallaby (*Petrogale rothschildi*) on at least two islands in Dampier Archipelago is smaller than on the adjacent mainland. The quokka on Rottnest Island is smaller than the nearest mainland population (Byford), and the four cranial features measured are less variable on the island (Shield 1967). Rottnest and Bald Island populations are also differentiated from mainland populations on other characteristics (Sharman 1954; Sinclair 1998). The tammar on Garden and West Wallabi islands is slightly heavier than the mainland (Tutanning) population studied (males 5.5, 5.0 versus 4.4 kg; Kelsall 1965). However, a study of the cranial characteristics of this species indicated that the island populations consist of smaller animals than on mainland south-west WA (Poole et al. 1991). The mala (rufous hare-wallaby; *Lagorchestes hirsutus*) on Bernier and Dorre islands is larger than on the mainland (Richards et al. 2001), although no comparison with populations of the adjacent mainland were possible because these are extinct there. The boodie (burrowing bettong; *Bettongia lesueur*) is slightly larger on Dorre Island than on Bernier Island, and both populations are larger than the population on Barrow Island (J Short & Turner 1999). All three insular populations are smaller than on the mainland. The smaller body size of the golden bandicoot on Barrow Island is not a genotypic response to selective pressures. When translocated to the mainland, their offspring increase in body mass and reproductive output. This suggests that the small size on the island is a phenotypic response to resource limitation (J Dunlop pers. comm.).

Several reptile species exhibit morphological differences between island and mainland populations. The gecko *Gehyra occidentalis* occurs on Kingfisher Island (Kimberley region) as a dwarf form (R Palmer et al. 2013b). The skink *Proablepharus reginae* is slightly smaller on Barrow Island than on the adjacent mainland (LA Smith 1976). The skink *Egernia napoleonis* on Daw (Christmas) Island, Archipelago of the Recherche, has been described as exceptionally large (LA Smith & Johnstone 1996). The bobtail (*Tiliqua rugosa*) on Rottnest Island has a snout–vent length c. 10% less than on the mainland, which seems contrary to the hypothesis (Schwaner & Sarre 1990) of supposed reduced availability of prey on islands being the cause (Shea 1989). On Barrow Island the spiny-tailed goanna (*Varanus acanthurus*) is smaller than on the mainland (Case & Schwaner 1993, LA Smith 1976). The mulga snake (*Pseudechis australis*) exhibits dwarfism on Barrow Island relative to the mainland (LA Smith 1976). The dugite (*Pseudonaja affinis*) on Rottnest, Boxer and Figure of Eight islands is smaller than on the mainland (Rottnest Island Management Planning Group 1985b; S Wilson & Swan 2013).

The perentie (*Varanus giganteus*) on Barrow Island appears larger than on the mainland (AA Burbidge pers. comm.). The tiger snake on Carnac Island exhibits larger size than on the mainland, with snout–vent length of 90 cm and 79 cm respectively, and body mass of 452 g and 243 g respectively (Aubret & Shine 2007). On Garden Island, the carpet python shows very marked sexual dimorphism in size, with females more than ten times heavier than, and twice as long as, on the mainland. Males and females respectively exhibit nanism and gigantism in comparison to the nearest mainland (Dryandra) population (Pearson et al. 2002a). Other WA island populations also show this characteristic, but not to the same extent. This has been attributed to differences in the size of available prey (Keogh et al. 2005; Pearson et al. 2002b).

The most striking distinction in colour between WA island and mainland populations of any species is that of the white-winged fairy-wren. On Dirk Hartog and Barrow islands the blue plumage of the mainland population is replaced by black (Carter 1917; Whitlock 1918). Black and white specimens have, however, been recorded occasionally on the mainland (Ashby 1929; Sedgwick 1967). Once thought to be island-endemic species, molecular studies have demonstrated that the insular populations are not each other's closest relative (Driskell et al. 2002). It could not, however, be established if the black plumage of the island populations arose from blue convergently or if black plumage arose once and was followed by re-evolution of blue plumage on the adjacent mainland.

Differences in coloration or dorsal skin patterning between Rottnest Island and mainland populations of the singing honeyeater and squelching froglet (*Crinia insignifera*) respectively have also been described (Lawson 1905; AR Main 1959, 1961b). The skink *Eremiascincus isolepis* on Barrow Island has a different colour pattern from that on the adjacent mainland (LA Smith 1976). The spiny-tailed skink (*Egernia stokesii*) on Houtman Abrolhos and Baudin Island (Shark Bay) differs in coloration and patterning of the dorsal surface from mainland populations (Pearson 2012). The bobtail on Rottnest Island is darker than on the mainland (B Bush et al. 2010). Garden and West Wallabi island populations of the tammar have a tawny coloration on the shoulders, forearms, flanks, hind legs to tail, and up on to the face, whereas in the mainland population studied (Tutanning) this was confined largely to the shoulders, forearms and hind legs (Kelsall 1965). According to Gould (1863), animals of the latter population are darker and have less rufous on the shoulders and rump. The golden bandicoot is more reddish on Barrow Island than on the mainland (Butler 1970), although this is disputed (AA Burbidge pers. comm.).

Invertebrates have received little attention. Males and females of the spider *Aganippe raphiduca* are smaller on Rottnest Island than on the mainland (BY Main 1957). There has been no investigation of brachyptery (shortening of wings) or aptery (atrophy of wings) of insects such as beetles on WA islands. Populations on islands far offshore should have evolved reduced dispersal capability (Darwin 1859; Wollaston 1864, 1877; Darlington 1943; Ås 1984). The usual explanation is that it is disadvantageous for an organism to emigrate from a remote island, but natural selection in favour of flightlessness is equally plausible.

## Changes in niches

Species on islands sometimes have broader niches than on the mainland. This is attributed to the decreased level of interspecific competition as a result of reduced species richness, particularly the absence of congeners (ecological release). However, the role of other plausible factors (such as vegetation type) is seldom considered adequately (for example, by JM Diamond 1970). Niche shifts are well documented for landbirds (Crowell 1961, 1968; Lack 1971, 1976; MacArthur et al. 1972; Vassallo & Rice 1982; Keast 1996) and mammals (Grant 1970). In Australia attention has been directed to measuring changes in foraging methods used by bird species in Tasmania, islands in Bass Strait, Kangaroo Island (South Australia) and Heron Island (Queensland) (Keast 1968, 1970; Abbott 1973, Schlotfeldt & Kleindorfer 2006; Scott et al. 2003). Comparable studies have not yet been undertaken on WA islands, probably because no conspicuous broadening of foraging niches is evident.

## Genetic changes

During the millennia during which species have been isolated on the continental islands of WA, populations should have experienced at least one major type of severe disturbance. This includes drought, wildfire caused by lightning strike, and tsunami or tropical cyclone. The consequence is a sudden reduction in population and a potential genetic bottleneck.

Genetic studies of populations of plant species on WA islands have been limited to *Parietaria debilis* (Urticaceae), *Acanthocarpus preissii* (Asparagaceae) and *Callitris preissii* (Cupressaceae). Genetic divergence between populations of *P. debilis* on Rottnest and Garden islands and one of the two coastal mainland sites studied was low. Island populations did not show reduced heterozygosity compared to the mainland sites (Coates & Hamley 1995). *Acanthocarpus preissii* populations on Garden Island showed no genetic differentiation from mainland populations (Bussell et al. 2006). The population of *C. preissii* on Rottnest Island is clearly distinct genetically from all other populations examined, whereas the population on Garden Island showed little differentiation (Bussell et al. 2006).

It is well established that island populations of animals exhibit reduced genetic diversity and increased levels of inbreeding (Frankham 1997, 1998). Mammal populations on 17 WA islands (Bigge, Capstan, Purrungku, Boongaree, Koolan, Dolphin, Barrow, Bernier, Dorre, North [Abrolhos], West Wallabi, East Wallabi, Whitlock, Boullanger, Rottnest, Garden and Bald) have been genetically assessed. All (northern quoll *Dasyurus hallucatus*, euro *Macropus robustus*, tammar *M. eugenii*, mala *Lagorchestes hirsutus*, banded hare-wallaby *Lagostrophus fasciatus*, black-footed rock-wallaby *Petrogale lateralis*, dibbler *Parantechinus apicalis*, quokka *Setonix brachyurus*) show increased fixation of alleles (Alacs et al. 2011; Eldridge et al. 1999, 2004; How et al. 2009; AJ MacDonald et al. 2013; Miller et al. 2011; HR Mills et al. 2004; BJ Richardson & Sharman 1976; Sinclair 2001; Spencer et al. 2013a; Spencer et al. 2013b), presumably as a result of genetic drift or bottleneck.

Genetic studies of other vertebrates have been limited. The skink *Ctenotus inornatus* has lower levels of genetic variation on islands distant from the mainland (Kimberley region) relative to inshore islands (Harradine et al. 2015). Heterozygosity of the singing honeyeater on Garden and Rottnest islands is lower than on the mainland (S McKenzie 1996).

The population of quokka on Rottnest Island, where no *Gastrolobium* species occur, has a lower tolerance to fluoroacetate than do populations on Bald Island and the mainland (Mead et al. 1985). This presumably reflects genetic change on Rottnest Island.

One of the consequences of reduced genetic diversity is high levels of inbreeding (Van Noordwijk & Scharloo 1981) and increased frequency of morphological abnormalities. Examples of the latter include kinked tails (47–60%) and unilateral testicular aplasia (3%) in tammars on islands in Houtman Abrolhos (Miller et al. 2011).

It seems likely that some invertebrate species on WA islands should exhibit colour polymorphisms (cf. Halkka et al. 1970, 1971; Järvinen & Ranta 1987), or variation in morphological traits (cf. Creed et al. 1964), but we know of no relevant research.

Molecular studies have revealed that endemism of land snails on islands of Kimberley region has not evolved in the past 10 ka, but existed well before the coastal mainland hills became isolated by rising sea level (MS Johnson et al. 2010; Köhler & Johnson 2012). High levels of phylo-endemism have also been discovered in island populations of the gecko *Heteronotia binoei* in Kimberley region (Moritz et al. 2016).

## CONCEPTUAL FRAMEWORK

The re-presentation here (Fig. 3) of the traditional framework of island ecology is informed and guided by Jenny's conceptual model of the processes that form the properties of soil (Jenny 1941, 1980). He invoked five factors (regional climate, organisms, topography, parent material, time) as a necessary and sufficient basis for fully understanding the properties of soils. Although these factors vary independently, they are interrelated and interdependent. Jenny's framework remains a useful perspective, and has been applied to plant ecology (Major 1951) and the Hawaiian Islands (Vitousek & Benning 1995). A monographic study of the vegetation of tropical islands in the Pacific Ocean adopted a similar scheme, with six factors involved: 1. geography/geology/geomorphology/soil substrate; 2. climate; 3. disturbance regime; 4. flora of the area/region/site; 5. access potential of plant species to reach the sites; and 6. the functional type or niche of the plant (Mueller-Dombois & Fosberg 1998).

An informal global comparison of islands, together with an understanding of the complexity and subtlety involved, indicates the need to consider explicitly at least 15 factors, five more than deemed by Van Balgooy (1969). He presented no detailed conceptual model, instead regarding island area, age, altitude, exploration and the richness of the source area as having a positive influence on island biodiversity. Isolation, latitude, adverse climate, poor soil and human influence were considered detrimental to island biodiversity. Plant lists compiled from 1500 localities on >200 islands south-west of Finland have been used to identify floristic gradients based on island area, bedrock, degree of human impact, maritime influence, insolation and presence of wetlands (von Numers & van der Maarel 1998).

The 15 factors recognised in our conceptual framework are listed below, but are not organised as a hierarchy. Examples, together with explanations based on first principles and linkages between the factors, are adduced for non-Australian islands, islands of Australia, and islands of WA, in that order. However, WA islands are emphasised. Our thesis is that all 15 factors should be explicitly assessed in studies of island ecology and evolution.

Eight of these 15 factors (degree of exposure to wave action and salt spray, substrate, topographic variation, maximum elevation, climate, distance from the nearest source area, time since separation or formation, and planar area) represent abiotic variables. Biotic factors include number and extent of vegetation and other habitat types; presence of humans (Aboriginals, Europeans or Asians); presence of seals, seabirds and turtles; and ecological interactions. Another factor refers to methodological issues with sampling. The remaining factor (*coups de foudre* or sudden unforeseen events) relates largely to abiotic events. This framework and causal model is intended to answer questions such as: Why are so many species that are present on the adjacent mainland absent from islands? Why are some species present and others absent? Why do some species and not others diverge morphologically from their mainland ancestors? What is the relative influence of habitat, food resources and competitor species on the morphology of island species? How dynamic are island biotas?

Both the Jenny framework and the expanded one outlined above relate to the important concepts of ß diversity, ecosystem diversity and landscape diversity. These all link with the inhibition of competitive exclusion and the occurrence of ecotones, edges and habitat mosaics (Vitousek & Benning 1995).

### Degree of exposure to wave action and salt spray

#### *Normal exposure*

As is well known, the height of waves is related to wind speed. During a gale blowing over an ocean, 75 km $h^{-1}$ winds can generate wave heights of 8 m. Direct wave action on small, low islands can thus remove soil and vegetation (Flood & Heatwole 1986). Along the Cornwall coast of Britain, vegetation on exposed cliffs does not usually begin until c. 6 m above high water mark (HWM). In contrast, on cliffs protected from the prevailing winds, vegetation commences just above HWM (Hepburn 1943). Small, low WA islands on an exposed coast experience the greatest impact of these factors, whereas similar islands leeward (sheltered) from the prevailing wind are less affected (Fig. 4). For example, the exposed (south-west facing) islets and bays of Rottnest Island are subject to maximum wave heights of 1.4–2.5 m, in contrast to the most sheltered (north-facing and east-facing) islets and bays, which receive maximum wave heights of only 0.1–0.4 m (Rottnest Island Management Planning Group 1985a). The importance of protection from direct wave action is also well illustrated by comparison of Vancouver Rock (5 m high) and Flat Rock (3 m), respectively outside and

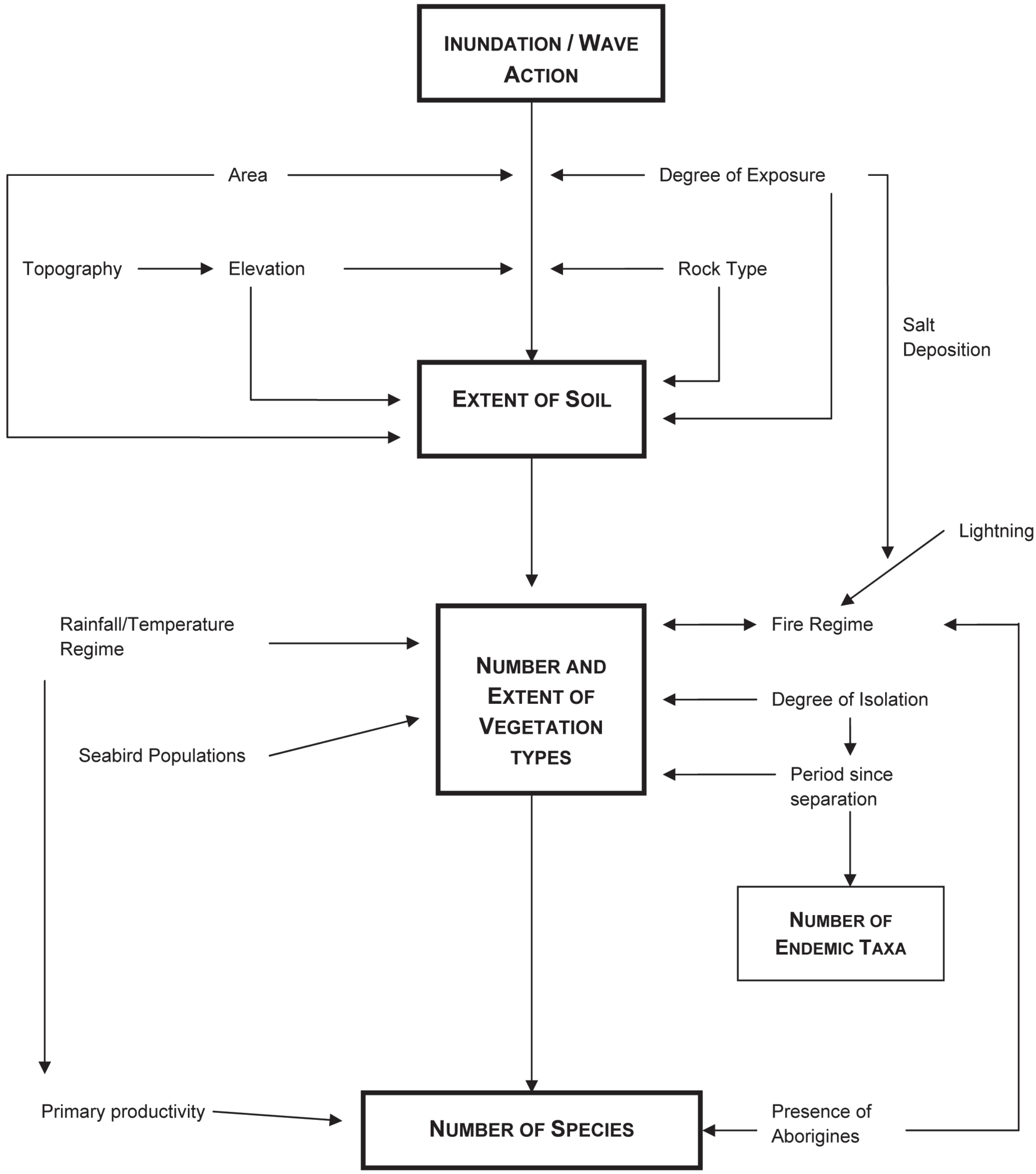



*Figure 3. Diagrammatic representation of the multifactorial conceptual model of island ecology proposed in this paper. See text for further explanation of the model.*

within King George Sound on the southern coast of WA. The former is exposed to swell, with waves washing continually over it, whereas the latter lies in calm waters in Frenchman Bay and supports a small patch of vegetation.

Small (c. 0.175 ha, 18 m elevation) sheltered islets in Barkley Sound (Vancouver Island, British Columbia) have taller vegetation than exposed islets, whereas larger exposed islands (c. 1.5 ha, 11 m elevation) are treeless and have only low vegetation (Cody 2006).

Studies of species richness on islands seldom assess exposure to, or protection by nearby islands from, waves and wind as relevant factors. These studies have produced inconsistent results. For example, exposure explained little of the variation in the size of the floras of small islands in the Bahamas (Morrison 2002a).

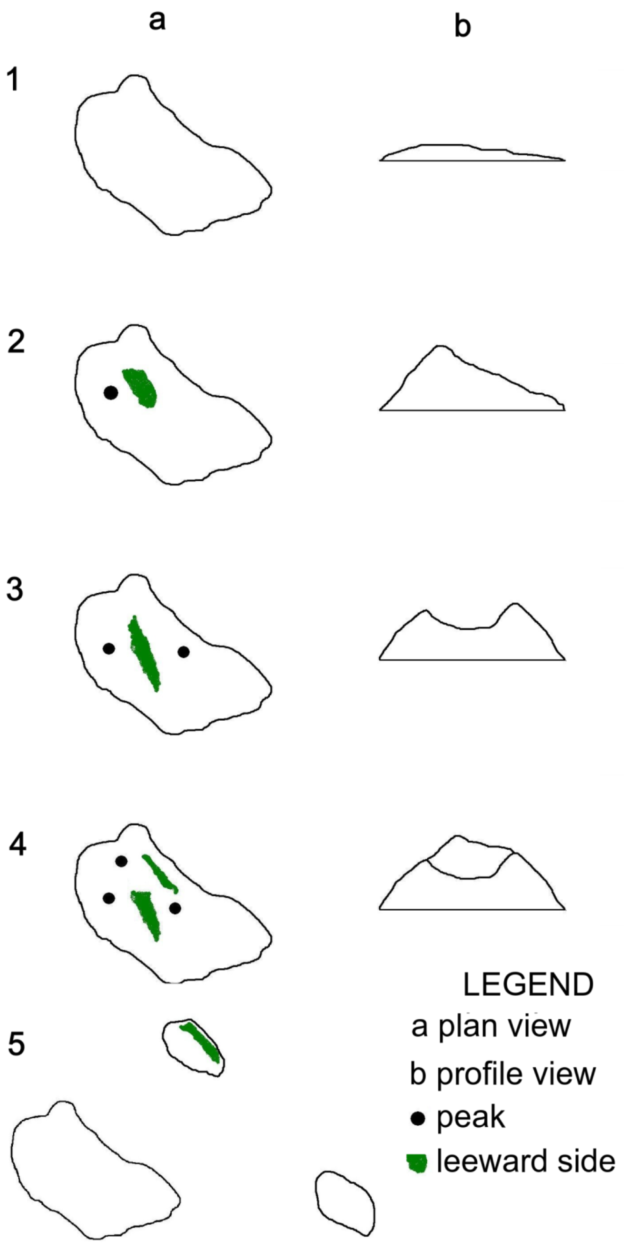



*Figure 4. Contrasts in island topographic relief, with island area held constant. Panels 1–4: a, plan view; b, profile view; ● = presence of a peak, shaded area = leeward side. Panel 5 shows the protective value of an island lying upwind. Direction of swell and prevailing wind is from the lower left of each panel.*

Configuration of the island and the accretion of sand (which increases elevation) together provide protection enabling the successful establishment of mangroves on cays near Jamaica (Asprey & Robbins 1953). A study of small islands (<0.0605 ha) in Barkley Sound (Canada) showed that the extinction rate of plant species increased with exposure of islands to the prevailing swell (Burns & Neufeld 2009).

Large waves, locally known as king waves, can suddenly appear, as was recorded at Albany on 1.4.1880 (The West Australian 13 April 1880: 3) and in 1964 and 1973 (Underwood 2013). Their impact on small islands remains undocumented.

Larger surface area contributes to reducing the influence of wave action, thereby increasing the retention of soil (habitat for plant species), the development of more plant biomass (vegetation, habitat for animal species), including the occurrence of trees (*Melaleuca, Eucalyptus, Allocasuarina*) and other non-halophyte plant communities (Davis et al. 1938; Fatchen 1982; T Robinson et al. 1996). The 14 insular occurrences of five *Eucalyptus* species in South Australia are restricted to larger islands (>81 ha), except for three small elevated islands (4–40 ha, 10–15 m) that are protected from sea spray (T Robinson et al. 1996).

As noted by BW Wells (1939), salt spray is a direct factor that depends on an indirect climatic factor (wind) for its effectiveness. Windborne salt spray results in the deposition of large quantities of chloride ions, making it either impossible for many plant species to persist (Boyce 1954; Okusanya 1979a, 1979b ) or resulting in zonation of vegetation (BW Wells & Shunk 1938; Hepburn 1943; Goodman & Gillham 1954; Parsons 1981). The quantity of sodium deposited is linked to the frequency of gale-force winds (Malloch 1972). Chloride deposition decreases rapidly with distance from the coast and is negligible at a distance of c. 500 m inland (Malloch 1972; Holton & Johnson 1979). This implies that an island without any topographic variation (i.e flat-topped) would need to be at least 0.75 $km^2$ in area to allow salt-intolerant plant species to persist. However, data provided by Lubke & Avis (1982) indicate that most chloride is deposited within 100 m of the coast, implying that salt-intolerant plant species are unlikely to persist on islands with areas <c. 3 ha. Apart from the overwhelming factor of salt deposition, particular combinations of wind strength, temperature and precipitation (even though infrequent and of short duration), may have lasting effects on future plant growth (Goodman & Gillham 1954).

Western Australian data reveal that up to 260 kg $ha^{-1}$ of sea salt are deposited in coastal areas (Hingston & Gailitis 1976). Most is deposited along the south-western coast, between Perth and Albany, with the greatest quantities (c. 100 kg of chloride $ha^{-1}$) precipitated within 5 km of the coastline. This suggests a more pervasive influence in south-west WA than in the countries cited in the preceding paragraph. The low chloride content of rainfall in the Kimberley region is attributed to tropical thunderstorms diluting the chloride washed from the atmosphere, as well as to other factors (Hingston & Gailitis 1976).

Maps of contours of soil salinity on two islands in the Sir Joseph Banks Group (South Australia) reveal the existence of steep gradients (T Robinson et al. 1996). Studies on these and other islands show promise in explaining local differences in the species composition and abundance of plants. In Britain, maritime (sea cliff) plant species are more prevalent where salinity is greatest (Malloch 1971; Malloch et al. 1985).

Many islands of New South Wales (NSW) are small, have shallow soils, and support only low-growing vegetation. Trees are generally absent and vegetation on the exposed side commences higher above the tideline than does vegetation on the protected side (AK Morris 1974). The various islands in the Solitary Group, NSW (SG Lane 1974a, 1974b, 1975a, 1975b; AK Morris 1975a, 1975b) and the Five Islands Group, NSW (Battam 1976a, 1976b, 1976c; JD Gibson 1976) are particularly instructive in showing the subtle interplay of area, maximum elevation, exposure and topographic variation in determining the vegetation type present. Similarly, islands near Wilson's Promontory (Victoria) show differences in the species richness of plants in terms of degree of exposure to spray-bearing winds (Gillham 1961c).

Data obtained for four groups of islands in WA show the connexion between small area and low elevation in jointly determining the presence or absence of vegetation (Fig. 5). Along a coast with waves of high energy, even relatively large and high islands (1 ha) are devoid of vegetation (Fig. 5c, 5d), whereas the presence of reefs and intertidal platforms dissipates wave energy, reduces the impact of waves, and is conducive to the development of vegetation on islands (thresholds of c. 0.01 ha and c. 5 m high, Fig. 5a, 5b). This is also linked to geological features. Granitic islands often have the shape of a dome and waves are able to run a great distance up the sides, in contrast to aeolianite islands that are always situated on a reef.

Much of the literature about island ecology attributes lower species richness on islands far from the source area to a distance effect. However, with plant species, distance may be confounded with exposure to sea spray. For example, islet #38 (0.014 ha, 4 m high) lies 4 m from Rottnest Island but is sheltered from salt spray and wave action (Abbott & Black 1980). It supports 13 native plant species, some of which are not

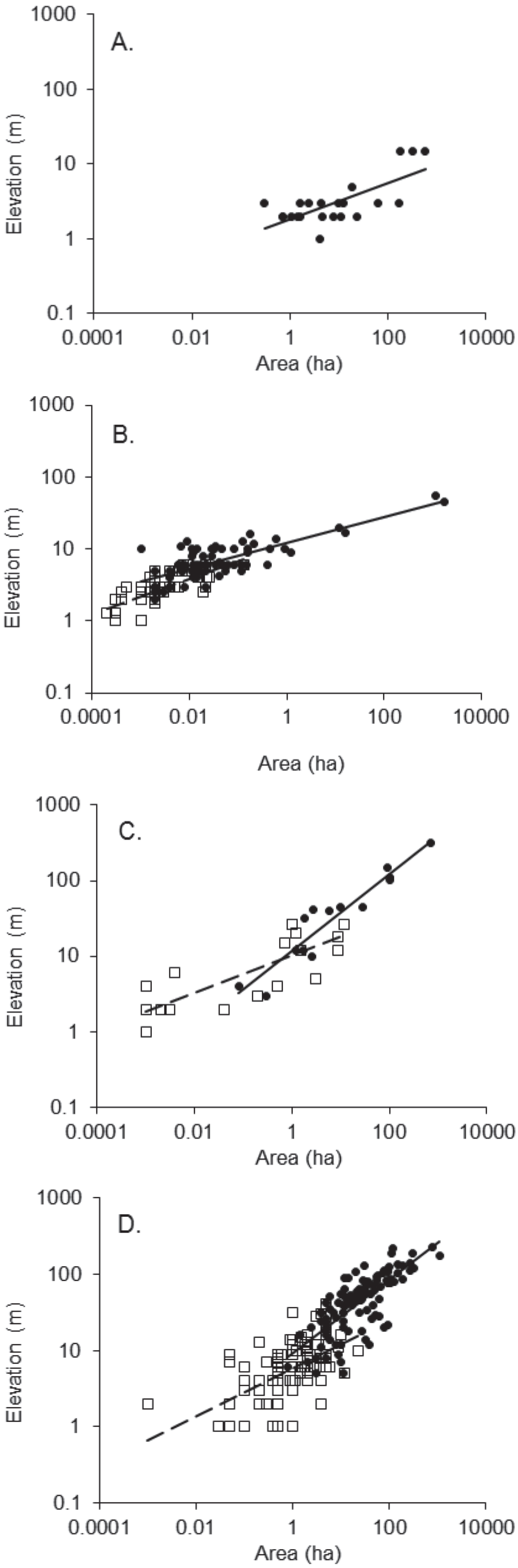



*Figure 5. Joint influence of area and maximum elevation in determining whether islands are vegetated or not ('bare' means that no plant species are present). A. Houtman Abrolhos vegetated islands (●, solid line); B. Fremantle vegetated islands (●, solid line) and bare islands (□, dashed line); C. Albany vegetated islands (●, solid line) and bare islands (□, dashed line); and D. Archipelago of the Recherche vegetated islands (●, solid line) and bare islands (□, dashed line). Data are from: Houtman Abrolhos islands, JM Harvey et al. (2001); Fremantle islands, Abbott and Black (1980); Albany islands, Abbott 1980e; and Archipelago of the Recherche, I Abbott, unpubl. data. Abrolhos vegetated islands: $log_{10}$ Elevation = 0.24($Log_{10}$ Area) + 0.27, $R^2$ = 0.52, n = 22, $p < 0.001$. Fremantle bare islands: $log_{10}$ Elevation = 0.24($Log_{10}$ Area) + 1.07, $R^2$ = 0.51, n = 54, $p < 0.0001$. Fremantle vegetated islands: $log_{10}$ Elevation = 0.18($Log_{10}$ Area) + 1.09, $R^2$ = 0.61, n = 70, $p < 0.0001$. Albany bare islands: $log_{10}$ Elevation = 0.25($Log_{10}$ Area) + 1.02, $R^2$ = 0.63, n = 18, $p < 0.0001$. Albany vegetated islands: $log_{10}$ Elevation = 0.51($Log_{10}$ Area) + 1.07, $R^2$ = 0.89, n = 14, $p < 0.0001$. Recherche bare islands: $log_{10}$ Elevation = 0.31($Log_{10}$ Area) + 0.77, $R^2$ = 0.29, n = 95, $p < 0.0001$. Recherche islands vegetated: $log_{10}$ Elevation = 0.48($Log_{10}$ Area) + 0.96, $R^2$ = 0.55, n = 107, $p < 0.0001$.*

found on other small islands. The most comparably-sized island is East Celia Rock (0.012 ha, 4 m high), also 4 m from Rottnest Island but exposed to wave action and spray. It has only three species present, all of which are tolerant of sea spray. A second example is equally illustrative. West Cathedral Rock (0.13 ha, 6 m high) and East Cathedral Rock (0.15 ha, 6 m high) differ mainly in distance from Rottnest Island, 133 m and 67 m respectively. The former has no plant species present, presumably because wave action has removed soil, and the latter has four plant species present (Abbott & Black 1980).

On Barrow Island, *Triodia wiseana*, the dominant plant species on inland limestone, is replaced by *T. angusta* or *T. pungens* on limestone headlands and small adjacent islands. This is probably in response to differential exposure to salt-laden winds (Buckley 1983).

Asymmetric growth of plants has been linked to chloride toxicity (Doutt 1941; Parsons & Gill 1968). Even on mainland coasts and relatively large islands with subdued topography, sites fully exposed to the prevailing winds result in trees being bent over (Backhouse & Pegg 1984). The mean compass bearing of such deformed trees planted on Rottnest Island is 001° and 017° for *Melaleuca lanceolata* (N = 11 and 15 respectively) and 018.5° (N = 13) for *Eucalyptus gomphocephala* (I. Abbott pers. obs.). The impact of exposure on *Acacia rostellifera* and *Melaleuca lanceolata* on Rottnest Island is described by Hesp et al. (1983). Strong winds also result in desiccation of soils (Hepburn 1943). Wind-pruned growth has also been described for *Alectryon oleifolius* and *Capparis spinosa* on Dorre Island (Royce 1962).

Photographs very clearly demonstrate that constant winds cause the planation of shrubs of *Astartea fascicularis* on Middle Island and of an unidentified species on Mondrain Island, Archipelago of the Recherche (JH Willis 1953: 12; Chester & McGregor 1997: 249). Mangal (mangrove low closed-forests) on Kimberley islands is confined to sheltered bays (AA Burbidge et al. 1978; Aklif 1999).

There is increasing evidence that shortage of sodium (in salt) reduces biomass and decreases plant decomposition (Kaspari et al. 2008). Sodium is unlikely to be limiting on small islands, but sheltered parts of large islands may experience reduced occurrence of sodium in soil.

## Extreme exposure and tidal surge

Tropical cyclones (low pressure systems with wind speeds >118 km $h^{-1}$) can generate wave heights >13 m and tidal surge. Small islands (0.02–0.34 ha) on reefs near Belize experienced local extinction of plant species after the passage of a hurricane, but the flora recovered within 10 years. Islands <0.1 ha have no plant species present probably because the combination of small area and low elevation cannot counteract normal wave action (Stoddart & Fosberg 1982). In the Bahamas, the degree of exposure of small islands to wind, wave action, and hurricanes jointly determines the presence/absence of vegetation. Large area tends to compensate for high exposure, whereas smaller islands sheltered by surrounding islets are vegetated (Morrison 2011).

On islands that have forest and woodland and are large and/or sheltered, tropical cyclones exert significant impacts (Lugo 2008). They increase vegetation heterogeneity and variability of ecosystem processes, rejuvenate the landscape and its ecosystems, and redirect succession. The numerous wooded islands in the Kimberley region of WA remain unstudied from this perspective.

In 1839, Dorre Island experienced a cyclone that caused a 17 m run-up, the height reached above sea level (Grey 1841). Evidence of a presumed cyclone was also noticed in 1840 on Barrow Island ('recent marks of the sea many feet above the ordinary reach of the tides', Stokes 1846 Vol. 2: 209). In 1976 a cyclone-generated wave 9 m high swept over Tuin Island (NEW Taylor 1987). Cyclone Vance in March 1999 generated winds of 267 km $h^{-1}$ resulting in a 3.6 m high surge at Exmouth. Waves pushed large boats over jetties that were 2 m high (Nott 2004). At North West Cape a run-up of c. 5 m above high tide level was recorded (Nott & Bryant 2003). Strong winds should also uproot vegetation and thus accelerate soil erosion. Low barometric pressure (<1000 kPa) raises sea level and, coupled with strong winds, can cause storm surges. Impact can be catastrophic if such surges coincide with high tide on a macrotidal coast. The islands of the Pilbara and Kimberley coasts are thus particularly vulnerable to the impact of tropical cyclones, with more than 120 detected during the period 1909–1980 (Lourensz 1981). Cyclone-force winds have been reported as scorching or stripping foliage, killing trees, uprooting vegetation and causing surges of seawater well above HWM on islands in Shark Bay (Grey 1841; Graham-Taylor 2012a). In 1998, Koojarra Island was washed away by a cyclone and is now merely a shoal (I Murray & Hercock 2008:162). One wonders how many propagules were transported by a cyclone to Dorre Island in 1839, along with the 'great forest trees' that were presumably washed across Shark Bay from the opposite mainland (Grey 1841 Vol. 1: 345). Tropical cyclones can also affect south-west WA, with 28 severe gales with gusts >120 $kmh^{-1}$ in recorded history (Hanstrum 1992). A gale in April 1843 created a tidal surge of 4 ft.

Woinarski et al. (1999a) have suggested that islands of elevation <10 m have probably been scoured of mammals during occasional inundations by tidal surges associated with cyclones and tsunamis. This might explain the general absence of mammals from many low islands adjacent to the Pilbara and Kimberley coasts.

Other taxa may be more resilient. In the Bahamas, cyclones reduced phytomass but did not result in any local extinction of plant species on small islands (Morrison 2003). Nor did ant species become locally extinct on these islands (Morrison 2002b).

Situated south-east of the Sunda Arc, the north-western coastline of WA is fully exposed to the impact generated by distant earthquakes and volcanic eruptions. No tsunami has impacted significantly on WA in historic (1863 onwards) times (Goff & Chagué-Goff 2014). The 1883 eruption of Krakatau caused a modest sea-level rise of 1–2 m (Victorian Express 29 August 1883; The West Australian 31 August 1883: 3, 18 September 1883: 3; Symons 1888), with coral boulders deposited 1 km inland (Bryant 2001). The tsunami of 26 December 2004 caused a sea-level change of only 0.35 m near Perth (Spencer 2007). However, in 1977 a 6 m wave was recorded at Cape Leveque, and on 3 June 1994, 2–4 m waves from an earthquake near Java were recorded at Exmouth and Onslow, and these penetrated 300 m inland. On 17 July 2006 an earthquake on Java resulted in a run-up of 9 m when a tsunami reached Steep Point (D Burbidge et al. 2008).

The presence of large boulders displaced from the coastline of Dirk Hartog, Dorre, Bernier, Koks, Barrow, Legendre, Dolphin and Lamarck islands has been interpreted as evidence of the occurrence of mega tsunamis within the past 5 ka (Playford 2014; Playford et al. 2013; Scheffers et al. 2008). Displaced boulders have also been observed on Darcy Island (K-H Wyrwoll pers. comm.). A tsunami is thought to have completely washed over Legendre Island (maximum elevation 17 m) c. 2.9 ka BP (Playford et al. 2013). In some places between Cape Leveque and North West Cape, headlands 20–60 m above sea level were overridden (Bryant 2001), and some tsunamis may have penetrated 30 km inland from the coast (Bryant & Nott 2001; Nott & Bryant 2003). At North West Cape, molluscan growth on boulders has been radiocarbon-dated to represent three separate events in the past 1700 years (Nott 2004).

A tsunami c. 1 ka BP deposited shells on the top of hills 15 m above sea level at Point Samson (Bryant 2001). Mega tsunamis would have completely washed over small, low (2–19 m) islands such as Adele, Browse, Lacepede, Delambre, North Sandy, Great Sandy (Beagle), Airlie, Thevenard, Bessieres (Anchor), Serrurier (Long) and Muiron islands, and would have removed plants and animals. This implies that the species that occur at present on these islands have colonised from the mainland within the past several thousand years; moreover, cays are unlikely to be more than c. 5 ka old.

Since the 1940s, cumulative evidence indicates that rising sea-levels in south-west WA following the end of the last glacial period overshot the present level by c. 2 m at c. 6 ka BP (Teichert 1947; Churchill 1960; Wyrwoll et al. 1995). This level lasted for c. 1 ka. In Shark Bay and Exmouth Gulfs, a lower peak of c. 1 m occurred at c. 4.5 ka BP (Brown 1983). Presumably this event significantly affected the soils, vegetation and biota of small, low islands. In Houtman Abrolhos, sea level reached a height of 0.5 m by 6.4 ka BP and remained at a height of c. +1 m until at least 4 ka BP (Collins et al. 1997).

Disturbance caused by elevated run-off that has resulted from the passage of tropical cyclones is not necessarily inimical to island biodiversity. Rafts of vegetation washed down coastal rivers may carry reptiles and other animals and could conceivably enable colonisation of some islands (R Palmer et al. 2013b). In June 1978, a large branch of a eucalypt c. 5 m in length was found lying above HWM on the western side of North Sandy Island (I Abbott pers. obs.).

Global warming is expected to raise sea-levels, which should expose small low islands to increased impact of wave action, resulting in changes in vegetation and habitat on these islands.

## Substrate

Soil properties influence the type of plant species present (and thus the habitat of animal species, e.g. Welter-Schultes & Williams 1999). A crude index is the number of soil types, a factor that is correlated with the diversity of vegetation structure on islands of the Seychelles (Mühlenberg et al. 1977), the number of plant species on islands of Britain (MP Johnson & Raven 1970, MP Johnson & Simberloff 1974) and north-eastern USA (McMaster 2005), and the number of mammal species on islands of Virginia (Dueser & Brown 1980) and Massachusetts (Adler & Wilson 1985).

Sedimentary and igneous rocks on the same island do not support the same plant species. Soils on granite and calcareous dunes are more fertile than siliceous sands (Byrnes et al. 1977). Soils derived from granite rocks are less fertile than soils derived from volcanic rocks, and support different plant species and vegetation types. On the islands in Bass Strait (Tasmania), soils on granite support different plant species from those on aeolianite (e.g. *Leucopogon parviflorus* versus *Threlkeldia diffusa* and *Acrotriche cordata*; S Harris et al. 2001). This is also the case in the Archipelago of the Recherche and other islands in WA, with *Astartea fascicularis, Dodonaea viscosa, Eutaxia myrtifolia, Hakea clavata, Kunzea sericea, Leucopogon obovatus* and *Pimelea ferruginea* growing in soils on granite, and *Acacia cyclops, Acrotriche cordata, Alyxia buxifolia, Boronia alata* and *Leucopogon parviflorus* growing on soils on aeolianite (JH Willis 1953). This is particularly evident in the Archipelago of the Recherche because some islands have both granite and aeolianite substrates (e.g. Boxer, Long, Middle, Goose, Salisbury, Daw), and others have only granite rocks (e.g. Figure of Eight, Woody, Sandy Hook, Thomas, Remark, MacKenzie [Round], Mondrain, Termination, North Twin Peak, South Twin Peak, Westall [Combe]) (Abbott & Black 1978; AA Burbidge et al. 1982; Fairbridge & Serventy 1954; Hopkins & Harvey 1989).

Islands with active volcanoes are also likely to have extensive areas of unvegetated lava flows. Even within the same archipelago, islands often differ in the amount of exposed rock that provides no suitable substrate for the growth of vegetation and hence no habitat for birds. For example, in the Archipelago of the Recherche, Ram, Remark, Frederick and Gunton islands have much bare rock whereas Sandy Hook, Long, Woody, Black, Observatory, Middle and Salisbury islands have little exposed rock. Similarly, Breaksea and Chatham islands have large areas of granite that are exposed as bare rock, the occurrence of which is not related to wave action (I Abbott pers. obs.).

If a fire were to ignite following a lightning strike, islands with large expanses of rock (such as granitic islands) would seem to provide a system of internal barriers to the spread of fire. Because the islands along the southern coast of WA were not visited by Aborigines, levels of combustible matter should have built up over decades. The presence of rock expanses should have provided refuges for invertebrates and other organisms from the spread of fire.

Along parts of the Queensland coast, islands of igneous rock are more densely forested than are those formed of metamorphic and sedimentary rocks (Steers 1929; Byrnes et al. 1977). In Torres Strait, the habitat on islands reflects their geology: Granitic islands have open woodland dominated by *Eucalyptus* and *Melaleuca*; cays have scrub dominated by *Casuarina*; volcanic islands have rainforest; and sedimentary islands predominately have mangroves (Draffan et al. 1983).

Islands in the Kimberley region consist of sandstone, volcanic and dolerite rocks, with laterites present on some islands (AA Burbidge et al. 1978; LA Gibson & McKenzie 2012a). On some islands exposures of rock are prevalent and vegetation there is sparse. Vine thickets (rainforest patches) are associated with basaltic rocks (Coate 2008a; Lyons et al. 2014; LA Smith et al. 1978). Thus, for example, Borda Island is composed of sandstone whereas Fenelon is doleritic with a lateritic plateau (Beard et al. 1984; AA Burbidge et al. 1978). Rainforest habitat on Borda Island is of limited extent in contrast to Fenelon Island. The occurrence of the mangrove golden whistler (*Pacycephala melanura*) only on Fenelon (LA Smith et al. 1978) may be linked to this. Sandy cays and other low islands offshore of the Kimberley coast are discussed by Teichert and Fairbridge (1948). Much of Depuch Island (Pilbara region) is unvegetated bare dolerite rock (Ride 1964a; Royce 1964).

Soil pH is largely influenced by rock type. Granite islands such as Eclipse and Chatham islands have acid soils (pH 3–6) in contrast to aeolianite islands (Carnac, Middle Shag, Seal, Garden, Rottnest), which have neutral to alkaline soils (pH 7–8) (I Abbott unpubl. data, Bancroft et al. 2005a, Hesp et al. 1983). However, the presence of breeding seabirds can override and obscure edaphic factors.

On the coral cay Lady Musgrave Island (Great Barrier Reef), soil depth is a prime determinant of the reduced composition of plants (Elsol 1985). The depth of sand is considered to have been decreased by exposure to spray-bearing winds, thereby reducing the size of the flora of Citadel Island, an 18 ha island near Wilson's Promontory, Victoria (Gillham 1961c; Norman & Brown 1979).

Sometimes the importance of substrate type is not apparent until conventional explanation of variation in species richness of plants in terms of island area and isolation fails (Buckley 1981). Analysis of 29 islands revealed considerable heterogeneity in terrain, resulting in the recognition of 11 types (Buckley 1981). Type of substrate does not, however, always affect the species richness of plants. Buckley (1985) classified an archipelago of small islands according to whether they were composed of silt, shell or a mixture of both. Island area was more influential than type of substrate. Similarly, for cays in the southern Great Barrier Reef, type of substrate had little influence on the species richness of plants (Heatwole 1984).

## Topographic variation

One of the earliest accounts, if not the earliest account, of this factor comes from the 1770s, with recognition of change in vegetation with elevation on Tahiti (Forster 1778: 163). On Gough Island, vegetation is related to rock type, which gives rise to differing topographies on weathering (Wace 1961).

The degree of slope increases the surface area of an island, with slopes of 35–40° increasing the surface area by 20% and slopes of 45° increasing surface area by 40% (Lazell 2005). Depending on maximum elevation, this may expand the extent of habitable space on an island.

Dissected topography results in the occurrence of a series of hills and valleys. This allows the differentiation of habitat, so that habitats are more diverse structurally and floristically than on islands that consist of only one hill or no hills (Heatwole 1991). This follows from the contrast between the leeward and windward side of hills (Fig. 4). Vegetation is taller on the leeward side, e.g. Little Broughton Island, NSW (SG Lane 1976b), Cabbage Tree Island, NSW (Priddel & Carlile 2004), Lion Island (SG Lane 1974c), Bowen Island, NSW (SG Lane 1976c), Brush Island, NSW (Carlile et al. 2012), Kangaroo Island, South Australia (Kirkpatrick 1972), in addition to zonation in vegetation types with distance from the shoreline (Kirkpatrick 1972). Chloride toxicity from airborne salt spray causes differences in vegetation height, asymmetrical canopies of trees, and zonation of plant species (Boyce 1954). On Lizard Island (Queensland), closed forest and low closed forest are restricted to gullies that receive run-off and seepage from hills. *Eucalyptus* woodland is found mostly on the sheltered side of the island (Byrnes et al. 1977). Only the steeper hills and riparian zones on granite islands in Torres Strait support rainforest (Draffan et al. 1983).

Topographic variation in New Zealand was regarded by Solem (1990) as promoting the high diversity of land snails there. This was attributed to gullies sheltering snails from desiccating winds. On islands off California, topographic diversity (measured as the number of arroyos per length of coast) strongly correlated with island area and elevation, but only weakly with number of species of birds and plants (Power 1976). A comparative study of the Collembola of 10 Australian islands (continental and oceanic) indicated that the complex topography of Lord Howe Island accounted for the highest species richness (as well as endemic species), rather than area or maximum elevation (Greenslade 2008a).

In the Archipelago of the Recherche, sheltered gullies on Boxer and Remark islands support trees (JH Willis 1953). On Ram Island (142 ha, 133 m maximum elevation), vegetation 2 m tall occurs on shallow rocky soils, whereas in gullies and depressions (presumably sheltered from wind) vegetation attains a height of 7 m (SG Lane 1982c). Similarly, in small gullies on nearby Remark Island vegetation dominated by *Eucalyptus* and *Melaleuca* reaches 9 m in height (SG Lane 1982b).

On WA's second largest island (Barrow, 23,000 ha), the two major vegetation types are controlled by topography and related soil type, with *Triodia wiseana* on shallow soils on uplands and *T. angusta* on deep soils in watercourses and lowlands (Buckley 1983). *Triodia pungens* occurs on sand near the coast and southern end.

Islands in the Kimberley region often support patches of rainforest at the foot of cliffs and in drainage lines (Coate 2008a; LA Gibson & McKenzie 2012a). Topographic variation and associated retention of moisture in soil may also provide protection from the spread of fire across an entire island and may explain the persistence of rainforest on some islands and not others (Lyons et al. 2014).

The distribution of some species appears to be associated with topographic position. On Penguin Island in Shoalwater Bay, six plant species (*Conostylis candicans, Clematis linearifolia, Cassytha racemosa, Exocarpos sparteus, Myoporum insulare, and Helichrysum cordatum*) are found only in the most sheltered part of the island (Hussey 1973).

## Maximum elevation

The role of this factor was recognised in the 1770s, with low islands in the Pacific Ocean observed to support fewer plant species than did high islands (Forster 1778). In the Galápagos Archipelago, island elevation explained almost half of the variation in plant species richness (Hamilton et al. 1963). For islands east of New Guinea and north-east of Australia, species richness of mammals increases with island elevation, although other factors have stronger correlations (Carvajal & Adler 2005). In the Philippines, maximum elevation of islands explains c. 40% of variance in the number of resident bird species, compared with c. 30% for island area (Peterson et al. 2000).

Elevation is usually correlated with island (planar) area (MP Johnson et al. 1968; MP Johnson & Raven 1970, 1973; MP Johnson & Simberloff 1974; Amerson 1975; Power 1976; Dueser & Brown 1980; Reed 1981, 1984; Heaney 1984; Deshaye & Morisset 1988; Woinarski et al. 1999b; Torres & Snelling 1997; Dennis et al. 2000a; Fernández-Palacios & Andersson 2000; Fattorini 2002; McMaster 2005). However, exceptions do occur, exemplified in Britain and WA by the combinations of large, low islands (Hascosay, Barrow) and of small, high islands (Ailsa Crag, Remark).

MacArthur and Wilson (1967) suggested that on large islands topography becomes more complex, resulting in greater heterogeneity of habitats, each of which can support somewhat dissimilar assemblages of species. Islands with high hills have also a greater surface area than do islands of low relief, resulting in more habitat space being available for occupation by individuals and species (Fig. 5). Elevation, which is easily measured from maps, is often assumed to be a proxy for habitat diversity (Crowell 1986; Losos 1986; Ricklefs & Lovette 1999; Welter-Schultes & Williams 1999). In NSW, higher islands do have more vegetation types present, e.g. Lion and Brush islands (AK Morris 1974; SG Lane 1975c). Higher islands also tend to have

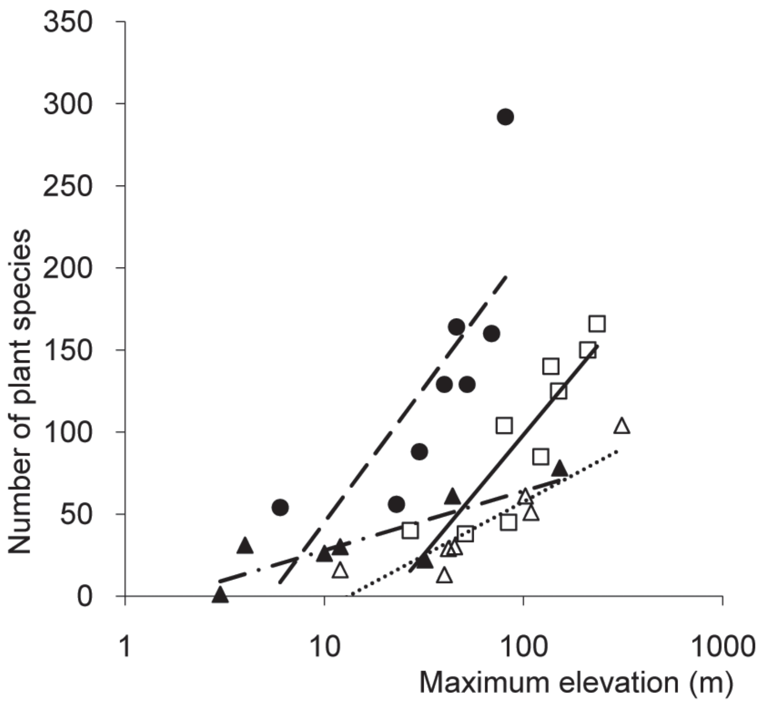



*Figure 6. Joint influence of exposure and maximum elevation on plant species richness for islands, peninsulas and promontories in Albany region (data from Abbott 1980e): exposed mainland sites (□, solid line); sheltered mainland sites (●, dashed line); exposed islands (△, dotted line); and sheltered islands (▲, dot-dash line). Mainland exposed: no. species = 145.82(Log$_{10}$ Elevation) – 193.34, $R^2 = 0.77$, $n = 9$, $p < 0.002$. Mainland sheltered: no. Species = 164.11(Log$_{10}$ Elevation) – 119.24, $R^2 = 0.58$, $n = 8$, $p < 0.03$. Island exposed: no. Species = 65.34(Log$_{10}$ Elevation) – 73.21, $R^2 = 0.83$, $n = 7$, $p < 0.005$. Island sheltered: no. Species = 36.16(Log$_{10}$ Elevation) – 8.29, $R^2 = 0.72$, $n = 7$, $p < 0.02$.*

more plant species than do low islands, unless the latter are sheltered from wave action and gales (Gillham 1961c; Fig. 6; Table 9, Table 10). A similar difference in elevation between forested versus grassy islands in Finland also explains the greater number of plant species on wooded islands with area c. >30 ha (Haila et al. 1982).

There are, however, exceptions. In the West Indies there is little correlation between island area and maximum elevation (Ricklefs & Lovette 1999). On islands in the Pacific Ocean, elevation has a spectacular influence on species richness of land snails. Irrespective of island area, high islands (with elevations >300 m) have 2–3 times as many species as low (<300 m) islands (Solem 1983, 1990). In the Galápagos there is a very strong correlation between island elevation and the number of plant species occurring in wet habitats. This is a function of exposure to tradewinds (van der Werff 1983).

Determining the threshold elevation above which habitat complexity increases varies with several factors, including area, exposure, and extent and depth of soil. Thus, in Victoria, Citadel Island (18 ha, 109 m tall) and Wattle Island (22 ha, 82 m) both possess scrub 2–3 m tall but only on the highest part, whereas nearby Dannevig Island (20 ha, 77 m) has restricted development of soil and lacks scrub (Gillham 1961c; Norman & Brown 1979; Norman et al. 1980a). The critical importance of maximum elevation for low islands is well illustrated by Coral Sea islands (Telford 1993b). Only 22 of the 46 cays support land plants (as herbfield), probably as a result of storm surges from frequent tropical cyclones. Open shrubland has developed only on those islands >3 m above sea level. Cays with elevation >3 m (to 5 m) may support closed shrubland or low forest (to 10 m tall). Heatwole (1991) had previously demonstrated the critical importance of island height instead of area for cays on the Great Barrier Reef, Queensland.

On Gough Island (southern Atlantic Ocean), plant communities are mainly influenced by the joint action of elevation above sea level and degree of exposure to the prevailing wind (Wace 1961). For the 61 small islands off Cape York Peninsula (Queensland) that were studied by Buckley (1985), plant species richness is better predicted by island elevation than by area, substrate or isolation. This was attributed to the effect of elevation on the soil-salinity profile. The reduced number of plant species on the Bromby Islands near Arnhem Land (Northern Territory) may be linked to their low elevation relative to other island groups in the same region (Woinarski et al. 2000).

Low islands may be prone to inundation by cyclones and high spring tides. This caused seabirds to abandon nests on Adele Island (Coate 1997). Cyclonic winds on Flag Island (Montebello Group) destroyed a colony of the crested tern (*Sterna bergii*; AA Burbidge et al. 2000). According to Veth et al. (2007), the limit of impact of a cyclone on land is c. 11 m above low tide.

## Climate

Climate has long been acknowledged as an influential factor. During the 1770s, differences between vegetation structure and floristics were described by Forster (1778) for tropical islands (particularly Tahiti) and islands occurring in high latitudes (Tierra del Fuego, South Georgia).

Climatic variables such as solar radiation or evaporative demand should influence species richness (the species/energy theory: DH Wright 1983; Wylie & Currie 1993) through the mechanism of high-energy areas supporting more individuals, thus enabling more species to occur (Evans et al. 2005). Glaciation is thought to have caused the local extinction of many species on islands in the northern Atlantic Ocean (Coope 1986). Climate as a relevant factor is usually silently excluded from most studies, as these examine islands only in the same climatic type. A notable exception is an investigation of plant species richness of 57 islands/archipelagoes (Hobohm 2000). It is clear from the species/area regression that islands with a low 'warmth index' (Campbell, Faroe, Iceland, Greenland, Svalbard) have fewer species than expected based on their area.

Climate is obviously an important factor, because islands without regimes of extreme rainfall and temperature support more species than islands that receive little rain or are very cold (Abbott 1974b). For example, Iceland (100,000 km$^2$) has fewer plant species (470 versus 6375) than the similar-sized Cuba (110,000 km$^2$); Greenland (2.1 million km$^2$) has few plant species (497 versus 2300) compared with the smaller island of Great Britain (220,000 km$^2$); and Antarctica (14 million km$^2$) has fewer plant species (two versus 16 000) than the smaller Australia (7.7 million km$^2$) (Hobohm 2000; Kent 1992; Orchard 1999). These data reinforce the obvious point that climate should not be overlooked as a first tier factor in explaining global differences in species richness on islands.

Much of Vestspitsbergen (39,000 km$^2$), situated at latitude 76–80° N, is covered with glaciers and in places supports only very low vegetation. Only two species of landbird breed there, the residential rock ptarmigan (*Lagopus muta*) and the migratory snow bunting (*Plectrophenax nivalis*; Løvenskiold 1964). Large islands situated at high latitudes in the Southern Hemisphere also show similar poverty of species: South Georgia (54 °S, 3,500 km$^2$) has only the South Georgia pipit (*Anthus antarcticus*; Prince & Payne 1979), and Elephant Island (61 °S, 56,000 ha) lacks any landbird species (Furse & Bruce 1975).

Islands around Britain show a negative correlation between latitude and number of plant species (MP Johnson & Raven 1970) and number of butterfly species (Hockin 1981). Presumably latitude is a proxy for temperature. Atoll floras in the Pacific Ocean reflect geographical variation in rainfall (Stoddart 1992). Macquarie Island lies c. 240 km north (on the warmer side) of the Antarctic Convergence and is well vegetated, whereas the much larger Heard Island occurs just to the southern (colder) side and is mostly glaciated (Hnatiuk 1993). Striking differences can also occur on the same island, as on Lizard Island (Queensland), where water is shed from hills, which support grassland dominated by *Themeda*. Soils in the lower parts of this island are more moist and support closed-scrub, woodland, rainforest and grassland with *Arundinella* as co-dominant with *Themeda* (Byrnes et al. 1977). On Isla Santa Cruz (Galápagos), species of plants from wet habitats dominate the vegetation of the windward side from 75 m upwards owing to orographic rainfall, whereas on the (drier) leeward side these species dominate only above 500 m elevation (van der Werff 1983).

Climate also moderates island productivity, as islands always experience higher minimum temperatures and lower maximum temperatures than the adjacent mainland (e.g. Troughton Island versus Kalumburu in Kimberley region; AA Burbidge et al. 1978). This is because of the high specific heat (= 1) of water. Forests cannot exist on islands with low annual rainfall. High islands are likely to intercept more rainfall than do low islands, as well as to produce rain shadows that diversify soil moisture regimes and habitats (Solem 1984).

The number of macropodoid species present on high-rainfall islands of WA is less than expected, and the number of macropodoid species present on low-rainfall islands is more than expected (Fig. 7). Climatic differences at the time of isolation were regarded by AR Main (1961a) as more important than interspecific competition in explaining why the two macropodoid species present in the Archipelago of the Recherche have differing patterns of distribution. In the Kimberley region average annual rainfall strongly influences the species composition of birds, reptiles and bats of large islands (NL McKenzie & Bullen 2012; R Palmer et al. 2013b; Pearson et al. 2013).

Average annual rainfall on the Kimberley islands is a prime determinant of species richness of camaenid land snails (LA Gibson and Köhler 2012). This factor, acting together with island area, topography and rock type, results in the development and retention of rainforest habitat, and thereby provides the humid and fire-resistant refugia required by these species. Rainfall gradients also contribute to explaining inter-island differences in the species richness of plants on these islands (Lyons et al. 2014).

Drought affects WA islands, just as it does the mainland coast (Foley 1957; Hunt 1929), and may kill trees and other vegetation (e.g. Bernier and Dorre islands, DEC 2007c; Dirk Hartog Island, Graham-Taylor 2012a) or alter the relative abundances of different species of plants (Heatwole et al. 1981). Drought also reduces the abundance of native mammals on islands (DEC 2007c; J Short et al. 1998; J Short & Turner 1999). On Bernier and Dorre islands, the size of marsupial populations is lowest two years after <200 mm of annual rainfall, and highest two years after >300 mm annual rainfall (Chapman et al. 2015). Introduced domestic cats are associated with the local extinction of native mammal species on Australian islands experiencing low rainfall (AA Burbidge & Manly 2002). A brief description of the effort that landbirds on Woody Island put into obtaining water from a leaking tank and under a metal roof implies that access to freshwater is highly sought during summer (WABN 1943–2016 No. 77: 10).

## Number and extent of vegetation and other types of habitat present

The number of plant communities present in an area, using a broad-scale classification, directly influences the number of animal species present (Jiménez-Alfaro et al. 2016). Recognition of plant communities ('vegetation diversity') is usually based on a combination of floristic

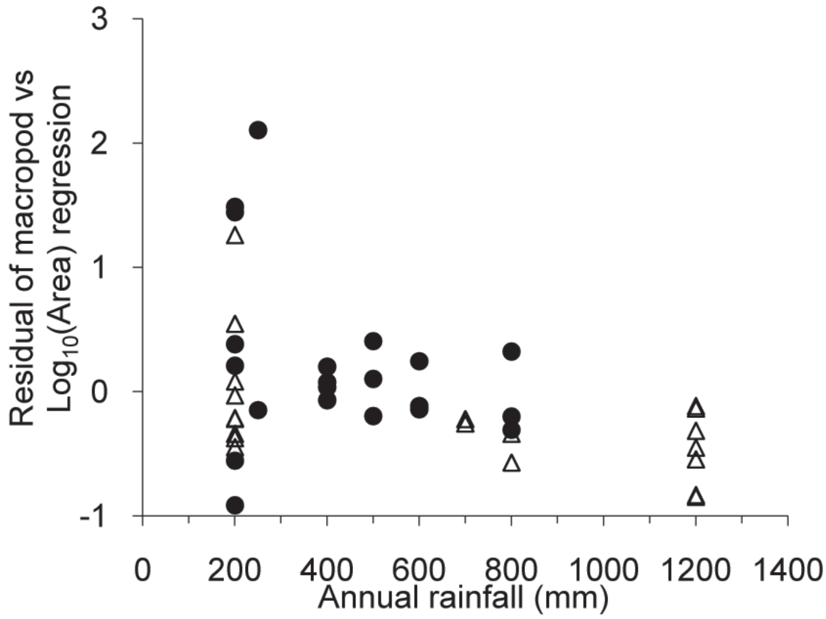



*Figure 7. The relationship between residuals of macropodoid species–area regression and average annual rainfall (based on data from Abbott 1980c, LA Gibson & McKenzie 2012b) for islands inaccessible to Aboriginal people (●) and accessible to Aboriginal people (△).*

composition and vegetation structure, and is itself influenced by temperature, rainfall, topography, elevation, and geology.

It seems that the earliest explicit recognition of the importance of habitat in determining the occurrence of particular bird species on Australian islands is the anonymous contribution in Commonwealth of Australia (1912: 51). This insightful account (probably written by AFB Hull) stated that the small islands of NSW with 'a densely stunted' vegetation supported certain bird species, whereas larger islands 'carrying trees of great girth' possessed additional species of birds.

The earliest quantitative study of the importance of habitat showed that as area increases from 1–100 ha, the number of species increases appreciably (CB Williams 1943). This was attributed to the inclusion of 'more and more variety of ecological formation due either to climate, soil, slope or other differentiating cause' (Williams 1943: 267). In addition, increased habitat complexity may decrease the extinction rates of species and thereby increase the number of species present on an island (MacArthur 1972: 102, 104). A small island with 'rich' vegetation is thus comparable to a large island with 'poor' vegetation (JM Diamond 1969). Similarly, in the Channel Islands (California), Anacapa is 'wooded' and has twice as many breeding bird species as on the 'barren' and equal-sized Santa Barbara, and more species than on the barren and much larger San Miguel and San Nicolas (HL Jones & Diamond 1976).

Large islands usually have more complex geomorphology and more vegetation types present than do small islands (GE Watson 1964; MP Johnson & Simberloff 1974; Byrnes et al. 1977; Mühlenberg et al. 1977; Reed 1981, 1984; Deshaye & Morisset 1988; T Robinson et al. 1996; AC Robinson et al. 2008a; Brothers et al. 2001; S Harris et al. 2001; Triantis et al. 2005, 2008; Jüriado et al. 2006). Exceptions do of course occur, as with Fuerteventura having only one vegetation type compared to La Palma and other smaller islands in the Canary Islands (Humphries 1979), and cold Baffin Island (510,000 km$^2$) having fewer vegetation types and sparse vegetation than does the smaller, tropical Cuba (110,000 km$^2$) (DA Walker et al. 2005). Islands with many vegetation types support more species than do islands that have only one vegetation type present (Mühlenberg et al. 1977; Dueser & Brown 1980; Haila 1981; Reed 1981. 1984; Adler & Wilson 1985; Boomsma et al. 1987; Ricklefs & Lovette 1999; T Robinson et al. 1996; AC Robinson et al. 2008a; Sfenthourakis 1996; Médail & Vidal 1998; Fernández-Palacios & Andersson 2000; Brothers et al. 2001; S Harris et al. 2001; Davidar et al. 2001). A study of plant species richness in eight habitat types on 160 islands in the Baltic Sea (Finland) demonstrated that almost all species occur on islands with area <20 ha. There was, however, a strong increase in species richness with the number of habitats present (Hannus & von Numers 2008).

Extreme climate also prevents the presence of trees and thus the formation of forests, as on cold Akpatok Island, Canada (Polunin 1934, 1935), St Lawrence Island, Alaska (Fay & Cade 1959), and Bear Island (Bjørnøya) and Spitsbergen, Norway (Summerhayes & Elton 1923; Løvenskiold 1964). None of the islands between the North Pole and the Canadian mainland support forest (Möller & Thannheiser 2011). In WA, the arid Barrow and West and East Wallabi islands lack trees (Buckley 1983; Storr 1965d). Absence of trees has obviously resulted in the absence of forest or woodland vegetation and of the bird species that require this habitat.

The concept that some landbird species do not occur in all island habitats but are instead restricted to one habitat type (Lack 1942) was first applied in Australia to the presence/absence of eucalypt forest/woodland or rainforest on islands of Queensland (Marshall 1934). On islands with pronounced habitat heterogeneity, it can be useful to examine species richness in relation to the area of each habitat unit and then sum over all units (Buckley 1982; Deshaye & Morisset 1988).

Despite being acknowledged as an important determinant of species diversity (Ouellet 1967; JM Diamond 1984a), habitat characteristics have been quantified in few studies. Island elevation is instead treated as a satisfactory proxy for, and shortcut measure of, habitat diversity (e.g. MP Johnson & Raven 1970; Heaney 1984). This assumption seems to be based on correlations with temperature, precipitation, humidity, evaporation and insolation (Fattorini 2002). Sometimes habitat diversity is partially linked with island area and elevation, as on seven of the Canary Islands (Lack 1976), although on all 11 Canary Islands only elevation (and isolation) were correlated with the number of habitats (Fernández-Palacios & Andersson 2000). Given the close association between Lack and Diamond with Robert MacArthur, it is puzzling why foliage height diversity (MacArthur et al. 1966) was not measured on the islands that they studied.

Crude or cursory typification, instead of finer distinction, of island habitats may predispose habitat not to be selected in species/area regressions (Mayr & Diamond 2001), and coupled with the assumption that small, low islands have fewer habitats than large, high islands, has frequently resulted in the habitat factor being undervalued. For example, habitats on northern Melanesian islands were classified into only six oversimplified types, with the most widespread type (rainforest) not subdivided further by structure or dominant plant species (Mayr & Diamond 2001; contrast with Beard 1944, and Mueller-Dombois & Fosberg 1998). This is also in contrast to a study of Fennoscandian islands that involved recognition of 10 habitat types and construction of rarefaction curves for several of these (Haila 1983). More bird species occurred on large forested islands. On islands around Britain, 3–26 habitat types relevant to landbirds could be identified (Reed 1981). A study of 17 islands in Torres Strait (between New Guinea and Queensland) recognised 34 habitat types (Lavery et al. 2012). Height of vegetation is also a useful indicator of mammal and ant species richness (Dueser & Brown 1980; Morrison 1998).

In a study of nine land and freshwater snail species on seven islands in the Bahamas, Maly and Doolittle (1977) characterised six island habitats on the basis of elevation, substrate and vegetation. A study of 42 land-snail species on 12 islands in the Skyros Archipelago adopted a similar method of recognising a habitat matrix based on eight types × six elements (Triantis et al. 2005). In the latter study, the habitat matrix was a better predictor of species richness than was the traditional approach of counting the number of vegetation types. Habitat complexity is a major determinant of species richness in both studies. A study of ants on 44 islands near Puerto Rico found that the number of habitat types was the best predictor of species richness (Torres & Snelling 1997). An early example of a simple, but successful, attempt to characterise habitats on two West Indian islands is provided by Wunderle (1985).

Seldom has detailed comparison of tree-species composition and vegetation structure between island and mainland been undertaken (SG Nilsson 1977; Vassallo & Rice 1982). The most detailed comparative study of habitats available is of Corsica and Provence (France). This island has habitats similar to those on the mainland, but bird species occurring in forest on the mainland are spread more broadly across habitats on Corsica (Blondel et al. 1988). Habitat diversity offers a better explanation of plant species richness in the Galápagos than does island area and isolation (van der Werff 1983). A detailed count of landbirds on Åland and Ulversö (the former island considered to act like the mainland for the latter island) implicated habitat unsuitability in explaining most absences of species. Ulversö lacks spruce forest, has a more mosaic-like landscape, denser undergrowth, and shorter trees (Järvinen & Haila 1984).

Another potentially useful measure of habitat diversity is the number of plant species present on an island. This factor strongly correlates with species richness of ants on islands of the Wadden Sea (Boomsma et al. 1987) and Bahamas (Morrison 1998), birds on Galápagos and Californian islands (MP Harris 1973; Power 1976), ants on continental islands of Mexico (Case 1975), butterflies on British islands (Hockin 1981), and Lepidoptera on islands in the Baltic Sea (Järvinen & Ranta 1987). However, a more empirical approach has merit. Deshaye and Morisset (1988) distinguished 22 habitat types on the basis of various combinations of five factors: Substrate, drainage, slope, aspect, and potential snow cover.

Joint consideration of island area and habitat diversity often provides a better prediction of species richness than area alone. These factors are thus better considered as mutually supplementary rather than mutually exclusive (Triantis et al. 2003). A remarkably comprehensive study of 521 islands in the Bahamas found that area and vegetation structure explained much of the variation in species richness of lizards and breeding birds (TW Schoener & Schoener 1983a). When the lichen flora of Estonian islands is divided into occurrence on substrate types, habitat is a better predictor of species richness than is island area (Jüriado et al. 2006). An important exception is the study of woody plant, beetle and land-snail species on 17 Swedish islands, which found that habitat diversity (involving the recognition of 19 types) did not contribute to species richness (SG Nilsson et al. 1988). In addition, a study of the carabid beetle fauna of 24 islands near south-western Finland failed to find that habitat diversity predicted species richness (Kotze et al. 2000).

Because of the possibility of latent ecological flexibility, it is not always a straightforward matter to explain the absence of species from islands on the basis of lack of suitable habitat. A notable instance is when a eurytopic species with many host plant species is studied on a large number of islands (91) differing in the extent of suitable habitat (Halkka et al. 1971). The absence of 18 bird species from Kangaroo Island (South Australia) has been attributed to the lack of 'suitable' habitat on the island relative to the adjacent mainland (Carpenter & Horton 1979). The most obvious demonstration for WA is the absence of freshwater vertebrate species from islands of south-west WA, none of which possess creeks or pools. These islands lack freshwater fishes and the oblong turtle (*Chelodina colliei*), all of which depend on water. Frogs (five species) are restricted to those islands with wetlands or seepages. Other obvious insular absentees are bird species dependent on *Eucalyptus* foliage (*Pardalotus* species, south-west WA) and those which depend on the presence of rainforest or mangal (Kimberley region).

Lack (1976) attributed the reduced number of bird species on islands in the West Indies to the reduced variety of habitats available. For bird species on small islands around Britain, the best model for predicting colonisation and extinction probability included four factors: Island area, distance to the presumed nearest source area, plus two measures of habitat (GJ Russell et al. 2006). In contrast, species richness of plants on small islands near Greece showed no link with the number of habitat types present (Panitsa et al. 2006). It is likely that a simple enumeration of habitat types is too coarse a measure of habitat heterogeneity.

For islands in the Torres Strait, a single habitat dominates most of the area of the two largest islands, whereas on other islands four habitat types cover much of the area (Lavery et al. 2012). Species richness of birds, mammals, reptiles and amphibians varied with the number of habitat types but weakly or not at all with habitat diversity. This may indicate that small areas of scarce habitat types may be disproportionately important for these vertebrate groups.

Sometimes the vegetated area of an island, a measure of habitable area, explains inter-island variation in species richness, as is the case for the floras of small islands in the Bahamas (Morrison 2002a). This factor explained more than area, elevation or degree of exposure.

A fruitful line of inquiry involves examination of the abundance of plant species on small islands in relation to island area and habitat availability. For five shrub species studied on islands of British Columbia, two species increased in abundance with island area but the other three species did not. Patterns in abundance were consistent with the distribution of the preferred habitat type (Burns 2005a).

Waterhouse Island (Tasmania, 290 ha, c. 3 km offshore) was cleared of its original vegetation for grazing by sheep (*Ovis aries*) and fallow deer (*Dama dama*) for many decades, then destocked (in 2005 and 2012), and planted with trees from 1979. No native bird species were recorded by Brothers et al. (2001), but after extensive planting of trees more than 10 landbird species have established (P Johns pers. comm.).

An analysis of the landbird fauna of 34 islands in the Torres Strait, ranging in area from 1 ha to 19,600 ha, found that area of habitat, not island area, was the factor that best correlated with species richness (Draffan et al. 1983). Similarly, although the number of plant species on islands adjacent to the Arnhem Land coast of Northern Territory is strongly correlated with island area, Woinarski et al. (2000) considered that larger islands have more species because of their greater environmental complexity. Small islands have few plant species because of low habitat heterogeneity. In terms of the mammal fauna of these islands, Woinarski et al. (1999b) regarded the absence or limited extent of grassland and *Eucalyptus* forest as important in explaining the absence of many species. Vegetation type is the major factor accounting for inter-island variation in bird species richness (Woinarski et al. 2001). The depauperate nature of the granivorous avifauna on Groote Eylandt (Northern Territory) has been linked to a lack of suitable habitat—grassy open woodland and grassland (Noske & Brennan 2002).

Studies on Lady Musgrave Island (Great Barrier Reef) have led to the idea that the survival of arriving plant species varies with both frequency of arrival of plants (as seeds or fruits) and the availability of suitable habitat for these diaspores (TA Walker 1991b). Habitat disturbance on this island between 1927 and 1989 was regarded as more important than dispersal of seeds by humans to the establishment of plant species there.

In the Archipelago of the Recherche, 13 major plant communities were identified and described, based on landings on 20 islands (JH Willis 1953). *Eucalyptus* forest (the tallest vegetation) was recorded on seven of these islands, and *Melaleuca* woodland was recorded on three islands. The most widely distributed vegetation types include 'woody mixed-shrub thicket', 'mat plants' and 'annual herbs'. The soil characteristics and other ecological factors that determine these vegetation types has not been established. On Depuch Island the three vegetation types identified are linked to three distinct soil types: White sands of beach dunes, red soils and limestone soils (Royce 1964).

For islands of south-west WA, vegetation structure explains most of the variation in number of breeding landbird species present that is not explained by island area for islands close to the mainland (Fig. 8). Michaelmas and Breaksea islands, which lie close together and are of similar planar area, show differences in the richness of bird species consistent with the effect of vegetation structure. Breaksea is more exposed to waves and wind than is Michaelmas. Chatham Island also has fewer breeding bird species than expected from island area, distance from the mainland, and vegetation structure. This may be related to the extensive area of the island that is bare rock.

The earliest study of WA islands that explicitly considered the variety of habitats was of the flora of islands in Shoalwater Bay (Storr 1961). This analysis was later expanded to all the islands south and west of

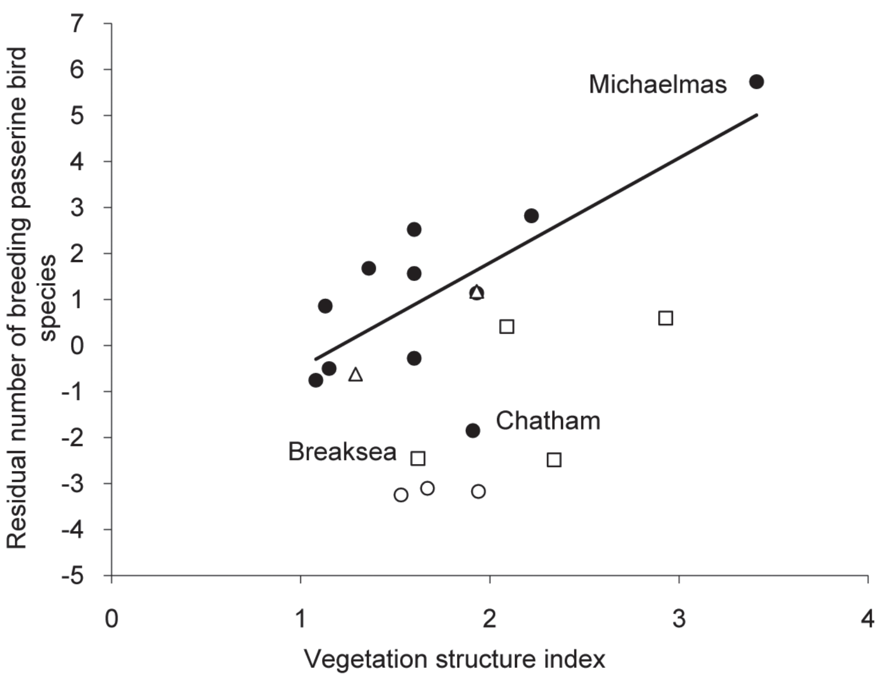



*Figure 8. The relationship between residual number of breeding passerine bird species (number of species versus $log_{10}$ island area) plotted against an index of vegetation structure (data from Abbott 1978a) for islands: <5 km from the mainland (●, solid line); 5–10 km from the mainland (□); 11–20 km from the mainland (△); and >20 km from the mainland (○). Species–area relationship: no. species = 3.57($log_{10}$(Island area(ha))) – 3.70 ($R^2$ = 0.69, n = 20, p < 0.00001). Relationship between residual of species–area regression and vegetation structure index: Residual = 2.28(VSI) – 2.76 ($R^2$ = 0.53, n = 11, p < 0.02) for islands <5 km from mainland.*

Fremantle, revealing a high correlation with number of plant species (Abbott 1977a). Another early study undertaken in WA demonstrated a gradient in height of vegetation, from 3–4 m on the leeward side of Hamelin Island to <1 m on the windward side (Gillham 1963).

In a study of the reptilian fauna of 36 islands between Dongara and Lancelin, J Ford (1963: 139) showed a perceptive understanding of the role of habitat diversity: 'The number of species on an island is a function of the habitat diversity which depends on the size of the island.' 'Habitat impoverishment and size reduction are continuous processes under the weathering action of the sea, wind and rain'. Weathering patterns on these islands result in talus slopes and strong winds have deposited sand as dunes (G Keighery et al. 2002). The number of habitat types present is significantly correlated with island area (Table 10). A study of species richness of lizards on 38 islands between Fremantle and Becher Point (Perth metropolitan region) found significant correlation with plant species richness, vegetation cover and vegetation structure (Coster 1977).

A biogeographic study of reptiles on 10 small to moderately sized (0.9 –140 ha ) islands in Dampier Archipelago found 2–10 habitat types present (Connell 1983). The species richness of reptiles was considered to be more influenced by habitat diversity rather than by island area, both of which were correlated.

In the Montebello Group, five habitat types have been recognised (FL Hill 1955). Trimouille Island consists largely of consolidated sand dunes dominated by *Sorghum* and *Sporobolus* grasses, with scattered shrubs. This is in contrast to nearby Hermite Island, which is more rocky. The grassland there is dominated by *Triodia* species. The intricate physical configuration of the coastline of this island, with many sheltered bays, has allowed the development of patches of mangal (AA Burbidge 1971; DEC 2006a). This demonstrates a habitat effect that is independent of island area.

The absence of particular habitats often seems to override flexibility in habitat preference. Few species are able to widen their choice of habitat. The presence and extent of rocky habitat (as scree, boulders, cliffs and gorges) contributes to the presence/absence of many saxicolous reptile species on high-rainfall islands in the Kimberley region (R Palmer et al. 2013b). Islands in the Kimberley region lacking mangrove or rainforest habitat do not support species totally or largely dependent on these habitats on the adjacent mainland (LA Smith et al. 1978; Coate 2008a; Pearson et al. 2013; Lamont et al. 2014).The mangrove-dependent and rainforest-dependent avifaunas each comprise 22 species (Johnstone 1990; Johnstone & Burbidge 1991). Some bird species (e.g. mangrove robin *Eopsaltria pulverulenta*) require particular species of mangrove. There is also little doubt that the presence of mangroves on outlying islands, as in the Montebello Group, accounts for the occurrence of several other bird species (Montague 1914).

A detailed study of the occurrence of isopods on islets around Rottnest Island recognised 10 microhabitats and found a significant correlation between the number of habitat types and island area (Bunn 1980; Table 10).

Accidents of geological history also result in the development of unusual habitats. For example, Rottnest Island is one of only two WA islands with permanent lakes (it has six of them), which comprise c. 10% of the island's surface area (Rottnest Island Management Planning Group 1985b). The island has two breeding species each of duck and wader, and supports populations of non-breeding migratory species of waders (Storr 1965b). The other island with a permanent lake is Middle Island in the Archipelago of the Recherche.

Deciding how to recognise habitats presents a formidable challenge to the island ecologist. Subjectivity is involved as understanding of how species select habitats is meagre. The appropriate choice of habitat variable will also vary from taxon to taxon (Williamson 1988).

What is lacking from most ecological studies of islands are estimates of the abundance of each species in relation to habitat. The reason for this is that most studies on islands are based on short visits. An exceptionally-detailed study on the Faroe Islands of four landbird species demonstrated that each had low density in the lowest quality habitat (as expected) but only one species had the highest density in the highest quality habitat. As habitat quality is inversely correlated with island area, the influence of other factors cannot be ruled out (Bengston & Bloch 1983).

## Degree of isolation from the nearest source area

Isolation influences the biota because many species present on the mainland cannot or will not cross water. Possibly the most extreme example concerns tropical landbird species. More than about half of the New Guinea bird species of appropriate habitat preference have not crossed the gap 10 m wide between New Guinea and Admosin Island (MacArthur 1972).

Darwin (1859) emphasised the filtering effect of distance from the source area based on his firsthand experience with oceanic islands (Armstrong 2004). Isolation, with its consequence of impeded dispersal, was until the 1960s regarded as 'the most important and effective factor relevant to understanding the nature of island biotas' (Allee & Schmidt 1951: 623). Isolation is, with area, one of the two island properties most emphasised in studies of island ecology and biogeography. However, it is often very difficult to apportion unequivocally their relative importance. For example, Isla Grande (Tierra del Fuego), with c. 61 breeding landbird species is much larger (47,000 km$^2$) but also much closer (3–7 km) to mainland South America than are the Falkland Islands, with c. 26 breeding landbird species (area 12,000 km$^2$, 460 km from the continent) (Humphrey et al. 1970; RW Woods 1975). The elevation of Isla Grande is also greater than the Falkland Islands.

Ideally, investigation of the effect of isolation on species richness should compare islands that are similar in terms of area, climate, soil, elevation, age, latitude, etc. This is seldom attempted. Nonetheless, biodiversity (measured as number of genera of plants) does decline with increasing distance from the presumed source area, although the most remote large islands still have more genera than the closest small islands (Van Balgooy 1969). Species richness of lichens strongly declines with increasing isolation from the Estonian mainland (Jüriado et al. 2006). Species richness of butterflies on British islands is negatively correlated with distance to Britain (Hockin 1981) or to Britain, France or Ireland (Dennis & Shreave 1997). Species richness of geckoes on islands in the Indian Ocean varies inversely with distance from Madagascar (Losos 1986). Species richness of landbirds on the Bahamas and Gulf of Guinea islands is strongly negatively correlated with distance to the mainland (Reed 1987). Species richness of mammals on islands of east New Guinea and north-east Australia decreases with distance from these source areas and increases according to the number of large islands in each archipelago (Carjaval & Adler 2005). Species richness of birds, mammals, reptiles and amphibians on the Torres Strait islands decreases with increasing isolation (Lavery et al. 2012).

In contrast, a study of 521 islands in the Bahamas revealed few significant correlations between species richness of lizards and breeding birds with distance to the nearest main island (TW Schoener & Schoener 1983a). However, these correlations were usually the expected negative. Similarly, correlations between distance and number of plant species on islands off California and around Britain are low (MP Johnson et al. 1968; MP Johnson & Raven 1970; MP Johnson & Simberloff 1974). Plant species richness in vegetated plots on islands in the southern Pacific Ocean is not linked to degree of isolation (Keppel et al. 2010). Species richness of other taxa on islands correlates poorly with distance from the mainland (ants, Frisian Islands, Boomsma et al. 1987; mammals, Massachusetts, Adler and Wilson 1985; birds, Britain, Reed 1981, 1984; forest birds, Andaman islands, Davidar et al. 2001; terrestrial isopods, Aegean Archipelago, Sfenthourakis 1996; beetles, Aegean Archipelago, Fattorini 2002; plants, Aegean Archipelago, Kallimanis et al. 2010). However, once allowance is made for habitat, a stronger relationship between number of landbird species and distance to the nearest land emerged (Reed 1984).

Isolation is a problematic concept with migratory bird species (Salomonsen 1976; Haila 1983) and some mammal species (Crowell 1986; Lomolino 1986). This is because colonisation (and extinction) are no longer easily defined events and instead are subsumed by regional population dynamics. Migratory bird species 'recolonise' the islands between Sweden and Finland each spring, and mammals can cross frozen water connecting some islands to mainland Canada and USA. Other mammalian species can swim to islands (e.g. moose and bear in Canada and Alaska; euro in WA, and black rats in New Zealand and Australia).

Isolation in the simplest instance is the shortest distance between an island and the nearest point of the mainland, but in some situations determining the distance is not straightforward. If a stepping stone (intervening) island is present, should isolation be calculated as the distance between stepping stone and island, or between island and mainland? In archipelagoes, should the relevant distance be to the central island, the nearest large island, the nearest high island, the nearest island, the nearest four islands, or measured as an average of the distance to all islands (Hamilton et al. 1963; Thornton 1967; Willerslev et al. 2002)? Furthermore, a small island will be more isolated than its geographic position would indicate because it presents a poorer target than does a larger island (Tryon 1970).

A detailed study of the avifaunas of Jamaica and other islands in the West Indies led Lack (1976) to reject isolation as playing any major role in determining the number of bird species present on each island. Lack developed this thesis in the late 1940s, regarding it at that time as 'quite inadequate as a full explanation' (Lack & Southern 1949: 608). This viewpoint is incorrect, because many of these records are of single birds during the non-breeding season (Ricklefs 1977; Grant 1977). Indeed, Lack's 10 months of residence in Jamaica does not support this proposition—only one vagrant species was recorded despite Lack's party being in the field 'almost every day' (Lack 1976: 81).

According to Salomonsen (1976) the Canary Islands also demonstrate that dispersal and not island ecology constitutes the primary difficulty in the colonisation of islands by birds. Although a large number of non-breeding landbird species have been recorded, most are passage migrants from Europe to Africa (Bannerman 1963). These species would not be expected to breed on the islands. Well-studied islands, such as Lundy and Cape Clear, indicate that vagrant bird species recorded are not a random sample of all species found on passage. Species differ in their dispersal ability (Reed 1987).

Remoteness (irrespective of island area) often facilitates speciation, as is the case with land snails on Pacific Ocean islands (Solem 1983, 1990). Evolutionary change on oceanic islands is caused by reduced gene flow, which occurs at a more rapid rate than the immigration of new species (Williamson 1988). On oceanic islands off Mexico, distance accounted for a substantial portion of the variance in species richness of lizards in contrast to continental islands (Case 1975).

On islands in the Torres Strait, the number of sedentary bird species (i.e. species occurring on continental islands) is correlated with distance to the nearest island with area >5 $km^2$ (Draffan et al. 1983). For most of WA, however, the maximum distance of islands from the coastline is only c. 60 km. There is little effect of isolation on the number of macropodoid species present (Fig. 9). The number of plant, isopod and reptile species on islands also shows little evidence of distance from the mainland as an important factor (Table 9, Table 10). This is also the case for islands near the north-eastern coast of Arnhem Land, Northern Territory (Woinarski et al. 1999b, 1998, 2000, 2001). Nevertheless, closeness does enable some mammalian species to visit islands, e.g. the Murray River (WA) delta islands. Western grey kangaroos (*Macropus fuliginosus*) swim between islands and mainland, and koomal (brushtail possums) make intermittent visits (Browne Cooper et al. 1989). However, based on genetic evidence, the tammar has been unable to disperse between West and East Wallabi islands in Houtman Abrolhos, a distance of 1.9 km and much of which is exposed at low tide (Miller et al. 2011).

Some species present on the mainland coast have been recorded on islands very close to the mainland but not on islands farther out to sea. For example, in the Kimberley region the striped rocket frog (*Litoria nasuta*) and the red-backed fairy-wren (*Malurus melanocephalus*) were recorded only on Boongaree Island, which is 140 m from the mainland (Doughty et al. 2012; Pearson et al. 2013). In Exmouth Gulf, the red fox is able to cross mudflats at low tide to Burnside, Tent, Sandalwood and Hope Point islands (Start & McKenzie 1992). The islands of the Murray River (WA) delta have the crawling toadlet (*Pseudophryne guentheri*), quacking frog (*Crinia georgiana*) and humming frog (*Neobatrachus pelobatoides*) present, and the motorbike frog (*Litorea moorei*) occurs on an island in Wilson Inlet (WAM 2015). None of these species occurs on offshore

**Table 9**

Correlations between physical and biological variables for islands between Dongara and Lancelin. Island area and elevation are $\log_{10}$ transformed. ns = $p > 0.05$.

| | Area | Elevation | Isolation (distance) | No. of vegetation types | No. of native plant species |
|---|---|---|---|---|---|
| Elevation | $r^2 = 0.56$<br>n = 17<br>$p < 0.001$ | | | | |
| Vegetation types | $r^2 = 0.52$<br>n = 30<br>$p < 0.00001$ | | ns | | |
| Native plant species | $r^2 = 0.78$<br>n = 30<br>$p < 0.00001$ | $r^2 = 0.41$<br>n = 17<br>$p < 0.01$ | ns | $r^2 = 0.51$<br>n = 30<br>$p < 0.0001$ | |
| Exotic plant species | $r^2 = 0.63$<br>n = 30<br>$p < 0.00001$ | $r^2 = 0.46$<br>n = 17<br>$p < 0.005$ | ns | $r^2 = 0.61$<br>n = 30<br>$p < 0.00001$ | |
| Reptile species | $r^2 = 0.77$<br>n = 30<br>$p < 0.00001$ | $r^2 = 0.17$<br>n = 17<br>$p < 0.05$ | ns | $r^2 = 0.58$<br>n = 30<br>$p < 0.00001$ | $r^2 = 0.80$<br>n = 30<br>$p < 0.00001$ |

Source: J Ford 1963, 1965; G Keighery et al. 2002.

**Table 10**

Correlations between physical and biological variables for islands between Fremantle and Becher Point. Island area and Elevation are $\log_{10}$ transformed. ns = $p > 0.05$.

| No. of species | Area | Elevation | Isolation (distance) | No. of habitat types |
|---|---|---|---|---|
| Native plants | $r^2 = 0.42$<br>n = 120<br>$p < 0.0000001$ | $r^2 = 0.25$<br>n = 120<br>$p < 0.0000001$ | ns | |
| Isopods | $r^2 = 0.36$<br>n = 48<br>$p < 0.00001$ | $r^2 = 0.28$<br>n = 48<br>$p = 0.0001$ | ns | $r^2 = 0.31$<br>n = 48<br>$p = 0.00004$ |
| Reptiles | $r^2 = 0.79$<br>n = 10<br>$p = 0.0006$ | $r^2 = 0.69$<br>n = 10<br>$p = 0.003$ | $r^2 = 0.69$<br>n = 10<br>$p = 0.003$ | |

Source: Abbott and Black 1980; Bunn 1980; MG Brooker et al. 1996; Coster 1977; LA Smith 1997; Storr 1961; Western Australian Museum reptile database; Wykes et al. 1999.

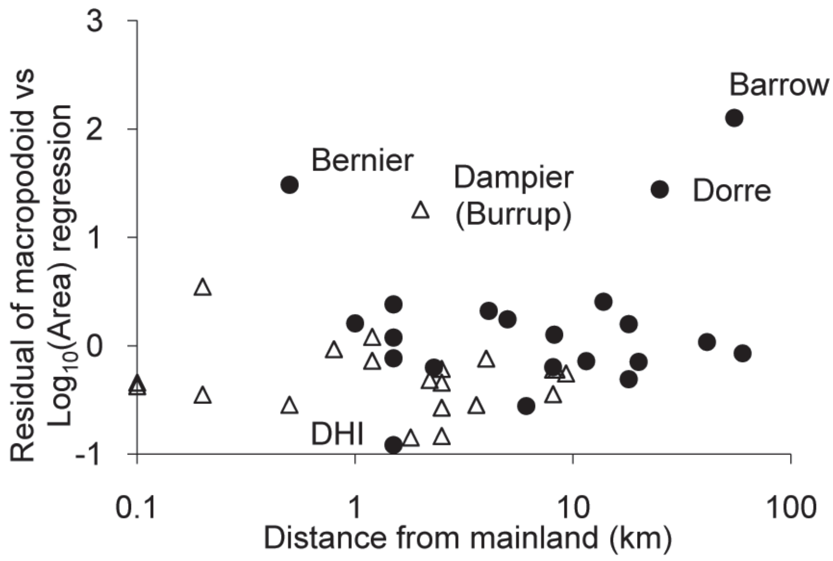



*Figure 9. The relationship between residual of macropodoid species–area regression and isolation (based on data from Abbott 1980c, LA Gibson & McKenzie 2012b) for islands inaccessible to Aboriginal people (●) and accessible to Aboriginal people (△).*

islands. The euro occurs on Simpson Island (57 ha), which is separated by a narrow channel 1.2 km wide, much of which dries at low tide.

Studies of species richness of plants on islands in Queensland demonstrate negligible influence of isolation (Buckley 1985; Heatwole 1991), as do studies of islands near the north-east coast of Arnhem Land, Northern Territory (Woinarski et al. 2000). Lack of significant correlation between species richness and isolation may not be infrequent (e.g. plants, Amerson 1975, Moody 2000, McMaster 2005; amphibians, Hecnar et al. 2002; reptiles, Wilcox 1978, Hecnar et al. 2002; birds, MP Harris 1973; mammals, Dueser & Brown 1980, Heaney 1984).

Given the frequent occurrence of tropical cyclones along the Pilbara and Kimberley coasts of WA and the occasional subsequent flooding of major rivers (from the Gascoyne to the Ord River), it seems possible that invertebrates, reptiles and small mammals could be transported to islands on floating vegetation and woody debris carried down rivers (MacArthur 1972; Heatwole & Levins 1972, 1973; Houle 1998). We have found no documented WA reports of such incidents but suggest that flotsam and floating islands be searched.

## History: Time since separation (or formation)

Island history may be a significant factor in explaining the nature of the biota present on an island (Soulé 1966). Islands in deep water have been isolated longer than those in shallow water. Continental islands in deep water are, however, usually those far offshore, making it difficult to separate distance effects from history.

The first demonstration of the importance of this factor, as a consequence of the mode of formation of islands, was by Wallace (1860). He noted striking differences in species composition between oceanic and continental islands in south-east Asia. These differences do not coincide with any differences in topography or geology. Many remote islands are of volcanic origin and were formed millions of years ago (Paulay 1994), in contrast to continental islands (all younger than c. 15 ka). The traditional view is that remote islands should—given enough time—have the same number of species as comparable areas close to the source area. However, we have found no evidence that supports this. It is self-evident that species in the source area will differ in dispersal ability, remote islands will (ceteris paribus) offer fewer habitats than do close islands, and resources (plant species, insect species) will be impoverished relative to the source area. Moreover, older remote islands will have experienced more time for species to have become extinct than have younger remote islands. Old remote islands may also have decreased in area as a result of erosion (Williamson 1988).

Taxa may differ in response to island age. In the Hawaiian archipelago, species richness in the weevil genus *Rhyncogonus* increases with island age. This is in contrast to the cerambycid genus *Plagithmysus*, which shows no relationship with island age (Paulay 1994).

On islands in the southern Pacific Ocean, the species richness of plants in vegetated plots in lowland rainforest increases with island age and to a lesser extent with island area (Keppel et al. 2010). New Caledonia, although smaller and more isolated than the Solomon Islands, has the richer flora. This discrepancy is attributed to the Gondwanan origin of New Caledonia and the Eocene origin of the Solomon Islands (Mueller-Dombois & Fosberg 1998).

Famously, Wallace (1881) noted that the landbird and mammalian faunas of Bali and Lombok differ far more from each other than do those of Japan and Britain. He concluded that 'distance is one of the least important of the causes' determining biotic similarity. In this case, geological history evidenced by the bathymetry between these islands is the explanation.

Another example illustrating the importance of history concerns the biota of the Alexander Archipelago, Alaska. Unlike most continental islands, these islands were glaciated when part of the mainland and possessed no relict biota following the post-glacial rise in sea level (Conroy et al. 1999). All of the mammalian species now present have therefore colonised the islands. Many islands in the higher latitudes of the northern hemisphere have been similarly affected, including Newfoundland, Manhattan, islands of Scandinavia and islands of northern Britain.

Time is as relevant to most continental islands (Crowell 1986) as it is for oceanic islands (Heatwole & MacKenzie 1967). A proxy for time since separation is the minimum depth of ocean at which an island separates from a larger landmass (mainland or adjacent larger island), assuming that only sea level (and not the height of the land) has changed. Although all continental islands became geographically independent of the mainland after the last glacial period, they are not all of the same age. For South Australian islands, T Robinson et al. (1996) estimated that a 90 m water depth corresponded to insularisation at 12.6 ka BP, in contrast to 5 m at 6 ka BP. In the Archipelago of the Recherche, the minimum water depth required for the isolation of large islands ranges from 82 m (Salisbury Island) to 18 m (North Twin Peak Island) (Abbott & Black 1978). For south-west WA more generally, island ages have been estimated to range between 3 and 13 ka BP (Abbott 1978a). Cays (comprised of sand or coral rubble) may be even younger (Kitchener & How 1982). The oldest WA islands are Salisbury (isolated c. 13–14 ka BP); Daw, Wilson and Westall (Combe) (c. 11-12 ka BP); West Wallabi, East Wallabi, Figure of Eight and Mondrain islands (c. 10.5–11.5 ka BP); and Sandy Hook Island (c. 10–10.5 ka BP) (AA Burbidge et al. 1982).

Older islands have had more time to experience extinction of populations of species than have younger islands. However, time since isolation is generally correlated with distance offshore for continental islands (Wilcox 1978; Heaney 1984; Abbott & Burbidge 1995; T Robinson et al. 1996). Another correlated factor, suggested by RW Fairbridge, is that the older islands in the Archipelago of the Recherche are occupied by rock wallabies rather than tammars because the former were more abundant 11–13 ka BP than the latter were at 8–10 ka BP (Serventy 1953). During a period of several millennia it is likely that climate will have varied. Thus, populations isolated in c 14 ka BP may have inherited an arid-adapted biota, whereas those isolated in c. 10 ka BP should be comprised of mesic species (Hopkins & Harvey 1989). The occurrence of six species of chenopods on Salisbury Island (AA Burbidge et al. 1982) may be linked to this.

The absence of the short-eared rock-wallaby (*Petrogale brachyotis*) from islands in the Kimberley region, as well as the predominance on the Kimberley islands of the Kimberley rock-rat (*Zyzomys woodwardi*) over the common rock-rat (*Z. argurus*), may indicate that the climate of the Kimberley coast may have been wetter when the islands separated from the mainland (NL McKenzie et al. 1978). Equally plausible is a hypothesis that dingoes extirpated the larger mammalian species on these islands.

For breeding passerine bird species, the graph of the residual of the species/area relationship versus time since isolation shows a reduction with increasing time (Fig. 10).

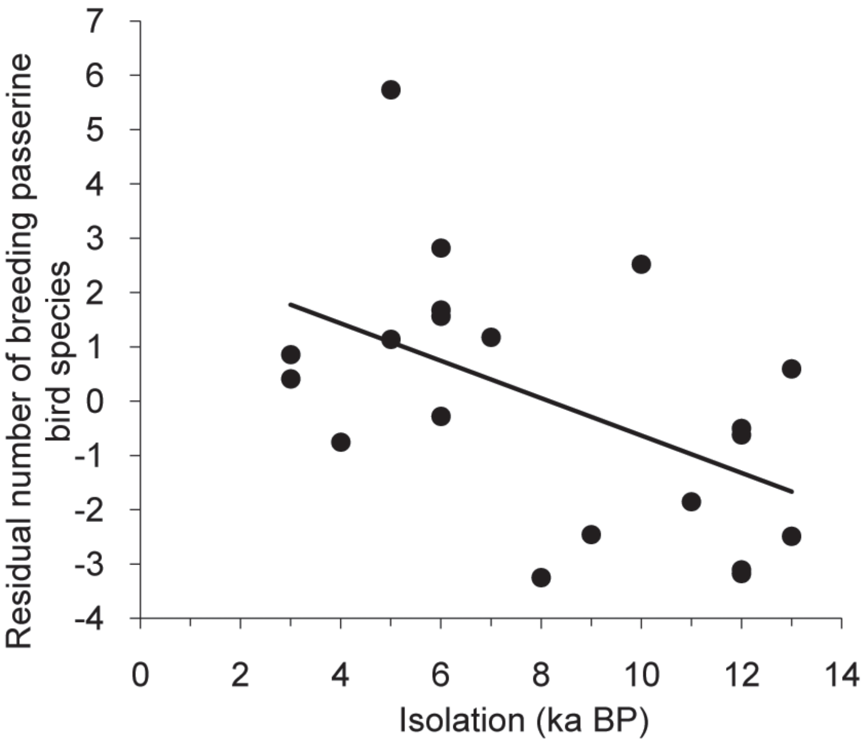



*Figure 10. Residual of breeding passerine bird species–area relationship versus isolation for Western Australian islands (data from Abbott 1978a). Residual passerine species = –0.00034(Isolation) + 2.81, $R^2$ = 0.26, n = 20, p < 0.03.*

## Planar area

Island area was first reported as relevant in explaining species richness by Forster (1778: 169): 'Islands only produce a greater or less number of species, as their circumference is more or less extensive'. Later studies of floras and faunas on islands often did not emphasise area as particularly important and some studies did not even provide a graph of species number versus area (e.g. Lack 1942; Asprey & Robbins 1953). Indeed, the first published graph and regression equation seems to be due to Lowe (1955). From the 1960s, presentation of a graph has become standard practice (EO Wilson 1961; Hemmingsen 1963; Levins & Heatwole 1963; Niering 1963; MacArthur & Wilson 1963; Hamilton et al. 1964; Moreau 1966), as has the use of regression analyses (Hamilton & Rubinoff 1963, 1964; Hamilton et al. 1963, 1964). The species–area relationship has come to be accorded primacy, so that other factors are viewed by some as 'disrupting' this relationship (Losos & Parent 2010). For example, Wissel & Maier (1992) advocated that Arctic and tropical islands should not be compared because this would obscure the detection of a species–area relationship.

Slud (1976) pointed out that while the double logarithmic species–area graph for the species richness of landbirds shows the familiar increase (although with great scatter), the semi-logarithmic graph does not. All islands smaller than 25,900 ha, and most islands smaller than 259,000 ha, have fewer than 50 species present. Above 25,900 ha, however, richness increases dramatically. Factors additional to area are therefore clearly relevant.

In addition, the correlation between species richness and island area is not always high (Hockin 1981), despite being statistically significant (Dennis et al. 2000a; Hobohm 2000; Lockwood 2006; Franklin & Steadman 2008; Jonsson et al. 2009). The low correlation of determination ($r^2$) surely points to the relevance and importance of other factors not measured. As succinctly expressed by Boecklen and Gotelli (1984: 67), 'the determinants of species diversity are often too complex to be modelled by area alone'. Yet, preoccupation with improved estimates of planar area (Fattorini 2007a) and sophisticated methods for estimating surface area (Triantis et al. 2008) still occur.

Planar area (often less than surficial area) allows more individual organisms to occur (via 'random placement') and this by itself will result in more species being present (WR Turner & Tjørve 2005). For example, Ireland (82,000 $km^2$) has fewer landbird species than Great Britain (210,000 $km^2$) (Lack 1969). However, area is correlated with other highly relevant factors, particularly the extent and variety of habitat types, which are often difficult to quantify (e.g. Reed 1981, 1984; GJ Russell et al. 2006). Not surprisingly, these factors have often been overlooked or omitted in statistical analyses. This is for the simple reason that pure area effects are difficult to separate from the effects of increasing environmental diversity as the sampled area is expanded (JD Sauer 1969; Haila 1983). Islands with similar species numbers may differ in area by several orders of magnitude. Some islands in the Galápagos of similar area do have similar plant species richness, whereas others do not (van der Werff 1983).

With Belizean reef-islands, area overrides distance (15–80 km) from the mainland. When the species–area relationship of these islands is compared with remote islands in the Pacific Ocean, the role of isolation (of the order of thousands of kilometres) becomes evident (Stoddart & Fosberg 1982).

An unexpected characteristic of islands of Sweden is that large islands attract more lightning strikes than do small islands. This results in changes in the species composition and biomass of plants, litter decomposition and other ecosystem properties (Wardle et al. 1997).

Clearly, island area is not necessarily the prime or only determinant of insular biodiversity. The relationship between species richness and area is complex, being influenced by many factors. Islands of equal area may differ widely in species number, even within assortments of islands selected for comparability (JD Sauer 1969). As a general rule, however, the number of taxa does increase with increasing area only if all other factors are equal (Van Balgooy 1969). Small, close tropical islands have more genera of plants than small, close temperate islands, and large continental temperate islands have more genera than large oceanic islands. Indeed, MP Johnson et al. (1968) regarded island area as a good predictor of species richness 'so long as the [islands] considered are reasonably homogeneous for other environmental variables'. MacArthur (1972) made a similar point when explaining why a large island may hold fewer species than expected—he invoked geology as responsible for impoverished habitat. For example, extensive areas of recent lava flows on several Galápagos islands support no vegetation. The habitable area of large islands may thus much be less than their actual area (Willerslev et al. 2002).

For small islands (<40 ha) off the coast of Connecticut, area is a weak predictor of the number of ant species in comparison to the vegetated area of these islands. Even better is a measure of the exposure of ant nests to the degree of open sky, a proxy for temperature (Goldstein 1975). Island area contributed little to explaining species richness of geckoes on 48 islands in the Indian Ocean (Losos 1986).

The direct effect of area on species richness can best be demonstrated in two ways. First, islands that consist of only one or a few plant species but differ in area minimise or eliminate the effect of habitat diversity (Simberloff & Wilson 1969; Rey 1981; J-L Martin 1983; J-L Martin & Lepart 1989). Second, fixed-area quadrats can be used on islands of differing areas. On Melanesian islands the local size of the ant fauna increases with island area (EO Wilson 1961). With the floras of small islands near northern Scotland, this approach showed an increase in small-scale species richness with increasing island area (Kohn & Walsh 1994). This is also evident from the comparison of mean species richness of plants in quadrats with the total area vegetated on five islands in the Bonaparte Archipelago WA (Henson et al. 2014). However, on the Channel Islands (California), quadrat-level richness of plant species did not increase with island area. This was interpreted to signify that positive correlations between plant species richness and island area are the result of increasing habitat and disturbance heterogeneity with increasing island area (Westman 1983).

MacArthur and Wilson (1967) conceded that species richness could increase if island area is correlated with elevation and proximity to the mainland. For the purposes of their mathematical analyses, they also assumed climate and topography to be uniform among islands. Nonetheless, they regarded area as the prime factor and viewed major differences in ecology among islands as distorting the species–area relationship. They also acknowledged that neither area nor elevation exerts a direct effect on species richness. Both are related to other factors, including habitat diversity.

Because planar area is easily measured on a map, this factor (together with the width of the water gap between island and mainland or between other islands in an archipelago) has been given the greatest attention, producing the famed species–area relationship ($S = cA^z$) and resulting in hundreds of published examples (Connor & McCoy 1979; Draffan et al. 1983; Woinarski et al. 1998, 1999a, 1999b, 2000, 2001, 2011). For WA, the first graphs of S versus A (without the calculated equation) were published by Storr (1961) and Armstrong (1979), and the first equations were calculated by Abbott (1977a) and Kitchener and How (1982). Subsequent examples for WA islands include plants (Fig. 11, 12), isopods (Fig. 13), land snails (LA Gibson & Köhler 2012), butterflies (Fig. 14), frogs (Doughty et al. 2012), reptiles (Fig. 15; R Palmer et al. 2013b), landbirds (Fig. 16, 17; Pearson et al. 2013) and mammals (Fig. 18; LA Gibson & McKenzie 2012b).

Large islands are likely to satisfy the minimum area requirements of more species than are small islands (Cole 1983; WR Turner & Tjørve 2005). This is because the extent of each habitat increases, allowing greater population size of species as thresholds are exceeded (Reed 1981). The length of food chains on islands increases with island area (Roslin et al. 2014).

Large Australian islands thus retain species that that did not persist generally on other Australian continental islands. For example, the four large sand islands off the south-eastern coast of Queensland have retained many plant species that seldom persist on smaller islands (Stephens 2011). The flora of North Stradbroke Island (28,500 ha) includes four *Banksia* species, seven *Eucalyptus* species and three *Xanthorrhoea* species. Fraser Island (165,400 ha) has five, nine and three of these species respectively, Moreton Island (17,000 ha) has four, six and three species respectively, and Bribie Island (14,700 ha) has four, three and one species respectively. Other examples include Kangaroo Island (4500 km$^2$, South Australia), with two *Banksia* species, 21 *Eucalyptus* species and one *Xanthorrhoea* species (A Kinnear et al. 1999); Tasmania (62,000 km$^2$), with three *Banksia* species, 30 *Eucalyptus* species and three *Xanthorrhoea* species (ML

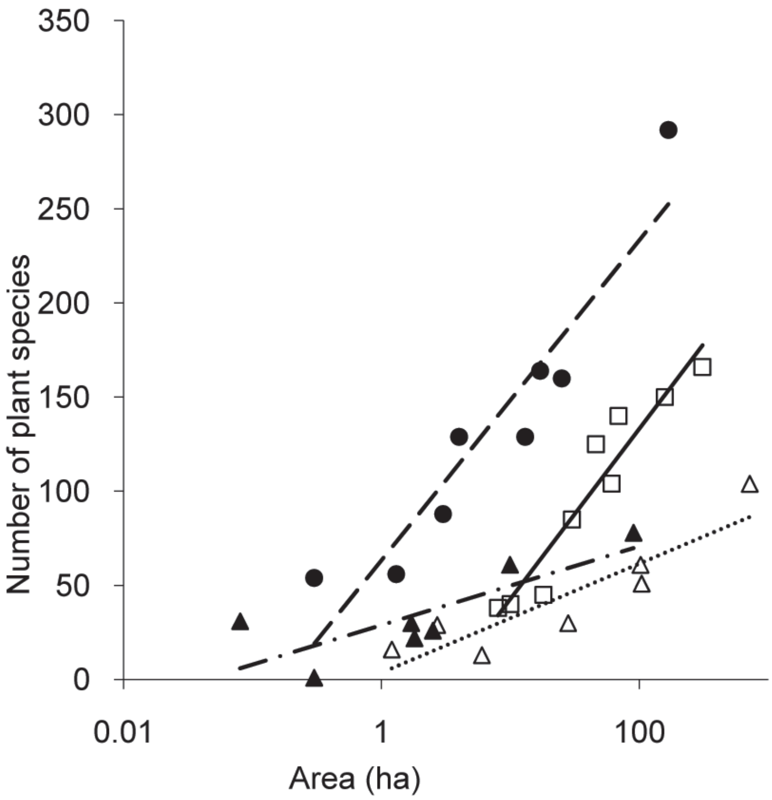



*Figure 11. Joint influence of exposure and area on plant species richness on islands, peninsulas and promontories in Albany region (after Abbott 1980e): exposed mainland sites (□, solid line); sheltered mainland sites (●, dashed line); exposed islands (△, dotted line); and sheltered islands (▲, dot-dash line). Mainland exposed: no. species = 90.39(Log$_{10}$ Area) – 47.53, $R^2 = 0.92$, $n = 9$, $p < 0.0001$. Mainland sheltered: no. species = 84.95(Log$_{10}$ Area) + 63.52, $R^2 = 0.88$, $n = 8$, $p < 0.0006$. Island exposed: no. species = 28.98(Log$_{10}$ Area) + 3.62, $R^2 = 0.82$, $n = 7$, $p < 0.006$. Island sheltered: no. species = 20.94(Log$_{10}$ Area) + 28.95, $R^2 = 0.65$, $n = 7$, $p < 0.03$.*

Baker & de Salas 2012); King Island (1100 km$^2$, north-west of Tasmania), with two *Banksia* species and four *Eucalyptus* species (DPIPWE 2012); Flinders Island (1,350 km$^2$, north-east of Tasmania), with two *Banksia* species, seven *Eucalyptus* species and one *Xanthorrhoea* species (S Harris et al. 2001); Cape Barren Island (46,200 ha), with four *Eucalyptus* species (S Harris et al. 2001); and Clarke Island (8400 ha), with one *Banksia* species, four *Eucalyptus* species and one *Xanthorrhoea* species (S Harris et al. 2001).

However, for islands between Shark Bay and the Kimberley region, area is evidently not a prime determinant of the number of *Eucalyptus* species present (information from Western Australian Herbarium 1998- unless otherwise indicated): Dirk Hartog Island (58,600 ha, three species); Barrow Island (23,400 ha, one species); Augustus Island (19,000 ha, one species); Bigge (17,900 ha, one species); Dorre Island (5200 ha, one species); Faure Island (5200 ha, two species); Boongaree Island (4900 ha, one species); Bernier Island (4300 ha, three species); Uwins Island (3200 ha, one species); Koolan Island (2700 ha, seven species, G Keighery et al. 1995); Depuch Island (1100 ha, one species); and Cockatoo Island (500 ha, two species). The larger islands of south-west WA show a similar anomalous pattern: Middle (Archipelago of the Recherche) Island (1000 ha, five species); Mondrain (800 ha, two species); Bald Island (720 ha, one species); North Twin Peak Island (270 ha, two species); and Michaelmas Island (93 ha, two species).

Large continental islands retain the dominant vegetation type that occurs on the adjacent mainland, well exemplified by large islands off Arnhem Land, Northern Territory (Specht 1958), North Stradbroke Island, Queensland (Clifford & Specht 1979); Kangaroo Island, South Australia (Wood 1930); and Tasmania off Victoria (WD Jackson 1999).

After navigating the southern coastline of Australia in 1801–1802 and landing on several islands, Matthew Flinders noted that 'the size of the kanguroo [present on each island] bore some proportion to the extent of land [island area] it inhabited' (Flinders 1814: 207). There is little doubt that every species has a minimum population size (and hence a minimum area), below which it is impossible to sustain a viable population as a result of deaths and emigration exceeding births and immigration. The size of the minimum area is not fixed

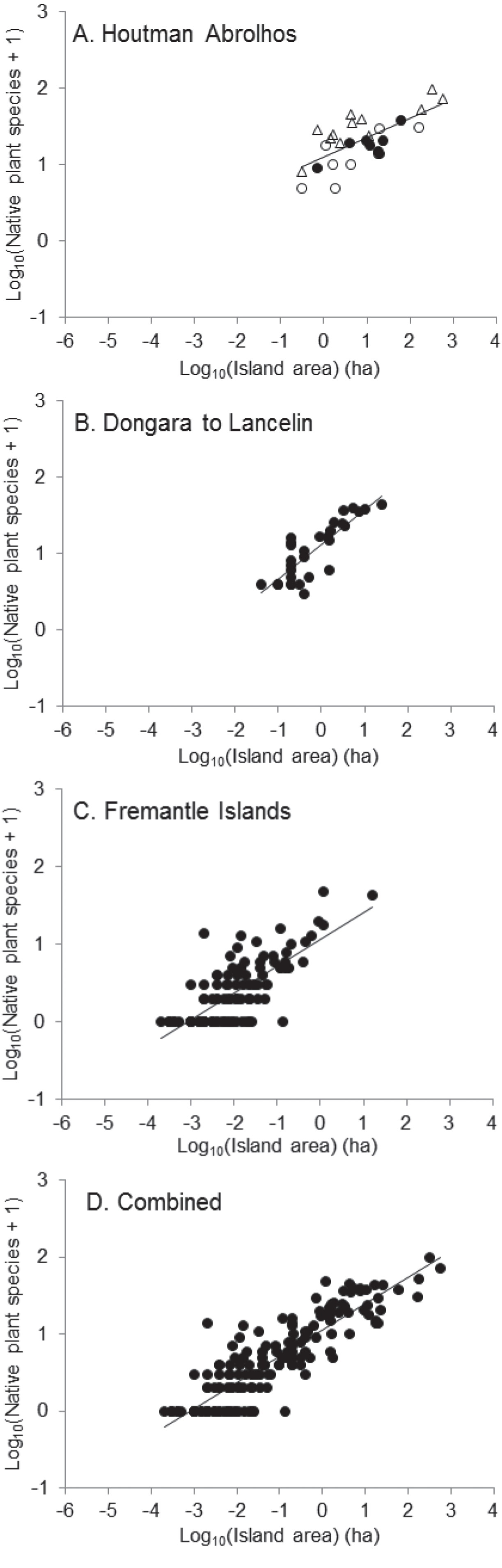



*Figure 12. The number of native plant species versus island area. A. The three island groups comprising Houtman Abrolhos: Easter Group (●), Pelsaert Group (○), and Wallabi Group (△); data from JM Harvey et al. 2001. $Log_{10}$(No. species + 1) = 0.25 ($Log_{10}$ Area) + 1.10, $R^2$ = 0.50, n = 28, $p < 0.0001$. B. The islands between Dongara and Lancelin; data from GJ Keighery et al. 2002). $Log_{10}$(No. species + 1) = 0.45 ($Log_{10}$ Area) + 1.12, $R^2$ = 0.70, n = 30, $p < 0.0001$. C. The islands between Fremantle and Becher Point; data from Abbott & Black 1980. $Log_{10}$(No. species + 1) = 0.35 ($Log_{10}$ Area) + 1.06, $R^2$ = 0.57, n = 120, $p < 0.0001$. D. Combined data from A, B and C. $Log_{10}$(No. species + 1) = 0.34 ($Log_{10}$ Area) + 1.06, $R^2$ = 0.79, n = 178, $p < 0.0001$.*

because the presence of habitat of high quality, presence of abundant resources, absence of competitor species, absence of predator species, and proximity to other conspecific populations may compensate for small areas of islands. For example, the squirrel glider (*Petaurus norfolciensis*) occurs on five islands off south-eastern Queensland, the smallest of which (Woogoompah) has an area of 630 ha. This species is absent, however, from the next smallest island studied (Peel, 400 ha; Bell et al. 2011). For WA islands, the minimum size of a population of wallaby/kangaroo for persistence during a period of c. 7 ka has been estimated at 200 animals, assuming that the entire island is occupied (AR Main & Yadav 1971).

The occurrence of two species of mammals (native rodents) on a 23 ha island close to the Kimberley mainland (How et al. 2006) is puzzling. It is the only island of five with an area <30 ha to have any mammal species present. This island shows, however, little difference to the other four in terms of the number of reptile species recorded. Thus, it does not seem that either substrate or distance from the mainland is responsible. Perhaps the direction and configuration of tidal currents are relevant factors. Evidence from islands north-east of Arnhem Land (Northern Territory) indicates that large species of reptiles are more likely to occur on large islands, although island area is not the only factor responsible (Woinarski et al. 1999b).

Deliberate introductions of wallabies to islands can be informative about the minimum area required by species. In 1905, tammars were released on Greenly Island (200 ha, South Australia). This population has persisted (T Robinson et al. 1996). In 1960, six individuals of the black-footed rock-wallaby (*Petrogale*

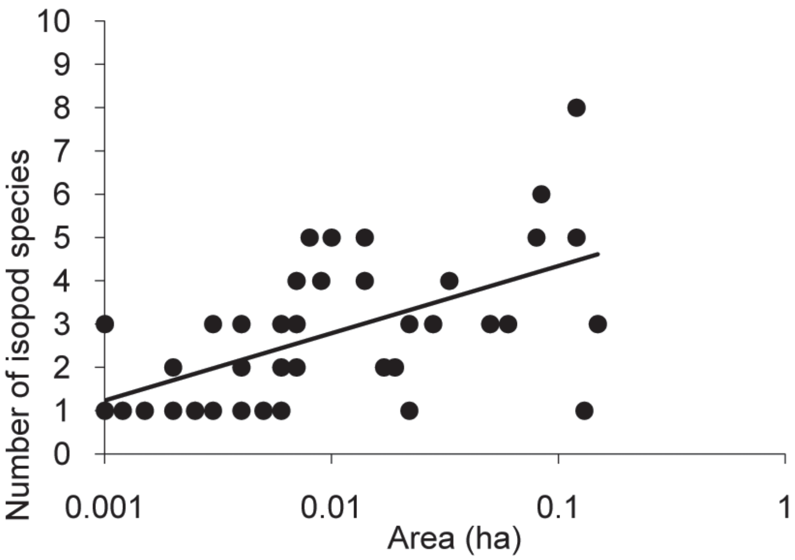



*Figure 13. The number of terrestrial isopod species versus island area for islets adjacent to Rottnest Island (data from Bunn 1980). No. species = 1.55($Log_{10}$ Area) + 5.89, $R^2$ = 0.36, n = 48, p < 0.00001.*

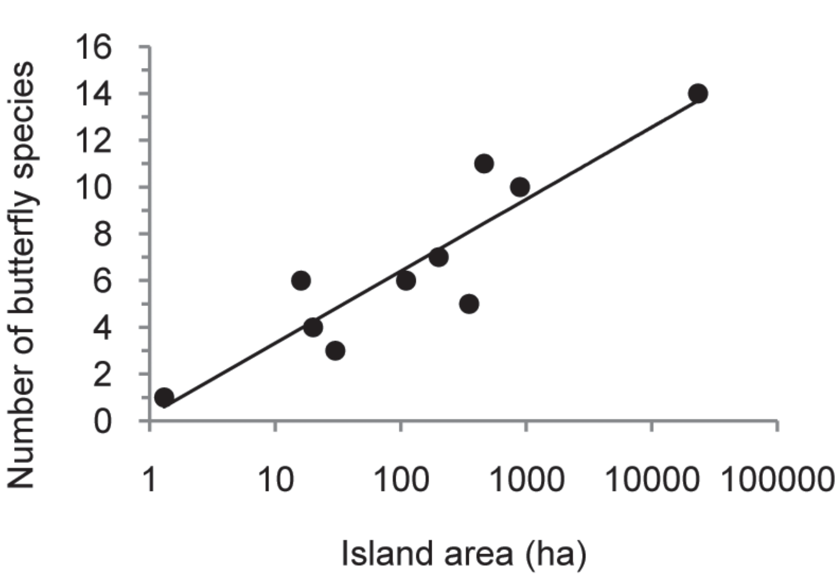
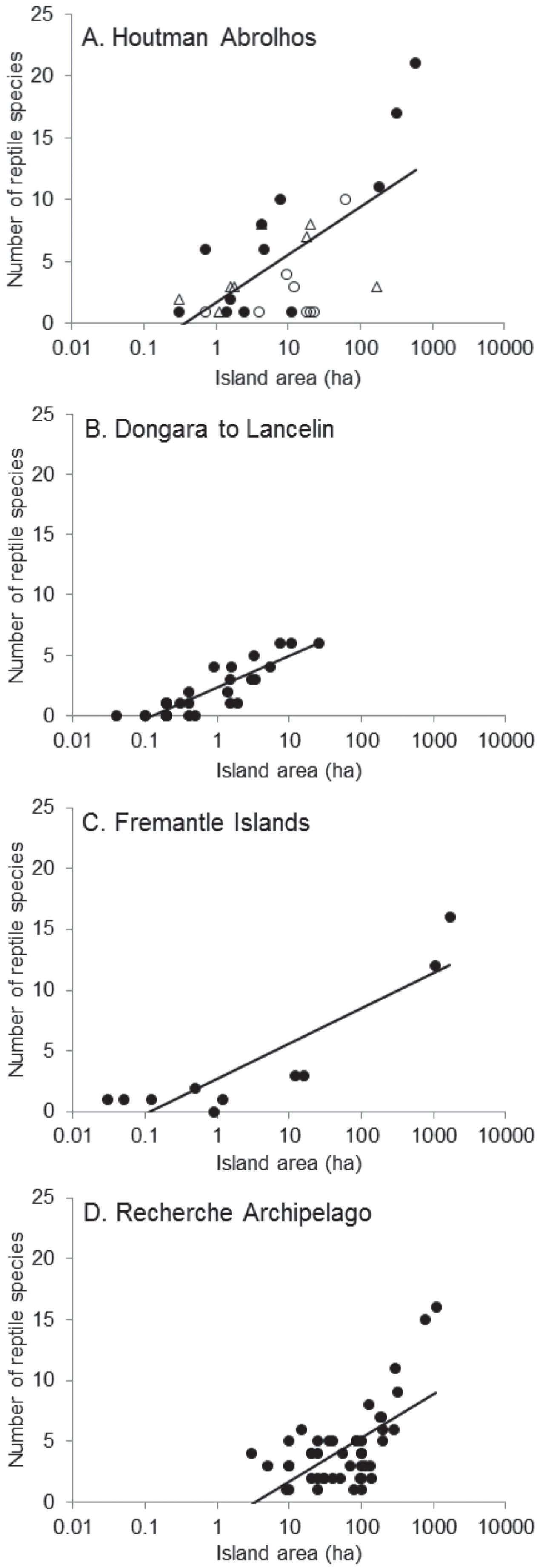



*Figure 14. The number of butterfly species versus island area for Barrow and adjacent islands (data from Smithers & Butler 1983). No. species = 3.08($Log_{10}$ Area) + 0.25, $R^2$ = 0.82, n = 10, p < 0.0003.*




*lateralis*) were collected for close study from North Pearson Island (c. 140 ha) and were accidently released on South Pearson Island (which is isolated by a rock-filled channel from North Pearson Island). Within 30 years this founder group had increased to 150 animals and still persists on this c. 70 ha island (T Robinson et al. 1996). In contrast, an attempt to establish tammars on West Island (10 ha, South Australia) failed (T Robinson et al. 1996), indicating that 10 ha is below the threshold area.

Data presented by Gillham (1961c) indicate that the species richness of plants on eight islands adjacent to Wilson's Promontory, Victoria does not increase with island area. The same result applies when only native plant species are considered. On the smaller islands in the Furneaux Group, Bass Strait, the correlation between species richness of plants and area is weak (S Harris et al. 2001). Species richness of plants on cays on the Great Barrier Reef, Queensland is weakly associated with area (Batianoff et al. 2009a; Buckley 1981; Stoddart & Fosberg 1991). Cays with limited extent of beach are likely to receive fewer propagules than are cays with long beaches (Buckley & Knedihans 1986).

For the frog fauna of the five largest sand islands in south-eastern Queensland, area is a weak predictor of species richness compared with the extent of wetland habitat present (Hines & Meyer 2011). In contrast, island area explained much of the variation in species richness of plants, reptiles, birds and mammals on 24 Kimberley islands across a range of areas from 300–18,900 ha (LA Gibson 2014). However, other factors also made significant contributions: Rainfall (plants, land snails), distance (plants, non-volant mammals), and extent of rock scree (plants).

Islands occupied by Indigenous people have usually experienced local extinctions of species (Holdaway et al. 2001; Steadman 2006). If these Holocene fossil species are not included in species–area comparisons, the equations developed are misleading and biased.

In conclusion, we agree with comments that island 'ecology starts after (and not with) the computation of species–area curves'; that 'the actual biological mechanisms producing the species–area relationship are the main issue, not the regression itself'; and that the species–area graph should be a 'starting point for future studies aimed at uncovering the biological, often

*Figure 15. The number of reptile species versus island area. A. Islands in the Houtman Abrolhos: Easter Group (●), Pelsaert Group (○) and Wallabi Group (△); data from How et al. 2004. No. species = 3.89 ($Log_{10}$ Area) + 1.68, $R^2 = 0.44$, $n = 28$, $p < 0.0002$. Additional captures included (best available information). B. Islands between Dongara and Lancelin; data from Ford 1963. No. species = 2.61($Log_{10}$ Area) + 2.32, $R^2 = 0.77$, $n = 30$, $p < 0.0001$. C. Islands between Fremantle and Becher Point; data from Coster 1977; Brooker et al. 1996. No. species = 2.89($Log_{10}$ Area) + 2.69, $R^2 = 0.79$, $n = 10$, $p < 0.001$. D. Islands in Archipelago of the Recherche (data from LA Smith & Johnstone 1996). No. species = 3.56($Log_{10}$ Area) – 1.81, $R^2 = 0.37$, $n = 47$, $p < 0.0001$.*

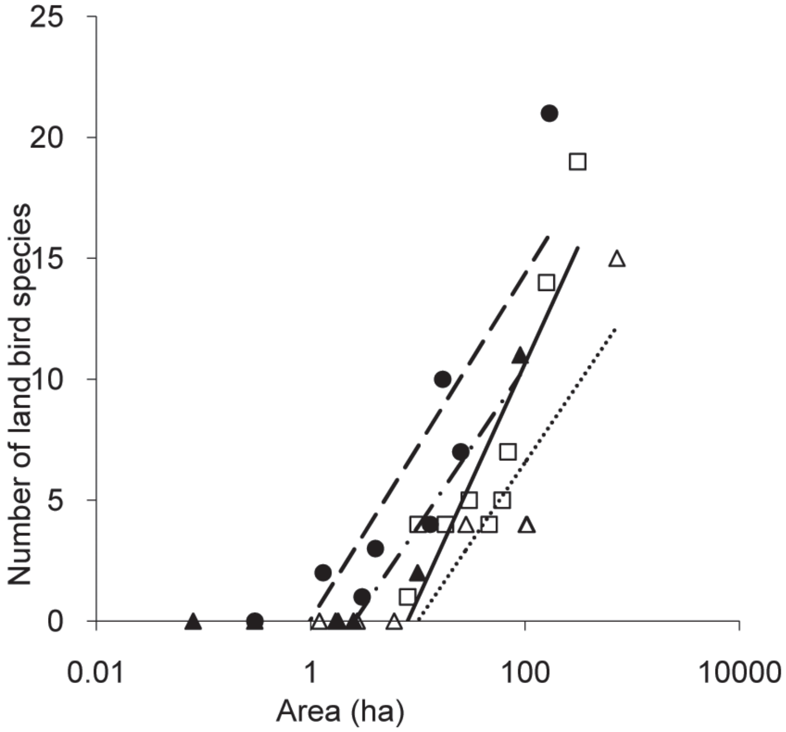



*Figure. 16. Joint influence of exposure and area on landbird species richness near Albany (after Abbott 1980e): exposed mainland sites (□, solid line); sheltered mainland sites (●, dashed line); exposed islands (△, dotted line); and sheltered islands (▲, dot-dash line). Mainland exposed sites: no. species = 9.72($Log_{10}$ Area) – 8.77, $R^2$ = 0.79, n = 9, p < 0.002. Mainland sheltered sites: no. species = 7.15($Log_{10}$ Area) + 0.07, $R^2$ = 0.77, n = 8, p < 0.005. Exposed islands: no. species = 6.56($Log_{10}$ Area) – 6.54, $R^2$ = 0.80, n = 5, p < 0.05. Sheltered islands: no. species = 6.59($Log_{10}$ Area) – 2.68, $R^2$ = 0.94, n = 4, p < 0.05.*

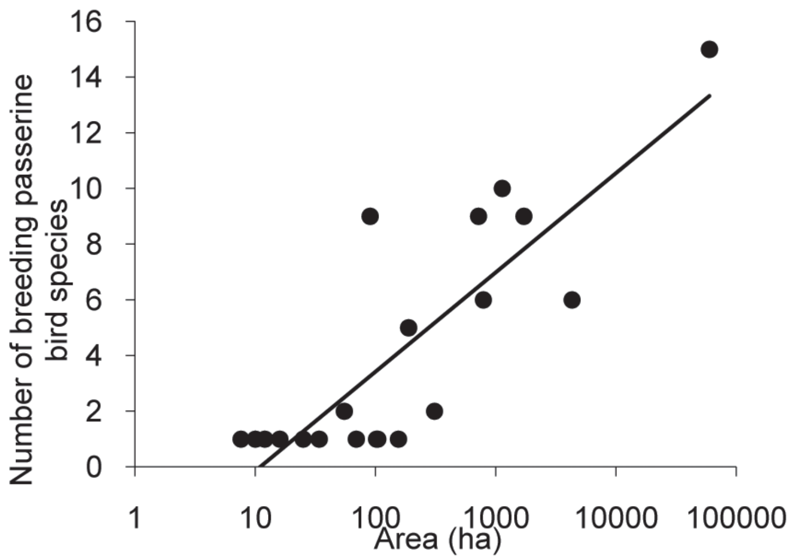



*Figure.17. The number of breeding passerine bird species versus island area for WA islands studied by Abbott (1978). No. species = 3.57($Log_{10}$ Area) – 3.70, $R^2$ = 0.69, n = 20, p < 0.00001.*

population-level processes behind the pattern observed' (Järvinen & Ranta 1987: 251). In the ensuing decades few of the new numerical techniques that have become available have been applied to (real) islands. Newer approaches have introduced new problems with unrealistic assumptions (e.g. Chisholm et al. 2016).

## Presence of breeding seals, seabirds, and turtles

On many islands seabirds provide a significant linkage between the land and the surrounding sea. Seabirds have been described as chemical and physical engineers because they affect soil properties, vegetation and the composition of island floras (Ellis 2005). On the island of St Kilda (Scotland), seabird colonies are dominated by plant species usually found on arable land (Petch 1933). This change of vegetation is attributed to the elevated input of nitrogen from the seabirds. It is well known that dense populations of seabirds can trample vegetation, burrow in soil, and transfer nutrients from the ocean to island soils (Davis et al. 1938; Norman 1967; Warham 1996; Zed et al. 2006). Indeed, the excreta and remains of seabirds and seals provide ‘a richly nitrogenous top dressing’ of parts of islands (McVean 1961). Areas made bare by seabirds trampling vegetation and soil also have less organic matter and water present in the soil (Goodman & Gillham 1954).

Physical disturbance and increased soil fertility also alter plant ecology, particularly floristic and structural components (Gillham 1956, 1960, 1961a, 1962; Sobey & Kenworthy 1979; D Walsh et al. 1997), and animal ecology (Soulé 1966; Sale & Arnould 2012). More than 300 WA islands support breeding populations of one to 25 seabird species (AA Burbidge et al. 1996; Johnstone & Storr 1998). Some populations are very large (tens of thousands of pairs; AA Burbidge et al. 1996) and some islands are used for breeding by many seabird species (e.g. 17 species on Pelsaert Island; AA Burbidge & Fuller 1989). Burrowing seabirds are usually only present where soil is of sufficient depth, although cover provided by dense vegetation or rock ledges can compensate (SG Lane 1975a, 1975b, 1975c, 1975d, 1976a, 1976b, 1976c). Dense vegetation is usually unsuitable for surface-nesting species such as gulls, terns and cormorants.

The most striking characteristic of small islands or parts of larger islands in WA supporting breeding seabirds is the bright green colour of the vegetation. This is induced by the manuring effect of seabird colonies in shaping the dominance of various native plant species, enhancing the chlorophyll content of leaf tissue, the prominence of exotic annual plant species, or both. It is for this reason that there are nine islands named ‘Green’ (I Murray & Hercock 2008; I Abbott unpubl.).

Changes in the chemical properties of soil on WA islands and adjacent mainland have attracted little botanical attention. pH appears to vary little but N, P and K of the soil increase, particularly on those islands with breeding seabirds (Rippey et al. 2002b; Wolfe et al. 2004). Comparison of physical and chemical properties of soil collected from a colony of burrowing shearwaters and from adjacent vegetation on Rottnest Island showed that seabirds cause drying of the soil and increase its bulk density, the concentration of N and P, and pH, but reduce soil C (Bancroft et al. 2005a).

The importance of seabirds in transferring nutrients from sea to land is particularly evident on unvegetated cays of the Great Barrier Reef, Queensland. Species of insects scavenging on carrion aid this process (Heatwole 1971). Cays in the southern section of the Great Barrier Reef with the largest populations of silver gulls also have the largest number of plant species dispersed by birds (Heatwole & Walker 1989). Many of these plant species are introduced to Australia.

The far-reaching and unexpected effects of sea-to-land nutrient transport by seabirds only becomes clear when the process becomes disrupted. Islands with rats present have reduced populations of seabirds, soil fertility, and soil fauna (Fukami et al. 2006). Islands with foxes have lower density of seabirds, reduced soil fertility, less phytomass, and altered vegetation relative to islands without foxes (Croll et al. 2005).

On small islands in the Isles of Scilly near Cornwall UK, large colonies of nesting gulls are thought to put spatial and predation pressure on the potential landbird community (Reed 1984).

Two pinniped species breed on WA islands (Abbott 1979), but only one of these (Australian sea lion *Neophoca cinerea*) hauls out onto vegetated parts of islands, often as far as 300 m from the shoreline (F Péron in Cornell 2006; Abbott 1979). This species has been recorded breeding on 27 WA islands and hauling out on another six islands (Gales et al. 1994). Sea lions trample vegetation or modify vegetation structure by tunnelling beneath 2-m-tall bushes of *Nitraria billardierei* (Gillham 1961a; J Ford 1965; Johnstone 1978; Gales et al. 1992, 1994). The other species, the New Zealand fur seal (*Arctophoca australis forsteri*), confines itself to rocks and boulders close to shore (Abbott 1979; Shaughnessy et al. 1994) and therefore has no material impact on the terrestrial ecology of islands.

The occurrence of seabird colonies on islands usually results in a greater abundance of various plant species (Goldsmith 1973; Abbott 1980d). Small mammal species, such as the dibbler in WA and swamp antechinus (*Antechinus minimus*) in Tasmania, occur at very high densities on islands as a result of the transfer of nutrients from sea to land by breeding seabirds (Wolfe et al. 2004; Sale et al. 2006). However, J Ford (1963) attributed low species richness of reptiles on some islands to the activity of sea lions and seabirds, particularly on small islands. Arthropods are more abundant on islands with seabird colonies than on those without (Polis & Hurd 1996; Sánchez-Piñero & Polis 2000).

In contrast to seabirds and seals, the four species of turtle that breed in WA (green turtle *Chelonia mydas*, hawksbill turtle *Eretmochelys imbricata*, loggerhead turtle *Caretta caretta* and flatback turtle *Natator depressus*) lay their eggs in sandy beaches on tropical and subtropical islands south to Dirk Hartog Island (e.g. Waayers 2014). They therefore have less influence on the terrestrial ecology of these islands, except that hatchling turtles attract the attention of predators, and egg-laying turtles disturb vegetation (cf. Rogers 1989). Nonetheless, the quantities of nutrients transported by turtles are not insignificant (Bouchard & Bjorndal 2000) but are more localised on islands than are those of seabirds. Nesting turtles also destroy seedlings of drift seed plants, as noted on cays in the Coral Sea (Batianoff et al. 2009b).

## Presence of Indigenous people

*Homo sapiens* did not begin to colonise islands until after c. 70 ka BP, when humans expanded their geographical range outside Africa. Australia was colonised by c. 40–50 ka BP (RH Pearce & Barbetti 1982; O’Connor 1995; Turney et al. 2001), and most of the islands of the Pacific Ocean by c. 1200 CE. The concept of Indigenous people living on tropical islands with minimal impact on the environment was an enduring legacy of the Enlightenment (Hames 2007). However, recent evidence shows that colonisation of previously uninhabited islands by people had substantial impacts on their ecology (Grayson 2001; Curnutt & Pimm 2001). For example, Rapa Nui (Easter Island) had been deforested by the Pacific rat (*Rattus exulans*), introduced by the Polynesian settlers, and by fire and felling before its discovery by Europeans in 1722 (Hunt 2006; Hunt & Lipo 2009). The introduction of this rat in c. 1200 CE led to failure of the principal tree species to regenerate (Hunt & Lipo 2009). Such widespread habitat loss must have caused the extinction of many species of plants and associated species of invertebrates and birds.

Aborigines visiting Swan Island (Bass Strait) in 1830 'slew a great number' of little penguins (*Eudyptula minor*) for food. According to the European present, 'Numbers were killed wantonly', thus stimulating a surprising intervention by this European (Plomley 1966: 280). Great numbers of eggs of the mutton bird (*Puffinus tenuirostris*; short-tailed shearwater) were also collected from islands for food (Plomley 1966). Small mammals on Swan Island were also eaten (Plomley 1966).

Anthropogenic burning of island habitats was a necessary part of the acquisition of edible resources (Grayson 2001). Hunting or use of fire also reduces species diversity, well illustrated by Polynesians on the numerous islands in the Pacific Ocean (Pimm et al. 1995; Steadman 2006), the Māori in New Zealand (Worthy & Holdaway 2002), and Australian Aborigines (Abbott 1980c). This fire regime will differ from that caused by lightning strikes alone, and may alter the extent of particular plant communities. Edible species may be reduced in numbers (often to local extinction) through hunting or harvesting. Thus, the landscapes of those WA islands occupied or visited by Aborigines are artefacts in that they represent the imposition of cultural factors on underlying natural factors.

Indigenous peoples have also deliberately introduced mammals and unintentionally introduced invertebrates to islands occupied by them in both prehistoric and historic times (Grayson 2001, Heinsohn 2003). In contrast, Aboriginal people have had much less impact by this means, with the dingo likely to be the only animal species taken to islands by watercraft.

Aboriginal people also spent time on some islands conducting other cultural activities, including rock art (paintings and petroglyphs). Prolific evidence of this persists on Naturalists, Bigge, West Montalivet and Prudhoe islands in the Bonaparte Archipelago (Crawford 1968; Coate 2008a), Depuch Island (Crawford 1964), and islands in the Dampier Archipelago (Vinnicombe 2002, Donaldson 2009). Midden sites and artefacts occur on Dixon Island (K Palmer 1975).

Given that Aborigines have been present in south-west WA for at least 40 ka, it can reasonably be assumed that the entire coastline was rapidly occupied, perhaps in 5 ka. At the time of European contact in WA (1826–1886), 45 tribes (language groups) occurred along the coastline (Tindale 1974). There is also abundant evidence from dated artefacts of Aboriginal presence on soon-to-be-isolated 'islands' (Veth 1993; Bowdler 1995b; Dortch 1991; Marwick 2002). Therefore, these islands were either abandoned by humans while they could or populations that chose to remain eventually became extinct (Mulvaney & Kamminga 1999).

Between Shark Bay and the South Australian border, Aboriginal people belonging to the 24 tribes present along the coast did not access islands, at least in the period 1697–1829, except where water was shallow (below waist height) or flats were exposed at neap tides. There are two reasons for this: Inability to swim, and lack of watercraft. The evidence for this derives from observations by early visitors and colonists.

Aborigines living near New Norcia, Perth and Bunbury could not swim, except by dog paddling short distances (*The Perth Gazette* 30.3.1833: 51; derboween, *The Perth Gazette* 13.4.1833: 59; kowunyung, *The Perth Gazette* 14.9.1839: 148; Grey 1841 Vol. 2: 275-276, 278; kowanyang, GF Moore 1842; Berryman 2002: 241; JMR Cameron 2006: 163, 254, 285; Roth 1902; Stormon 1977: 129). In 1836 Henry Bunbury recorded Aborigines wading in Lake Preston 'up to their necks' but reported none swimming (JMR Cameron and Barnes 2014: 160). None of the early accounts of Albany allude to Aboriginal swimming (Flinders 1814: 66; Nind 1831: 32; Mulvaney & Green 1992: 248, 286; TB Wilson 1835: 249, 270, 283; McIntyre and Dobson 2011). An 1859 account from Nornalup Inlet noted Aborigines crossing water up to their necks (*Albany Advertiser* 3.3.1920: 4). Aborigines in south-west WA were evidently taught to swim by Europeans (e.g. Migo in Roe 20.11.1835, Hercock 2014). In contrast, Aborigines at Geraldton, between Cape Farquhar and North West Cape, at Nickol Bay, and along the Kimberley coast could swim (*The Perth Gazette* 13.2.1852: 5; *The Inquirer and Commercial News* 15.7.1868: 3; Coghlan 1885; *kiar'ree*, Durlacher 1900; WL Owen 1936: 45; Melville-Jones 2009: 57, 93, 105, 115, 121; Vigilante et al. 2013).

This absence of Aboriginal watercraft from south-west WA is well documented (The Perth Gazette 5 November 1836: 793; GF Moore 1842; NW Thomas 1905, RH Mathews 1907; DS Davidson 1935; Berryman 2002; McIntyre & Dobson 2011). As noted by Flinders (1814: 66), 'None of the small islands had been visited [by Aborigines], no canoes were seen, nor was any tree found in the woods from which the bark had been taken [by Aborigines] for making one.' No smoke was recorded issuing from islands, nor was freshly burnt ground reported on any of the four islands (Seal, Mondrain, Middle, Goose) visited.

From a global perspective, this absence of Indigenous people from islands is highly unusual. It is shared with the marine islands of South Australia, Victoria, Bass Strait, north-eastern Tasmania, and numerous remote islands in the Pacific, Southern, Indian and Atlantic Oceans. The larger islands in these oceans known to have been uninhabited before European discovery (Wace 1978) include: Juan Fernández, Alejandro Selkirk, Robinson Crusoe, Guadalupe, Socorro, Clarión, San Benedicto, Cocos, Galápagos, Midway, Raoul, Lord Howe, Norfolk (Pacific Ocean); Prince Edward, Marion, Kerguelen, Crozet, Heard, Macquarie, Campbell, Auckland, Antipodes, South Shetland, South Orkney, South Sandwich (Southern Ocean); Christmas, Cocos-Keeling, Seychelles, Diego Garcia, Aldabra, Mauritius, Réunion, Rodrigues (Indian Ocean); and Bermuda, Bahamas, Azores, Madeira, Cape Verde, St Helena, São Tome, Príncipe, Annobón, Fernando de Neronha, Tristan da Cunha, Gough, Falkland, South Georgia (Atlantic Ocean).These islands were therefore the only places on Earth where humans had no impact on the biota. When discovered by Europeans the vegetation and populations of the conspicuous species were in an obvious state of acheiropoieta. Clearly these islands (including those of south-west WA) provide an important benchmark, though few remain pristine.

The consequential long absence of anthropogenic fire on islands of south-west WA has favoured plant species capable of regenerating from seed over resprouters, evidenced by Garden Island (49% versus 25–36% on the adjacent mainland; Baird 1958; Bell et al. 1987; B Keighery & Keighery 1995), Middle Island (90%; Hopkins & Harvey 1989), and Carnac Island (72%; Abbott et al. 2000, G Keighery pers. comm.).

Although log rafts are known to have been in use in the 1850–1870s by four coastal tribes present between the mouth of the Gascoyne River and North West Cape (The Perth Gazette 20 June 1851; Austin 1855; DS Davidson 1935; Bowdler 1995a; Melville-Jones 2009), these records are all close inshore. Although FT Gregory (1858-1859: 43) recorded Aborigines wading to Babbage Island (at the mouth of the Gascoyne River) in May 1858, he did not record rafts when he traversed the coast north for c. 10 km.

In 1875 the castaway Stefano Skurla noted many tree trunks floating on the sea north of Cape Cuvier after a storm (Melville-Jones 2009). NW Thomas (1905) suggested that the logs found at the mouth of the Gascoyne River had been washed down this river from inland. There are no records of Aboriginal presence on islands in Shark Bay during the period 1697–1858 (F Péron in Cornell 2006; King 1827; Grey 1841; Stokes 1846; Caldwell 1934; Robert 1972). Claims of smoke on Dirk Hartog Island (Bowdler 1990), suggestive of Aboriginal presence, are inconsistent with the weight of evidence available. The claim by Tindale (1974: 254) and repeated by Bowdler (1995b), that these islands were accessed via watercraft, is therefore mistaken.

Nor were there records of Aboriginal presence in 1840 on Barrow Island and the Montebello Islands (Stokes 1846 Vol. 2). Islands in the Bonaparte and Buccaneer Archipelagoes (i.e. from Cape Talbot to Cape Leveque) were visited by raft (Stokes 1846 Vol. 1; Chief Protector 1909a; Basedow 1925), and islands in the Dampier Archipelago (from Point Samson to Cape Preston) were visited by sitting astride a log (King 1827; FT Gregory 1862; Durlacher 1900; Tindale 1974; K Palmer 1975). Despite no watercraft being observed, signs of Aboriginal presence (camp fires, huts) were found in 1801 and 1840 on Depuch Island, which could be walked to at low water spring tide (F Péron in Cornell 2006; Wickham 1842; Stokes 1846 Vol. 2; Ride 1964a). Lacrosse Island was reported to be ablaze with Aboriginal fires in October 1884 (Government Gazette 12 March 1885 supplement: 126).

Rafts, not canoes, were in use along the coast of the Kimberley region, except for Cambridge Gulf (Coghlan 1885). Detailed descriptions and photographs show these to be remarkably sturdy, (J Martin 1865; Love 1917; Basedow 1918, 1925), and capable of conveying two Aborigines and two dogs (*Canis familiaris*) together (The Western Mail Christmas Number 24 December1919: 23, 42; EJ Stuart 1923). Aborigines in the Kimberley could raft offshore at least as far as 10 km, as evidenced by signs of their visits to Parry and Baudin islands (Bassett-Smith 1894) and to Sir George Moore, Red, Long, Osborn, Bigge and Montgomery islands (EJ Stuart 1923; Beard et al. 1984), and smoke on islands around Sunday Island (R Pratt & Millington 1986). They were capable of travelling even farther offshore, evidenced by smoke seen on the Champagny Islands in 1906 (R Pratt & Millington 1986). Indeed, it can be assumed that all islands of the Kimberley, up to 50 km offshore, were accessed by Aborigines, either by raft or by swimming (Vigilante et al. 2013). The length of occupation depended on the availability of fresh water (Vigilante et al. 2013).

Islands of WA show a strong influence of Aboriginal presence (either as visitors or semi-permanent residents) on the number of macropodoid species present in relation to island area (Fig. 18), with more species on inaccessible islands than on accessible islands of the same area. Furthermore, of the 21 islands accessible to Aborigines and known to possess at least one macropodoid species, the median area is 1970 ha, and the smallest island is 300 ha. This is in marked contrast to the 21 islands not accessible to Aboriginal people, where median area is 650 ha and smallest area is 70 ha. There is also a remarkable difference in the smallest island with three species present, 11,800 ha (accessible islands) versus 4200 ha (inaccessible islands). A complementary analysis is to compare the proportion of WA islands with an area of 100 ha or more relative to their accessibility to Aboriginal people. The proportion of islands with at least one macropodoid species present is 50% for islands inaccessible to Aborigines versus 12% for islands that were accessible. It is likely that dingoes left behind by visiting Aborigines were responsible for the local extinctions, not hunting per se.

Another major impact of Aboriginal presence on islands was the seasonal harvesting of seabirds and their eggs, and turtles and their eggs, as on islands in the Dampier Archipelago and the Kimberley region (KD Morris 1989a; Vigilante et al. 2013; WABN 1943–2016 No. 101: 12-13). The key ecological difference, however, between islands not visited and those visited is the lack of anthropogenic fire for many centuries on the former. On several of the larger inaccessible islands long-term exclusion of fire has resulted in the development of small areas of tall forest lacking any undergrowth (Weston 1985). The predominance of seed-regenerating species

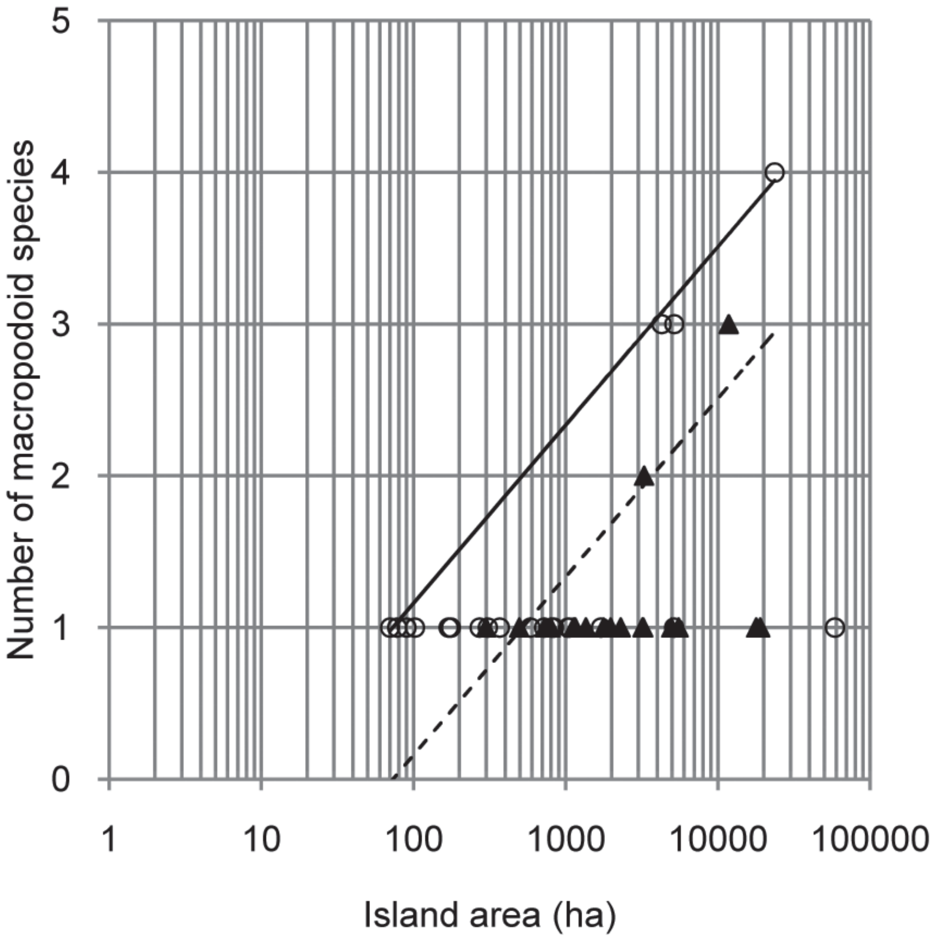



*Figure. 18. The number of macropodoid species versus island area for WA islands with Aboriginal access (▲) and without Aboriginal access (○). Data from Abbott 1980c; LA Gibson & McKenzie 2012b. The minimum island area required to sustain a given number of species is calculated as the regression of number of species versus area for the smallest islands carrying a given number of species (no. species = 1.17($Log_{10}$ Smallest Area) – 1.19, $R^2 = 0.9981$, $n = 3$, $p < 0.03$). This is assumed to be a threshold and is delineated by the solid line. If these islands carried one less species the dotted line would apply as the threshold. Thus, island data points to the left of the dotted line carry the expected number of species and data points to the right of the dotted line carry less than the expected number of species. Regression equation for all islands: no. species = 0.52($Log_{10}$ Area) – 0.36, $R^2 = 0.24$, $n = 41$, $p < 0.005$. Deltaic islands excluded.*

of plants over resprouting species on islands of the southern coast of WA may be linked to the long absence of anthropogenic fire (Barrett et al. 2009).

As Aboriginal culture has become more westernised, islands of the north Kimberley region have been less visited and thus burnt less frequently. This may have favoured some species and disadvantaged others. Indeed, Beard et al. (1984) speculated that fire-sensitive patches of rainforest have responded by colonising eucalypt savannah since the 1940s. Bird species dependent on rainforest should have become more abundant and the increased area of rainforest should allow any absent species to colonise and establish on these islands. On Marchinbar, a large island visited by Aborigines near Arnhem Land (Northern Territory), there is an unexpectedly large number of mammal species possibly linked with increased habitat heterogeneity resulting from an intricate scale of burning by Aborigines (Woinarski et al. 1999b).

It is very likely that most of the small islands (<5 ha) around south-west WA have remained free of fire for at least 7 ka. This is a consequence of lack of Aboriginal visits, the deposition of salt-laden sea spray (which appears to act as a fire retardant for some plant species; Hart 1914; Department of Defence 1980), the low amount of fuel (dead plant biomass) present, and the presence of much rock and sparseness of vegetation (which should limit the spread of any ignition caused by lightning strike).

## Activities of Europeans

Technological change has increased the capability of Europeans to modify island landscapes (LR Walker & Bellingham 2011). In Britain, the introduction of cereal growing led to deforestation. During the Bronze Age, trees were felled to make charcoal to melt metals and alloys. The Iron Age accelerated the rate of deforestation.

Following the development of large watercraft, Europeans invaded their first islands outside Europe (Canary Islands). During the 1400s CE the Indigenous people of these islands were conquered through violence and disease, and European animals and plants were introduced (Crosby 1984). The hunting of game and the introduction of rats and cats seems to have first entered the consciousness of the literate public with publication of 'The Life and Strange Surprizing Adventures of Robinson Crusoe', a fictitious (but attentive to fact) journal based on the title character's residence of 28 years on 'Despair' island after being shipwrecked (Defoe 1719).

Humans with advanced technology subsequently have interfered with many islands, ultimately with profoundly destabilising consequences that have resulted in species extinctions (e.g. Pimm et al. 1995). Human habitation on islands for only short periods can have significant long-term consequences (Holdgate & Wace 1961; Sachet 1963). When disturbance involves only the living components of island ecosystems, recovery tends to be rapid because of the high reproductive potential of most species. In contrast, disturbance that alters the physical environment or involves the introduction of exotic species often results in permanent change (Fosberg 1963).

Intrusions and imprints have included the following impacts, some of which result from deliberate actions whereas others are unintentional:

- Physical destruction (Table 11; Stoddart 1968; Daley & Griggs 2006). The landscape may be transformed by extraction of iron ore (Cockatoo and Koolan islands in the Kimberley region of WA), removal of guano (islands in Houtman Abrolhos and Great Barrier Reef), military usage (Phillip Rock), and infrastructure (Slope Island, East Intercourse Island). The area may also be reduced (Great Barrier Reef cays; Flood & Heatwole 1986).
- Habitat destruction with the use of iron or steel tools such as axes and machinery. This is most visible on densely and long-settled islands, for example Singapore (Corlett 1992), Manhattan, Hong Kong, Malta, Britain and Ireland. It is also evident on some Australian islands, including North Stradbroke Island (Queensland; G Moore 2011), King Island (Tasmania; DPIPWE 2012), Althorpe Island (South Australia; Radford 2005), Flinders Island (South Australia; Laurence et al. 2008), Barrow Island (WA; AA Burbidge & Main 1971), and the islands of Sydney Harbour (Wagner 1971; S Davies 1984; Frame 1990; MS Clark & Clark 2000). Fosberg (1983) rated this factor as by far the most frequent on oceanic islands.
- Creation of new habitats, such as the planting of woods and gardens and the establishment of cultivated land, favours so-called synanthropic species and adventive species (plant species that have reached islands unassisted by humans). Such changes have resulted in many bird species breeding on islands around Scotland (Lack 1942; Reed et al. 1983) and on the larger of the Isles of Scilly (Reed 1984), and the establishment of three landbird species on Kangaroo Island (South Australia; HA Ford 2006). An example from WA is the successful colonisation of the bird species western gerygone on Rottnest Island following the establishment of plantations of *Eucalyptus gomphocephala* (Storr 1965c).
- Ongoing introduction and spread of exotic (so-called anthropochorous) species such as weeds, Asian house gecko (*Hemidactylus frenatus*), ants, rats, rabbits (*Oryctolagus cuniculus*), goats (*Capra hircus*), cattle (*Bos Taurus*), pigs (*Sus scrofa*), dogs and cats (Ridley n.d.; RP Cooper 1948; Roberts 1957; Gillham 1962; Duffey 1964; Plomley 1966; Norman 1971a; Fatchen 1982; Møller 1983; Chaloupka & Domm 1986; Lebel 1991; G Keighery 1993; NL McKenzie et al. 1995; GIEAC 1998; Fensham & Cowie 1998; Longman et al. 2000; Long 2003; Priddel et al. 2000, 2011; AC Robinson et al. 2008b; Lach & Hooper-Bùi 2010; Callan et al. 2011; Majer et al. 2013; R Palmer et al. 2013b), whether through deliberate release or accident (e.g. shipwreck; Montague 1914; Migaud 2011).

  James Cook was very liberal in the distribution of European plants and animals in the 1770s on islands in the Pacific Ocean (Hoare 1982), as was James Ross in the 1840s on various southern islands (Ross 1847). It is known that whaling ships infested with rats visited King George Sound as early as 1800 (Dickson 2006). In 1841 a French whaling ship used an unidentified island in Rossiter Bay to grow vegetables and keep sheep, pigs, and giant tortoises (Eyre 1845 Vol. 2). Bird and mammal species introduced on islands are well documented from a global perspective by Long (1981, 2003). Species totally dependent on humans (introduced to islands by humans and persisting only in human-made habitats) have been termed serf colonisers (Enckell et al. 1987).
- Release on the mainland of animals, such as the red fox, rock dove (*Columba livia*) and cane toad (*Rhinella marina*), which have then spread naturally to accessible islands (Sandland 1931; B Williams in Storr MSb; Gillham 1962; J Ford 1965; Norman 1971b; Serventy 1972; GIEAC 1997, 1998; Rippey et al. 1998; JE Kinnear et al. 2002; Shine 2010; Ziembicki et al. 2015). In the Gulf of Carpentaria, cane toads have spread to islands by means of freshwater flooding from the mainland. It is expected that the same will eventuate in the Kimberley region; to date, cane toads have been reported only on Adolphus Island (Anon. 2014).
- Human predation of sea lions and seabirds (Ling 1999a, 1999b; 2002; Plomley 1966), with inevitable indirect impacts on soil fertility and plant ecology.
- Increased provisioning of food scraps and discarded bait (GC Smith 1992), leading to larger

populations of silver gulls, as for example on Rottnest Island (Rottnest Island Management Planning Group 1985a), Carnac Island (Dunlop & Storr 1981), Seal Island in Shoalwater Bay (Abbott 1977d), Penguin Island (Dunlop 1988), Houtman Abrolhos (Surman & Nicholson 2009), Barrow Island (Sedgwick 1978) and Lacepede Islands (WABN 1943–2016 No. 103: 17). There are several consequences, including detrimental impact on other breeding seabirds; increased risk of introduction of weed species to breeding islands; and changes in soil nutrients and distribution of plant and other species (Brown & Paczkowska 2016; Gillham 1960; Garcia et al. 2002; Vidal et al. 1998, 2000; Orgeas et al. 2003).

- Summer wildfire caused by Europeans can alter successional dynamics of plant communities, usually in combination with browsing by herbivores (Shield 1959; Hesp et al. 1983).
- Killing of fauna. Some species are persecuted deliberately because of their destructive activities (e.g. eagles; Lack 1942; Austin & Kuroda 1953), as food (Plomley 1966), for their skins (e.g., wallabies; Plomley 1966), or for their feathers (Plomley 1966). Sometimes pleasure was the reason, as when 'splendid shooting' was advertised for Rottnest Island (Joske et al. 1997). The killing of seals for their fur was so severe in WA that it took more than 140 years for recolonisation of former haul-out sites on islands (Abbott 1979). In 2007, fur seals were recorded for the first time in more than 200 years on Rottnest Island, although breeding has not yet been substantiated (H Shortland-Jones pers. comm.). At Houtman Abrolhos, populations of sea lions have not yet regained the abundance reported in 1727 and the 1840s (Abbott 1979; R Campbell 2005; GF Moore in The Perth Gazette 9 February 1840: 23–24; The Geraldton Guardian 27 December 1996: 5). The presence of sealers along the southern coast of WA was first recorded in 1803 (Cornell 1974, 2003).
- Benign human presence (e.g. tourism, recreation and scientific study) may result in frequent disturbance of nesting seabirds (e.g. Storr 1964a), including trampling of burrows and causing surface-nesting species to leave the nest and thereby allow predators such as King's skinks and silver gulls to prey on seabird eggs exposed when the adults take flight (Nicholls 1974; WABN 1943–2016 No. 103: 17). The quest for 'unspoiled' places accelerated by the demands of mass tourism is ongoing (Wace 1978). A glance at the travel pages of any current newspaper or casual study of island tourism websites demonstrates how easily previously remote islands can now be reached by cruise ships.
- Disturbance by mechanical means results in slower recovery of vegetation than disturbance caused by fire (AA Burbidge & Main 1971).
- Grazing by introduced livestock may improve the habitat of some native species, as has been the case with the presence of pasture grasses, grazing by goats, and the occurrence of the largest flock of Cape Barren geese seen in the Archipelago of the Recherche (DF Dorward 26 March 1973, letter on Department of Fisheries and Fauna file; Dorward 1977). Halse et al. (1995) also recorded the largest flock on Cull Island.
- Deployment of poison baits to eradicate introduced mammals. The earliest instance of the compound 1080 being distributed on an island occurred in 1951 on Amchitka Island (Kenyon 1961). Strychnine pellets were dropped from the air. Dogs, cats and foxes, but not the rats, were eliminated. One wonders, however, about the impact of these poisons on the indigenous fauna of this island. On WA islands, 1080 and other poisons have been used responsibly and successfully to eliminate rabbits, rats, foxes and cats (Table 12). The eradication of mammalian species introduced to islands usually improves the conservation status of native species of mammals, seabirds, landbirds and other biota present (HP Jones et al. 2016, Newman 1994).

Information for WA islands is summarised in Table 11. Probably the most obvious WA examples of the impact of European settlers are from Rottnest Island, on which there has been extensive loss of tree cover since 1838 (Pen & Green 1983), and Faure and Dirk Hartog islands, the only two island pastoral stations in WA, on which sheep and/or goat grazing occurred for more than 100 years and was only terminated as recently as 1999 and 2009 respectively (Fraser 1876; DEC 2011; Graham-Taylor 2012a). On Dirk Hartog Island, there were c. 26,000 sheep in the 1920s, and sheep were kept during the 1930s at a density of one sheep/6 ha (Ride & Tyndale-Biscoe 1962). Sheep were kept on West Lewis from 1890 to 1900 and on Bernier Island at least in 1906, but no further information is available (Ride & Tyndale-Biscoe 1962; DCLM 1990). Grazing by (feral) goats on Bernier Island has caused extensive erosion and sand drift (Royce 1962).

The assessment by J Martin (in Anon. 1864: 4; also comments by FK Panter) that Augustus, Byam Martin and Heywood islands (Kimberley region) contain c. 80,000 acres of the 'richest pastoral land…capable of carrying 80,000 sheep' is without foundation, and happily did not lead to any grazing disturbance on these islands.

Few WA islands, however, have experienced the level of degradation that has resulted from a long period of unregulated settler activity on many of the islands in Bass Strait, Tasmania (S Harris et al. 2001; DPIPWE 2012). The clearing of vegetation on islands for residential settlement or open-cut mining can be extensive, as on the large islands of south-eastern Queensland (Bribie Island 40%, South Stradbroke Island 28%, North Stradbroke Island 24%; Stephens 2011). Both of these activities are at present limited on WA islands,

**Table 11**

Synopsis of activities of Europeans on Western Australian islands. Impacts considered to be significant are in **bold**. Activities are listed in approximate chronological order. Islands are listed from north to south.

| Activity | Islands | Impacts | References |
|---|---|---|---|
| Sealing (killing of seals for their skins) | All islands with seal populations (Houtman Abrolhos to Archipelago of the Recherche) | **Long-term reduction in nutrient transfer** by sea lion populations | Abbott 1979, Berryman 2002: 278, Grey 1841 vol 2: 125, GF Moore in *The Perth Gazette* 8.2.1840: 23–24, Mulvaney & Green 1992: 281, Rottnest Island Authority 1995b |
| Collection of firewood | Thevenard, Rottnest, Garden, Middle (Recherche) | Short-term to long-term | Flinders 1814: 88, Joske et al. 1997, WAPET 1987 |
| Firing of vegetation (including some natural fires ignited by lightning) | SW Osborn c. 1978, Steep Head c. 1978, Naturalists 1992; Uwins; Degerando 1957; Sunday 1912; Legendre 1982; Angel 1979, 2002; Dolphin 1987; Hauy 1988; Collier Rocks 1989; Rosemary 1863; Enderby 1863; Barrow 1864, 1961; Dorre 1874, 1909, 1973; Dirk Hartog 1850; Rottnest 1880s?, 1903, 1909, 1917, 1941, 1955, 1997; Garden 1829, 1834, 1880, c.1910, c. 1920, 1956, 1991, 1997; Culeenup 1972; Eclipse 1968; Mistaken 1803; Michaelmas 1923, Figure of Eight 1971; Boxer <1950, 1974; Observatory; Woody 1904, 1935, 1949-50; Mondrain 1802, 1944, 2002; Remark <1950; Sandy Hook <1950, 1983; Long 1930s; Charley <1950; Pasco 1994; Frederick 1980; North Twin Peak c. 1936; South Twin Peak 1989?; Gulch 1984; Middle (Recherche) c.1799–1800, 1972–73, 1977; Goose 1801, <1950; Salisbury 1992–1993; Daw [Christmas] <1950 | Infrequent (except Rottnest). High intensity fire kills extensive areas of vegetation, but secondary succession is initiated<br><br>Construction of firebreaks as preventive measure (limited destruction of vegetation, spread of weeds)<br><br>Prescribed burning trials (Garden Island only) | *Albany Advertiser* 24.1.1923: 2, Anon. 1864, 1975; Beard et al. 1984, Brockman 1987: 46, AA Burbidge pers. comm., AA Burbidge et al. 2012, Butler 1989, Coate 2008a, P Collins 1990 unpubl., I Cooke 1984 unpubl., Cornell 1974, DCLM 1990, Department of Defence 1980, Errington 2012, Flinders 1814: 83, Fowler 1945, Fullagar & Van Tets 1976, Garden Island Working Group 1974, GIEAC 1997, Graham-Taylor 2012b, Hopkins 1981, Hopkins & Harvey 1989, Hussey et al. 1992, Joske et al. 1997, SG Lane 1982g, NG Marchant & Abbott 1981, McArthur 1996b, R Palmer et al. 2013b, Pearman 1971, Pearson et al. 2005, *Pilbara News* 12.11.2003: 3, Rippey & Hobbs 2003; Ride & Tyndale-Biscoe 1962: 124, *The Perth Gazette* 7.2.1851, 27.1.1865: 2; Vallance et al. 2001: 116, Weston 1985, Whitley 1944, JH Willis 1953 |
| Construction of buildings associated with settlement (e.g. pilot station, wool store) | Forestier, West Lewis, Rottnest, Garden, Penguin | Limited vegetation destruction | Errington 2012, Goodlich 2015, Joske et al. 1997, *The Inquirer & Commercial News* 18.7.1883: 12, *The Sunday Times* 10.3.1912: 9, *The West Australian* 6.12.1889: 3 |
| Whaling base | Malus, Rottnest, Carnac, Migo, Middle (Recherche) | Short-term | JMR Cameron 2006, Dickson 2007, Gibbs 2010 |
| Fishing (rock lobster, finfish, trepang, clam, turtle) base | Ashmore (East, West), Carronade, Cassini, Lacepede, Rosemary, Houtman Abrolhos (22 islands, March-June), Rottnest, Carnac, Boxer, Middle (Recherche) | Limited vegetation destruction caused by construction of cottages; **introduction of weeds** | Abbott 1980a, Abrolhos Islands Task Force 1989, AA Burbidge & Prince 1972, Cornell 2003: 166, DCLM 1990, Fairbridge & Serventy 1954, *Geraldton Guardian* 23.11.1907: 4, J Green 1982, JM Harvey et al. 2001, Helms 1898, Johnstone & Storr 1994, Joske et al. 1997, D Serventy 1952, Sowden 1906, *The Inquirer & Commercial News* 28.2.1877: 3, *The West Australian* 7.12.1907: 5, *The Western Mail* 20.6.1981: 18 |

| Activity | Islands | Impacts | References |
|---|---|---|---|
| Collection of biological specimens (dead or alive) by naturalists and scientists | Kimberley to Archipelago of the Recherche | Limited and intermittent | See Table 1 |
| Procurement of native animals (and their eggs) for sport, fur or food, including seabirds and turtles | Ashmore (East, West, Middle), Bedout, Delambre, Rosemary, Trimouille, Barrow, Thevenard, Faure, unidentified islands in Freycinet Estuary (Shark Bay), Slope, West Wallabi, East Wallabi, Rat, Garden, Rottnest, Breaksea, Green (Oyster Harbour), Observatory, Thomas, Middle & other islands in the Archipelago of the Recherche | Limited and intermittent | Abbott 2001; Andrews 1959; Anon. 1864: 52; Berryman 2002: 277, 279, 280; AJ Campbell 1890a; Carter 1917; Cornell 2006: 160; Dash 2003; Dunlop 2013; Errington 2012; Flinders 1814: 54, 83, 88; J Gilbert 1843 in Whittell 1942; J Gregory 1941; Hall 1902: 199-200; Hercock 1996; Joske et al. 1997; Labillardiere 1800; Select Committee 1887; Serventy 1952, Stokes 1846; *The Inquirer & Commercial News* 28.2.1877: 3; *The Perth Gazette* 20.8.1842: 3, *The West Australian* 6.12.1907: 7, *The Western Mail* 7.8.1924: 30, 21.8.1924: 42; JJ Walker 1897 |
| Capture and sale of young birds for aviculture trade | Rottnest | Abundance of rock parrot much reduced in 1940s and 1950s | Storr 1965c |
| Castaway from shipwreck or damaged ship, or careening of a ship | Dirk Hartog 1841, Beacon 1629, East Wallabi 1629, West Wallabi 1629, Gun 1727 (Houtman Abrolhos); Garden; Middle 1824, 1920 (Recherche); Salisbury | Short-term and infrequent | Errington 2012, Johnstone & Storr 1994, Stanbury 2000 |
| Cultivation (agriculture, horticulture) | Sir Graham Moore, Sunday, Rottnest, Garden, Green (Oyster Harbour), Cheyne, Middle (Recherche) | **Vegetation destruction** caused by construction of buildings and by cropping; **introduction of weeds** | Abbott 2001, Aborigines Department 1904: 24, Andrews 1959, Crawford 2001, Department of Defence 1980, Errington 2012, Garden Island Working Group 1974, Joske et al. 1997, Rottnest Island Authority 1995b, Stokes 1846 |
| Grazing of livestock (seasonal agistment or pastoral station): sheep, goats, pigs, horses, camels | Sir Graham Moore, Sunday, West Lewis, Barrow, Bernier, Dorre, Dirk Hartog, Faure, Salutation, Rottnest, Garden, Archipelago of the Recherche (Figure of Eight, Boxer, Observatory, Cull, Rabbit, Charley, Thomas, Gunton, Woody, Sandy Hook) | **Extensive reduction in biomass of vegetation and density of palatable plant species**<br><br>**Erosion of vegetation causing blow outs of sand dunes** | Abbott 2008, Abbott & Burbidge 1995, AA Burbidge et al. 2012, Carter 1917, DCLM 2000b, Durlacher 1900, Errington 2012, Fairbridge & Serventy 1954, Fitzgerald 1907, Fraser 1876, Graham-Taylor 2012a: 349-352, Joske et al. 1997, Ride & Tyndale-Biscoe 1962: 124, Serventy 1947, Serventy 1953, *The Inquirer & Commercial News* 28.2.1877: 3, *The West Australian* 6.1.1882: 2, Tingay & Tingay 1982c, JH Willis 1953, B Wilson 2008b |
| Manned lighthouse (construction and operation)<br><br>All now automated | Jarman 1888, Dirk Hartog 1910, Rottnest 1851 & 1896, Eclipse 1926, Breaksea 1858 | Limited vegetation destruction caused by construction (including cottages and other buildings); introduction of companion animals (dog, cat, monkey), working animals (horse, donkey), or source of fresh meat (sheep, rabbits); accidental introduction of weeds via hay | *Albany Advertiser* 26.9.1932: 4, AJ Campbell 1890a, Joske et al. 1997, Lindesay n.d., WL Owen 1936, Rottnest Island Authority 1995b |

| Activity | Islands | Impacts | References |
|---|---|---|---|
| Erection of automatic light tower or navigation beacon | Lacrosse 1961, Lesueur, Troughton, Browse, Cunningham 1960 [Imperieuse Reef], Degerando 1960, Adele 1951, Caffarelli, Tanner 1951, Cockatoo, East Lacepede, Bedout 1909, Legendre, Malus, Rosemary, North West, Trimouille, Barrow 1950, Double, Mary Anne 1950, Airlie 1913, Bessieres [Anchor] 1913, North Sandy 1913, Great Sandy 1959 [Beagle], Bernier 1937, Dorre, North (Abrolhos), Pelsaert 1974, Escape 1930, Phillip Rock, Hamelin, Figure of Eight, Cull | Minimal vegetation destruction caused by activities associated with construction and maintenance of access tracks for amphibious vehicle | Australia Pilot 1972, 1973 |
| Reduced Aboriginal presence (via massacre or introduction of diseases) | Mary, Sheep, New, Sunday | Disruption of traditional cultural activities, **including reduced burning** | Crawford 2001, R Palmer et al. 2013a |
| Detention (gaol, internment, barracoon, lock hospital, lazaret) or church mission | Long (Eclipse Group), Bathurst, Sunday, Bezout, Lacepede, Delambre, Bezout, Enderby, Barrow, Bernier, Dorre, Rottnest, Carnac, Garden, Boxer, Woody, Mondrain | Reduction in abundance of edible animals?<br><br>Erection of buildings from locally derived materials | Aborigines Department 1912, Bain 1982, Chief Protector 1909ab, Crawford 2001, WS Davidson 1978, Executive Council 1841, Forrest 1996, Graham-Taylor 2012b, N Green & Moon 1997, Jebb 1984, Joske et al. 1997, Lipfert 1912; I Murray & Hercock 2008: 15, 289; Rintoul 1964, Rottnest Island Authority 1995b, Serventy 1953 |
| Storage of munitions & explosives | Garden, Fly [Geake Point] | Limited vegetation destruction | Garden Island Working Group 1974, HA Sunter-Smith pers. comm. |
| Pearling base | Montebello Group (1884–), Burnside, Dirk Hartog | **Introduction of rats and cats**<br><br>Equipment dumps | AA Burbidge 2004ab, Montague 1914, I Murray & Hercock 2008: 42, Start & McKenzie 1992, *The Daily News* 23.6.1909: 7 |
| Bombardment (naval, aerial) | Target Rock, Lancelin, Breaksea | Probably limited and infrequent | Abbott 1978b, G Keighery et al. 2002, I Murray & Hercock 2008: 294 |
| Mining (extraction of iron ore, guano, natural gas, oil, salt) and associated activity | Lesueur, Jones, Stewart, Booby [White], Browse, Lacepede (4), Bedout, Turtle, Finucane, E Forestier, Cockatoo, Koolan, East Intercourse, Trimouille, Hermite, Varanus, Barrow, ‘two islands near Barrow’, Beagle, Airlie, Thevenard, Shark Bay (at least 15), Houtman Abrolhos (West Wallabi, Rat, Pelsaert &c), Rottnest, Carnac, Middle (Recherche) | **Extensive or frequent vegetation destruction** caused by construction of buildings, tramways, roads, gravel pits, wells, and extraction of the resource; use of horses<br><br>Dumping of rubbish<br><br>Sewage disposal, providing habitat for weeds | Andrews 1959; Béchervaise 1954; Berryman 2002: 279; Browne-Cooper & Maryan 1990, AA Burbidge & Fuller 2000, Butler 1970, 1987, 1989; AJ Campbell 1890a; Coghlan 1885; Dampier Mining Co. n.d.; Dunlop 2013; Fairbridge 1948ab; Fuller & Burbidge 1992, 1998a; *WA Government Gazette* 27.6.1876: 138, 22.6.1880: 219-220, 12.3.1885 suppl: 134; Graham-Taylor 2012b; GA Green 1972; Helms 1898; Johnstone & Storr 1994; Joske et al. 1997; G Keighery et al. 1995, 2006; LeProvost, Semeniuk & Chalmer 1987; Lind 1994; Moro & Lagdon 2013; I Murray & Hercock 2008: 103, Rottnest Island Authority 1995b; Select Committee 1881, 1887, 1902; D Serventy 1952, 1972; Stanbury 1982; *The Inquirer & Commercial News* 28.2.1877: 3; *The West Australian* 6.12.1907: 7, AJ Wells 1897; Woodward 1917 |

| Activity | Islands | Impacts | References |
|---|---|---|---|
| Pollution from fuel oil | Hood | The 1991 wreck of the Sanko Harvest threatened seals on the nearest island | I Murray & Hercock 2008: 133 |
| Joining to the mainland by causeway or bridge | Finucane, Dampier [Burrup Peninsula], East Intercourse, East Mid Intercourse, Mistaken [Dampier Archipelago], Babbage, Slope, Garden, Fly [Geake Point] | Potential increased immigration of alien organisms | AA Burbidge & Fuller 2000, DCLM 1990, I Murray & Hercock 2008, Serventy 1972 |
| Increased population of silver gulls caused by rubbish dumps on mainland (and decrease when landfill sites are closed) | Rottnest, Carnac, Garden, Penguin | Introduction of weed species; predation on eggs of other surface-nesting seabirds<br><br>Hampering of ecological restoration (gulls pull out planted seedlings and trample plots) | Brown et al. 2015ab, Hercock 1998b: 400, *Post* 12.9.2009: 11, Saunders & de Rebeira 2009, Storr 1964a,b; Wykes et al. 1999 |
| Establishment of scientific research facility | Enderby, Hermite, Rat, Rottnest, Garden | Potential increased immigration of alien organisms | Abbott 2006, AA Burbidge 1997, DCLM 1990, Hodgkin 1959, Joske et al. 1997 |
| Increased population of native herbivorous mammals caused by fire-induced vegetation change | Rottnest, Garden | **Suppression of regeneration of palatable plant species** by quokka & tammar wallabies | Anon. 1975; McArthur 1996b, 1998; Rottnest Island Authority 1995b, Storr 1968 |
| Defence base/facility (construction and operation) and military occupation | Sir Graham Moore, West Montalivet, Champagny, Rottnest, Garden | **vegetation destruction & soil erosion** caused by construction of buildings; mortality of mammals caused by road traffic; risk of unnaturally high populations of mammals causing grazing pressure on natural bushland | BK Chambers et al. 2010, Choo 2001, Department of Defence 1993, Douglas n.d.: 102, Garden Island Working Group 1974, GIEAC 1997, Joske et al. 1997; McArthur 1996a, 1998; Rottnest Island Authority 1995b, *Western Suburbs Weekly* 14.5.2002: 8 |
| Introduction (inadvertent or deliberate) of exotic species including invertebrates (via importation of firewood), companion animals (cats, dogs, monkeys, cockatoo, kangaroo), tortoises, pigs, hares, rabbits, rats, mice, red deer, domestic pigeons, poultry, snails, earthworms, butterflies, honeybees, red-backed spider, disease organisms (e.g. *Armillaria*), and weeds | Kimberley to Archipelago of the Recherche | **Unremitting predation of native species**<br><br>**Reduction in density of palatable species**<br><br>**Competition with native plant species** | Abbott & Burbidge 1995, Abbott 2008, Aborigines Department 1904: 24, Acclimatisation Committee 1905, Andrews 1959, Bettink 2015, Buckley 1983, AA Burbidge & Fuller 2000, Carter 1917, Errington 2012, Eyre 1845 Vol. 2: 71, Fullagar & Van Tets 1976, GIEAC 1999, *WA Government Gazette* 22.10.1879: 282, GA Green 1972, Helms 1898, Jebb 1984: 77, MS Johnson & Black 1979, Joske et al. 1997; Longman et al. 2000, Majer et al. 2013, McArthur 1996a, Michaelsen & Hartmeyer 1907, 1908; Mulvaney & Green 1992: 281; WL Owen 1936; Rintoul 1964; Sedgwick 1940: 143; Serventy 1949, 1952, 1972; Serventy & Storr 1959; Serventy & White 1943; J Short et al. 1992; Start & McKenzie 1992; *The Australasian* 22.8.1891: 18; *The West Australian* 7.12.1907: 5, 7.3.1918; *The Western Mail* 21.8.1924: 42, 28.8.1924: 38; Warham 1956a; *WA Government Gazette* 22.10,1879: 282, AAE Williams 1997 |

| Activity | Islands | Impacts | References |
|---|---|---|---|
| Beautification (planting of exotic & native trees, lawns) | Cockatoo, Barrow, Thevenard, Faure, Rottnest, Garden, Penguin | Dependent upon species planted and the resources that these species supply to other species | Butler 1970, Edmiston & White 1974, Goodlich 2015, G Keighery 1998, G Keighery & Muir 2008, McArthur 1996a, Rottnest Island Authority 1995b, Rottnest Island Management Planning Group 1985b, Sten 1959, WAPET 1987 |
| Recreation and tourism (legal & illegal) | Kingfisher, Cockatoo (1980s), Tyri, Delambre, Dampier Archipelago (Dolphin, Gidley, Angel, Malus, East Lewis, West Lewis, Goodwyn, Enderby, Rosemary, several other smaller islands), Steamboat, Fortescue, Mardie, Sholl, Thevenard, Direction, Doole, Dorre, Dirk Hartog, Pelsaert, Wedge, Rottnest, Garden, Penguin, Hamelin, Woody, Middle (Recherche) | **Vegetation destruction** caused by construction of buildings and golf course, and visitors walking through vegetation<br><br>**Increased risk of wildfire** after annual grasses have cured; disruption to wildlife<br><br>Ferry service and high boat ownership with **increased potential risk of introduction of exotic species,** including companion animals<br><br>Use of buildings by birds for nesting sites | Conservation Commission of Western Australia 2009, Dans 1996, DCLM 1990, DEC 2012a, de Garis 1983, Department of Defence 1980, Fuller & Burbidge 1992, Goodlich 2015, Hercock 2002, Johnstone & Storr 1994, Joske et al. 1997, G Keighery et al. 2002, Kilpatrick 1932, KD Morris 1989a, *Northern Guardian* 16.6.2004: 3, Onton & Webb 2009, *Pilbara News* 3.7.2002: 1, Reid 1949, Rippey 2015, Rottnest Island Authority 1995b; Serventy 1943, 1950; EJ Stuart 1923; *The Post* 7.8.2010: 80, WABN No. 4: 10, *The West Australian* 4.7.1980: 26–27, *The Western Mail* 13.6.1981: 15 |
| Construction of jetty, pier or wharf | Cockatoo, Koolan, Varanus, Barrow, Thevenard, Houtman Abrolhos (numerous islands, including West Wallabi, East Wallabi, Rat, Gun, Pelsaert), Rottnest, Garden, Penguin, Breaksea, Woody | Increased potential for accidental introduction of cats, rats, mice and weeds; used for nesting sites by birds | Dampier Mining Co. n.d., Errington 2012, Goodlich 2015, Helms 1898, Kilpatrick 1932, Kinhill Stearns 1986, Moro & Lagdon 2013, WAPET 1998 |
| Construction of airstrip | Cockatoo, Koolan, Barrow, Rosemary, Varanus, Sholl, Thevenard, Faure, Dirk Hartog, North (Abrolhos), East Wallabi, Rat, Rottnest | Increased potential for accidental introduction of rats, mice and weeds; **vegetation destruction; nesting seabirds killed by aeroplanes** | Butler 1970, de Garis 1983, KD Morris 1989a, Joske et al. 1997, Storr 1964a, WAPET 1987, B Wilson 2008b |
| Provision of fresh water | Garden | Establishment of lawns facilitated & habitat for some exotic plant species provided; increased density of marsupials | G Keighery 1998, McArthur 1996b |
| Logging of forests (for firewood, fencing, building) | Rottnest, Garden, Woody | **Vegetation destruction** | Errington 2012, Rottnest Island Management Planning Group 1985a: 47, JH Willis 1953 |
| Removal of sandalwood (for export to Asia) | Bernier, Dirk Hartog | | Ride & Tyndale-Biscoe 1962: 124 |
| Construction of helicopter pad (to service automatic light, mining settlement or defence base) | Browse, Naturalists, Helipad, Varanus, Barrow, Airlie, Thevenard, Garden, Eclipse, Breaksea, Figure of Eight, Cull | Decreased risk of introducing weeds or vermin; possible disturbance of breeding seabirds | Fuller & Burbidge 1998a, SG Lane 1982i, McArthur 1998, I Murray& Hercock 2008: 136, Kinhill Stearns 1986, WABN No. 103: 17, WAPET 1993 |
| Quarantine facility | Barrow, Gun (for dogs), Carnac, Mistaken (King George Sound) | Increased potential for accidental introduction of rats, mice and weeds; vegetation destruction | De la Rue 1979: 99; *WA Government Gazette* 14.1.1892: 14, 29.9.1892: 772; WA Parliamentary Debates 9: 344 (8.9.1884); Whittle et al. 2013 |

| Activity | Islands | Impacts | References |
|---|---|---|---|
| Detonation of atomic bomb | Montebello Group (1952, 1956) | Unknown, but probably severe and apparently short-term | AA Burbidge & Fuller 1998, Kendrick 2003; *The Sydney Morning Herald* 23.5.1952: 3, 31.5.1952: 2 |
| Publication of management plan | Rowley Shoals (Bedwell, Cunningham), Dampier Archipelago, Montebello Islands, Muiron Islands, Shark Bay islands, Houtman Abrolhos, islands between Dongara–Lancelin, Rottnest, Carnac, Garden, Shoalwater Bay islands, Archipelago of the Recherche | Improved and coordinated management | Abrolhos Islands Task Force 1989; Conservation Commission of Western Australia 2009, DCLM 1990, 2000b, 2003, 2004; DEC 2007b, 2012ab; Department of Defence 1980, 1993; NPNCA 1992, 1999; Department of Parks and Wildlife 2016, Rottnest Island Management Planning Group 1985a; Rottnest Island Authority 1995a, 2003, 2009; DEC 2006a, 2007ab; 2012 |
| Visitor management: Construction of board walk and/or erection of signage prohibiting entry to parts of island; establishment of camping grounds | Lancelin, Rottnest, Garden, Penguin, Woody | Minimisation of trampling of vegetation and erosion; prevention of disturbance of breeding seabirds; reduced damage to burrows of seabirds | GIEAC 1997, Goodlich 2015, Joske et al. 1997, WABN No. 3: [3–4] |
| Education | Cockatoo (1948-1963), Koolan, Houtman Abrolhos (North, Pigeon, Rat, Little Rat), Rottnest, Breaksea | | Abrolhos Islands Task Force 1989, de Garis 1983, GA Green 1972, Hodgkin 1959, Hodgkin & Shield 1959, Lindesay n.d., Joske et al. 1997; O'Loughlin 1965, 1966, 1969; Rottnest Island Authority 1995b |
| Physical destruction | Slope, Phillip Rock (Rottnest), Anglesea [Pig] | **Habitat destruction** | Joske et al. 1997, G Keighery et al. 2006, I Murray & Hercock 2008: 5, Serventy 1972 |
| Creation of new island | Avocet, Ibis, Sandpiper | | I Murray & Hercock 2008: 9, 146, 263 |
| Vandalism | Rottnest | **Destruction of tern nests** | Kilpatrick 1932, Reid 1949 |
| Formal designation of purpose as 'reserve for native game' or nature reserve, 1898- | Houtman Abrolhos, Pelican, Dorre & Barrow (the first islands so designated); subsequently many others | Prohibition of shooting, cultivation, pastoral activity (with some exceptions) | Graham-Taylor 2012b, *WA Government Gazette* 2.8.1907 |
| Ecological restoration | Dirk Hartog, Faure, Rottnest, Seal (Shoalwater Bay), Penguin | Eradication of exotic animal species and re-introduction of native mammal species; Increased distribution of native vegetation (through planting) and bird species dependent on trees; eradication of weed species | Brown et al. 2015ab, DEC 2011, K Koch et al. 2014, Rottnest Island Authority 2009; Mather 2009, 2011; Rippey 2015, Table 12, Table 13 |

**Table 12**

Fauna management activities on Western Australian islands, including re-introductions of native species and removal of introduced species. Islands are listed from north to south and then west to east for each species.

| Island | Species | Action | Outcome | Reference |
|---|---|---|---|---|
| **Native birds (re-introduction)** | | | | |
| Hermite | *Malurus leucopterus* | Translocation of 37 birds in 2010–11 from Barrow Island | Successful; self-introduced to Renewal Island (c. 150 m distant, c. 300 m between the vegetated parts of both islands) | AA Burbidge pers. comm., AH Burbidge & N Thomas pers. comm., Johnstone et al. 2013, N Thomas et al. 2014 |
| Hermite | *Eremiornis carteri* | Translocation of 47 birds in 2010–11 from Barrow Island | Successful; self-introduced to Renewal Island (c. 150 m distant, c. 150 m distant, c. 300 m between the vegetated parts of both islands) | AA Burbidge pers. comm., AH Burbidge & N Thomas pers. comm., Johnstone et al. 2013, N Thomas et al. 2014 |
| **Native mammals (re-introduction)** | | | | |
| West Lewis | *Petrogale rothschildi* | Translocation of 15 animals from Enderby Island in 1982 and an unknown number in 1985 | Successful | Pearson 2012 |
| Boodie | *Bettongia lesueur* | Translocation of 36 animals from Barrow Island in 1993 to replace extinction in 1985 caused by baits deployed to eradicate black rats | Successful (breeding and recolonisation of entire island by 1998) | KD Morris 2002, J Short & Turner 1993 |
| Hermite | *Isoodon auratus* | Translocation of 165 animals from Barrow Island in 2010 | Successful; self-introduced to Buttercup Island (at low tide?) | DEC 2013, B Johnson 2010, N Thomas et al. 2014 |
| Hermite | *Lagorchestes conspicillatus* | Translocation of 111 animals from Barrow Island in 2010 | Successful | DEC 2013, B Johnson 2010, N Thomas et al. 2014 |
| Faure | *Perameles bougainville* | Translocation of 20 animals ex Heirisson Prong enclosure in 2005 | Successful | DEC 2012c |
| Faure | *Bettongia lesueur* | Translocation of 36 animals ex Barrow Island in 1993 and 17 animals in 2002 | Successful | DEC 2012c, Richards 2007 |
| Faure | *Pseudomys fieldi* | Translocation of 108 animals in 2002 from Perth Zoo (ex Bernier Island) | Successful | Richards 2007 |
| **Native bird (introduction)** | | | | |
| Bald | *Atrichornis clamosus* | Translocation of 11 birds from Two Peoples Bay in 1992–1994 | Successful by 1997 | Comer et al. 2010 |

| Island | Species | Action | Outcome | Reference |
|---|---|---|---|---|
| **Native reptile (introduction)** | | | | |
| Favourite | *Ctenotus lancelini* | Translocation of 133 skinks in 2002–03 from Perth Zoo (ex Lancelin Island) | Successful by 2013 | Hartley & Pearson 2008, D Pearson pers. comm. |
| **Native mammal (introduction)** | | | | |
| North West | *Pseudomys fieldi* | Translocation of 59 animals from Perth Zoo in 1999 (ex Bernier Island) | Successful | AA Burbidge 2004b, B Johnson 2010 |
| Alpha | *Bettongia lesueur* | Translocation of 40 animals from Barrow Island in 2010–2011 | Breeding occurring; active warrens throughout the island | DEC 2013, N Thomas pers. comm. |
| Trimouille | *Lagorchestes hirsutus* | Translocation of 30 animals from Tanami Desert NT in 1998 | Successful | AA Burbidge 2004b; AA Burbidge et al. 1999, 2000; Langford & Burbidge 2001 |
| Serrurier [Long] | *Leggadina lakedownensis* | Translocation of 65 animals in 1996 from Thevenard Island | Successful | DCLM 2000b, K Morris pers. comm., Woinarski et al. 2014b |
| Doole | *Isoodon auratus* | Translocation of 92 animals from Barrow Island in 2010–2011 | Successful | K Morris pers. comm. |
| Doole | *Pseudomys fieldi* | Translocated from Bernier Island in 1993 & 1995 | Successful at first, but absent by 2005 possibly from a tidal surge generated by a cyclone or because of predation by goannas | AA Burbidge, K Morris pers. comm., Woinarski et al. 2014b |
| Dirk Hartog | *Lagostrophus fasciatus* | Translocation of 11 animals ex Dorre Island to pens in 1974; these increased to 36 by 1976; released in 1977 | Failed because of cat predation & drought | AA Burbidge & George 1978, DEC 2012c, J Short et al. 1992, Woinarski et al. 2014b |
| Faure | *Lagostrophus fasciatus* | Translocation of 57 animals ex Heirisson Prong enclosure during 2004–2012 | Presumed successful | DEC 2012c, Richards 2007, Woinarski et al. 2014b |
| Faure | *Leporillus conditor* | Translocation of 16 animals from St Peters Island (South Australia) in 2006, and 6 from Salutation Island in 2006 | ?Successful | Richards 2007, Woinarski et al. 2014b |
| Salutation | *Leporillus conditor* | Translocated from Monarto Zoo (ex Franklin Island, South Australia) in 1990 | Successful | Woinarski et al. 2014b |
| North (Abrolhos) | *Macropus eugenii* | Unauthorised introduction in 1985; c. 800 animals culled in 2008 | Reduced damage to vegetation | Miller et al. 2011 |
| Escape | *Parantechinus apicalis* | Translocated from Perth Zoo (ex Boullanger [Long] and Whitlock islands) in 1998 | Breeding recorded | Moro 2003 |
| Gunton | *Parantechinus apicalis* | Translocation in 2015 of 28 animals from Perth Zoo and 1 wild animal born in 2015 | Too early to evaluate | *Parks and Wildlife News* October 1015: 16 |

| Island | Species | Action | Outcome | Reference |
|---|---|---|---|---|
| Michaelmas | *Potorous gilbertii* | Translocation of 7 animals in 2016, rescued after wildfire in November 2015 at Two People Bay and held in captivity | Too early to evaluate | https://www.dpaw.wa.gov.au/news/item/2697-gilbert-s-potoroo-head-to-a-new-home [accessed 31.7.2016] |
| Bald | *Potorous gilbertii* | Translocation during 2005–2007 of 10 animals from Two Peoples Bay | Successful | Bougher & Friend 2009, Woinarski et al. 2014b |
| Woody | *Macropus fuliginosus* | Unauthorised introduction <1948 | Successful | Abbott & Black 1978, Goodsell et al. 1976, J Short et al. 1992 |
| **Introduced native bird (extirpation)** | | | | |
| Rottnest | *Trichoglossus moluccanus* | Removal of 8 birds, including 1 young, in 2012–13 | Successful | Blythman & Sansom 2015 |
| **Introduced mammals (extirpation)** | | | | |
| Three Bays | *Mus musculus* | Poisoned with Brodifacoum in 2010 | Successful | R Palmer et al. 2013a |
| Adele | *Rattus exulans* | Ground baiting in 2011 (failed), aerial baiting (2013) | ?Successful | R Palmer pers. comm. |
| Bedout | *Rattus rattus* | Pindone baiting in 1981 | Successful | KD Morris 1989b |
| Montebello Islands (all islands in archipelago) | *Rattus rattus* | Brodifacoum baiting in 1996, 1999 (on ground), 2001 (aerial) | Successful after aerial baiting in 2001 | AA Burbidge 1997, 2004b; AA Burbidge et al. 2000 |
| Barrow | *Rattus rattus* | Pindone baiting in 1990–1991 on a small area near the southern tip where the rats were known to occur | Successful | AA Burbidge pers. comm., KD Morris 2002 |
| Boomerang | *Rattus rattus* | Pindone baiting in 1983 | Successful | KD Morris 1989b, 2002 |
| North Double | *Rattus rattus* | Pindone baiting in 1983 | Successful | KD Morris 1989b, 2002 |
| South Double | *Rattus rattus* | Pindone baiting in 1983 | Successful | KD Morris 1989b, 2002 |
| Middle (Barrow) | *Rattus rattus* | Pindone baiting in 1991 | Successful | KD Morris 2002 |
| Boodie | *Rattus rattus* | Pindone baiting in 1985 | Successful | KD Morris 1989b, 2002 |
| Pasco | *Rattus rattus* | Pindone baiting in 1985 | Successful | KD Morris 1989b, 2002 |
| Rat (& adjacent islands in Houtman Abrolhos) | *Rattus rattus* | Pindone baiting in 1991 | Successful | AA Burbidge & Morris 2002 |
| Penguin | *Rattus rattus* | Brodifacoum baiting in 2013 | Successful | Bettink 2015 |
| Dolphin | *Vulpes vulpes* | Aerial 1080 baiting 1984, 1987 | Successful | KD Morris 1989b |
| Angel | *Vulpes vulpes* | Aerial 1080 baiting 1984, 1987 | Successful | KD Morris 1989b |

| Island | Species | Action | Outcome | Reference |
|---|---|---|---|---|
| Gidley | *Vulpes vulpes* | Aerial 1080 baiting 1984, 1987 | Successful | KD Morris 1989b |
| Keast | *Vulpes vulpes* | Aerial 1080 baiting 1984, 1987 | Successful | KD Morris 1989b |
| Collier Rock | *Vulpes vulpes* | Aerial 1080 baiting 1984, 1987 | Successful | KD Morris 1989b |
| Legendre | *Vulpes vulpes* | Aerial 1080 baiting 1984, 1987 | Successful | KD Morris 1989b |
| Hermite | *Felis catus* | Aerial 1080 baiting & trapping, 1999 | Successful | Algar & Burbidge 2000, Algar et al. 2002, AA Burbidge et al. 2000 |
| Serrurier [Long] | *Felis catus* | 1080 baiting in 1996 to kill the one animal present | Successful | Moro 1997 |
| Dirk Hartog | *Felis catus* | 1080 aerial baiting 2011–2014 | In progress | Algar et al. 2013 |
| Faure | *Felis catus* | Aerial 1080 baiting in 2001 | Successful | Algar & Angus 2008, Richards 2007 |
| Rat | *Felis catus* | 1992–c. 2000 | Successful | Dunlop 2013 |
| Rottnest | *Felis catus* | 2001–2002 | Successful | Algar et al. 2011c |
| Wooded (Houtman Abrolhos) | *Oryctolagus cuniculus* | 1080 baits deployed in 1973 | Successful | KD Morris 1989b, Young 1981 |
| Morley (Houtman Abrolhos) | *Oryctolagus cuniculus* | 1080 baits deployed in 1973 | Successful | KD Morris 1989b, Young 1981 |
| Leo (Houtman Abrolhos) | *Oryctolagus cuniculus* | 1080 baits deployed in 1976 | Successful | KD Morris 1989b, Young 1981 |
| North & South Green Islet | *Oryctolagus cuniculus* | 1080 baits deployed in 1974 | Successful | KD Morris 1989b, Young 1981 |
| Carnac | *Oryctolagus cuniculus* | 1080 baits deployed in 1969 | Successful | KD Morris 1989b, Young 1981 |
| Penguin | *Oryctolagus cuniculus* | >1939, probably shot out | Successful | Sedgwick 1940: 143 |
| Mistaken | *Oryctolagus cuniculus* | 1080 baits deployed in 1977, 1978, 1979, 1980 | Successful 1980, but rabbits re-invaded by swimming | KD Morris 1989b, Young 1981 |
| Rottnest | *Lepus capensis* | Released in 1871 | Initially bred but extinct <1878 presumably because of predation by feral cats or shooting | Joske et al. 1997, Storr 1965c |
| Bernier | *Capra hircus* | Culled in 1971; shot from helicopter in 1984 | Successful | Chapple 1972, KD Morris 1989b |
| Faure | *Capra hircus* | Removed by 2007 | Successful | Clarke 1976, B Wilson 2008b |
| Dirk Hartog | *Capra hircus* | Removed & shot, except for a few Judas goats | Successful | AA Burbidge pers. comm. |
| Dirk Hartog | *Ovis aries* | Removed and shot | Successful | AA Burbidge pers. comm. |
| Faure | *Ovis aries* | Effectively removed by 2007 (restricted to a single paddock) | Successful | B Wilson 2008b |
| Gull [Cull] | *Cervus elaphus* | 5 released 1904–1905 | Failed | Acclimatisation Committee1905 |

although Cockatoo and Koolan islands have experienced significant clearing of vegetation in recent decades for mining of iron ore (G Keighery et al. 1995; I Abbott pers. obs.).

The enforced stay of 88 men from the wrecked ship *Zeewijk* for 10 months in 1727–1728 on Gun Island, Houtman Abrolhos, presumably had significant (but undocumented) direct and indirect impacts on edible fauna (particularly sea lions and seabirds) and vegetation on this and nearby islands. The direct actions of humans and their obvious impacts, however, may also mask subtle effects. For example, Arctic foxes (*Vulpes lagopus*) introduced to the Aleutian Islands have reduced the abundance of seabirds (a predictable impact), but the disruption of the non-obvious process of transfer of nutrients from ocean to island, and the ensuing changed composition of vegetation (Maron et al. 2006) were not expected.

On those islands not visited by Aborigines and thus lacking anthropogenic ignitions, the arrival of Europeans often led to conflagrations that burnt out large portions. Records exist for more than 20 islands (Table 11).

The most extreme disturbance on a WA island is surely the testing of atomic weapons in the Montebello Group in 1952 and 1956. Yet, as noted during a visit to Trimouille Island in 1958 by Serventy and Marshall (1964: 18), 'Apart from the damaged blockhouses or pill-boxes on the site it would be difficult to imagine that an atomic explosion had taken place in the vicinity'. This is of course an exaggeration, as other activity associated with the weapons-testing remains obvious, including disused roads, rubbish, decaying buildings and the remains of vehicles and aircraft. Although baseline biological surveys were incidental to other activities (FL Hill 1955), it is surprising how many plant, reptile and bird species have been recorded subsequently (Serventy & Marshall 1964; AA Burbidge 1971; AA Burbidge et al. 2000). However, radiation was not evenly spread across the archipelago, enabling reinvasion by feral cats and black rats.

Another extreme action is alteration of the physical configuration due to mining. Examples include extraction of guano (Egg Island and other islands in Shark Bay during the 1850s, numerous islands in Houtman Abrolhos from the 1870s), mining of iron ore (Cockatoo and Koolan islands), and harbour works associated with mining or production and export of solar salt (Slope Island, East Intercourse Island, East Mid Intercourse Island and Mistaken Island in the Pilbara region). The next most extreme action is to link an island to the mainland, thus nullifying its insularity (Table 11).

Many of the activities listed in Table 11 are localised and indirect, and thus are easily overlooked. For example, lighthouses are situated on islands close to ports or shipping lanes and one important duty (until the 1970s) was continuous monitoring of shipping, thus requiring the presence of three families (and thus three cottages). Provision of fresh milk (before refrigeration) necessitated a cow, and transport of supplies and equipment from the landing to the lighthouse and nearby cottages required a horse (*Equus caballus*) or donkey (*E. asinus*). This led to the importation of hay, which elevated the risk of introduction of weeds such as cape weed *Arctotheca calendula*. Some lighthouse keepers also brought their pet cat or dog, resulting in predation of seabirds and mammals. Women established gardens around the cottages,which led to the escape of ornamental plants such as pig's ear *Cotyledon orbiculata* on Breaksea Island (after 1858) and arum lily *Zantedeschia aethiopica* on Eclipse Island (after 1926). Rabbits were also introduced to Eclipse Island by lighthouse staff.

One of the most subtle and indirect impacts of European settlement on mainland Australia is the presence of so many (often self-) introduced plant species on adjacent islands. In South Australia, exotic species comprise 10–55% of the flora of islands (T Robinson et al. 1996). Islands adjacent to Wilson's Promontory, Victoria have 4–44% of their floras composed of introduced species (Norman et al. 2010). The smaller islands of the Furneaux Group in Bass Strait have 32% of plant species introduced (S Harris et al. 2001). The 15 cays comprising the Capricorn–Bunker group of the Great Barrier Reef, Queensland, have 59% of their flora composed of exotic species (Batianoff et al. 2009a). The six cays situated in the Coral Sea are dominated by exotic plant species (40%) and their presence is linked to human activities (Batianoff et al. 2009b). Even some of the most remote of the South Australian islands, upon which there has been minimal human activity, have at least one exotic plant species present (e.g. Dorothee Island, four introduced species, 9% of the flora; Topgallant Island, three introduced species, 15%; South Neptune North Island, six introduced species, 17%; T Robinson et al. 1996, Lawley & Shepherd 2005). Remote islands in Bass Strait corroborate this point: Craggy Island (six introduced plant species, 19% of the flora; S Harris et al. 2001), and Curtis Island (two introduced plant species, 7% of the flora; Kirkpatrick et al. 1974).

Along the southern coast of WA, 116 weed species have been recorded on 43 islands (MT Lohr & Keighery 2014). For the rest of the WA coastline (as far north as the Tropic of Capricorn), 317 weed species have been recorded on 206 islands (MT Lohr & Keighery 2016). These compilations noted a frequent association with islands with a history of intensive human activity. For all of the WA islands so far surveyed by botanists, 374 introduced species have been recorded (I Abbott unpubl.). The 59 species, all exotic, reported on at least ten islands are listed in Table 13. Most species (287, 77%) have been recorded on 1–5 islands, and a further 47 species (13%) have been reported on 6–15 islands (Fig. 19). Most of the species (18) recorded on 1–5 islands are grasses (Poaceae), followed by Asteraceae (eight species), Caryophyllaceae (seven species) and Brassicaceae (four species). The threat status of many of these species is underestimated on islands, as a consequence of threat analyses focusing on pest status

**Table 13**

Introduced plant species (either exotic or indigenous) recorded on at least 10 Western Australian islands. Included at the end are three species of special interest. Information on management activities is provided.

| Species (Family) | No. islands recorded | Comment/management actions |
|---|---|---|
| *Sonchus oleraceus* (Asteraceae) | 160 | Seeds are wind-dispersed |
| *Mesembryanthemum crystallinum* (Aizoaceae) | 148 | Displaces native flora via osmotic interference by accumulation and release of salt (Vivrette & Muller 1977), and forms a monoculture on sites where seabirds nest (Bancroft et al. 2005b) |
| *Chenopodium murale* (Chenopodiaceae) | 64 | |
| *Ehrharta longiflora* (Poaceae) | 62 | Displaces native flora and when cured increases fire risk |
| *Cakile maritima* (Brassicaceae) | 54 | |
| *Bromus diandrus* (Poaceae) | 51 | |
| *Hornungia procumbens* (Brassicaceae) | 46 | |
| *Solanum nigrum* (Solanaceae) | 41 | Fruits eaten and seeds spread by birds |
| *Hordeum leporinum* (Poaceae) | 40 | |
| *Urospermum picroides* (Asteraceae) | 37 | |
| *Lysimachia arvensis* (Primulaceae) | 36 | |
| *Avena barbata* (Poaceae) | 34 | When cured increases fire risk |
| *Sagina apetala* (Caryophyllaceae) | 34 | |
| *Melilotus indicus* (Fabaceae) | 32 | |
| *Polycarpon tetraphyllum* (Caryophyllaceae) | 32 | |
| *Hypochaeris glabra* (Asteraceae) | 31 | |
| *Spergularia rubra* (Caryophyllaceae) | 30 | |
| *Cerastium glomeratum* (Caryophyllaceae) | 29 | |
| *Passiflora foetida* (Passifloraceae) | 28 | Displaces native flora; spread by birds (Pearson et al. 2013) |
| *Helichrysum luteoalbum* (Asteraceae) | 28 | |
| *Erodium cicutarium* (Geraniaceae) | 26 | |
| *Salsola kali* (Chenopodiaceae) | 26 | |
| *Lycium ferocissimum* (Solanaceae) | 24 | Seeds dispersed by birds; physically excludes other plant species and burrowing seabirds; impales birds (Lawley et al. 2005).<br>Removed from Pelsaert Island in 1990 (Fuller & Burbidge 1992); difficult to eradicate from Penguin Island (Rippey et al. 2002a); removed from Milligan and Lipfert islands and Orton Rock (G Keighery et al. 2002); poisoned or removed on Woody Island in 1990-1992 (CALM file 015057F3102) & Cull Island in 1993 (CALM file 034467F3102 Vol. 6); removed from 6 islands in Houtman Abrolhos (JM Harvey et al. 2001); removal under way on Beagle Islands (AA Burbidge pers. comm.) |
| *Parapholis incurva* (Poaceae) | 24 | |
| *Tetragonia decumbens* (Aizoaceae) | 23 | |
| *Medicago polymorpha* (Fabaceae) | 23 | |
| *Malva parviflora* (Malvaceae) | 22 | |
| *Stellaria media* (Caryophyllaceae) | 21 | |
| *Vulpia myuros* (Poaceae) | 21 | |
| *Sisymbrium orientale* (Brassicaceae) | 20 | |
| *Avena fatua* (Poaceae) | 20 | |
| *Arctotheca calendula* (Asteraceae) | 18 | |
| *Bromus hordeaceus* (Poaceae) | 18 | |
| *Lolium rigidum* (Poaceae) | 18 | |
| *Rostraria cristata* (Poaceae) | 18 | |
| *Centaurium spicatum* (Gentianaceae) | 17 | |
| *Poa annua* (Poaceae) | 17 | |
| *Urtica urens* (Urticaceae) | 17 | Favoured by manuring of soils by seabirds |
| *Cynodon dactylon* (Poaceae) | 16 | Invades the succulent plant community on Rottnest Island (G Keighery 1986) |

| Species (Family) | No. islands recorded | Comment/management actions |
|---|---|---|
| *Spergularia diandra* (Caryophyllaceae) | 16 | |
| *Cenchrus ciliaris* (Poaceae) | 15 | |
| *Phalaris minor* (Poaceae) | 15 | |
| *Raphanus raphanistrum* (Brassicaceae) | 15 | |
| *Euphorbia paralias* (Euphorbiaceae) | 14 | |
| *Conyza bonariensis* (Asteraceae) | 13 | |
| *Dischisma arenarium* (Scrophulariaceae) | 13 | |
| *Malva arborea* (Malvaceae) | 13 | Characteristic of seabird nesting areas and favoured by their manuring of soil; forms dense thickets on Bird Island & Green (Rottnest) Island; displacement of native flora and hybridisation with *M. australiana*; reduction in cover of other plant species and of seabird nesting sites (van der Wal et al. 2008); controlled on Seal (Shoalwater Bay) Island (Rippey 2004, Rippey et al. 2002a) |
| *Arctotheca populifolia* (Asteraceae) | 12 | |
| *Lolium loliaceum* (Poaceae) | 12 | |
| *Silene nocturna* (Caryophyllaceae) | 12 | |
| *Trachyandra divaricata* (Asphodelaceae) | 12 | Displaces native flora, as on Rottnest Island (Anon. 1975) |
| *Vulpia bromoides*(Poaceae) | 12 | |
| *Vulpia fasciculata* (Poaceae) | 12 | |
| *Aira caryophyllea* (Poaceae) | 11 | |
| *Briza minor* (Poaceae) | 11 | |
| *Juncus bufonius* (Juncaceae) | 11 | |
| *Polypogon monspeliensis* (Poaceae) | 11 | |
| *Geranium molle* (Geraniaceae) | 10 | |
| *Sonchus asper* (Asteraceae) | 10 | |
| *Zantedeschia aethiopica* (Araceae) | 6 | Garden escape; widespread infestation on Eclipse and Garden islands; displaces native flora; seeds spread by birds. On Eclipse sland in 1954 'chok[ing] the ground wherever the soil is deep enough' (Warham 1955), presumably having spread from its introduction after 1926 when the lighthouse was established. By 1975 it dominated about half of the island (Abbott 1981a) |
| *Opuntia stricta* (Cactaceae) | 5 | Garden escape; eradicated from Enderby Island (DCLM 1990) |
| *Bryophyllum delagoense* | 2 | Garden escape; dominates islands (MT Lohr & Keighery 2016) |

Sources: Abbott 1980a, 1981a; Abbott & Black 1978, 1980; Abbott & Watson 1978; Abbott et al. 2000, 2006; Buckley 1983, AA Burbidge & George 1978, Claymore & Markey 1999, Dinara Pty Ltd 1987, Friends of Woody Island 2004, Gillham 1963, JM Harvey et al. 2001, Henson et al. 2014; G Keighery 1995, 1998; G Keighery & Muir 2008; G Keighery et al. 1995, 2002, 2006; LeProvost et al. 1987; MT Lohr & Keighery 2014, 2016; Lyons et al. 2014, NG Marchant & Abbott 1981; Rippey et al. 1998, 2003; V & C Semeniuk Research Group 1989; WAPET 1991, 1992; Western Australian Herbarium 1998–, JH Willis 1953. Species names from these sources and their status as exotic have been updated using Western Australian Herbarium (1998–). Identifications not supported by a voucher specimen deposited in the Western Australian Herbarium have been accepted at face value.

on mainland Australia (see MT Lohr & Keighery 2014 for discussion). Such evaluations overlook the role of disturbance caused by breeding seabirds in favouring many of these introduced plant species.

In the Archipelago of the Recherche, the most remote islands have few introduced plant species compared to inshore islands (JH Willis 1953; AA Burbidge et al. 1982; G Keighery 1995): Spindle (0%), Six Mile (0%), Salisbury (0%), Douglas (0%), Termination (0%), MacKenzie (Round; 2%), Pasco (3%), New Year (4%), Westall (Combe; 4%), Mondrain (4%), Wilson (6%), Kermadec (Wedge; 7%) and Long (8%). However, two other offshore islands have a moderately high level of introduced plant species present: Daw (11%) and Anvil (11%). Several inshore islands that are known to have been grazed have a high proportion of introduced plant species: Woody (26%), Figure of Eight (23%) and Boxer (21%). Some other inshore islands also have a high proportion of introduced plant species, perhaps suggestive of past (undocumented) grazing: Taylor (23%), Wickham (Stanley; 22%) and Bellinger (13%). However, others such as Remark (12%) and South Twin Peak (15%) are unlikely to have been grazed. Some large islands were never grazed and these have few introduced species: Sandy Hook (5%) and Middle (1%).

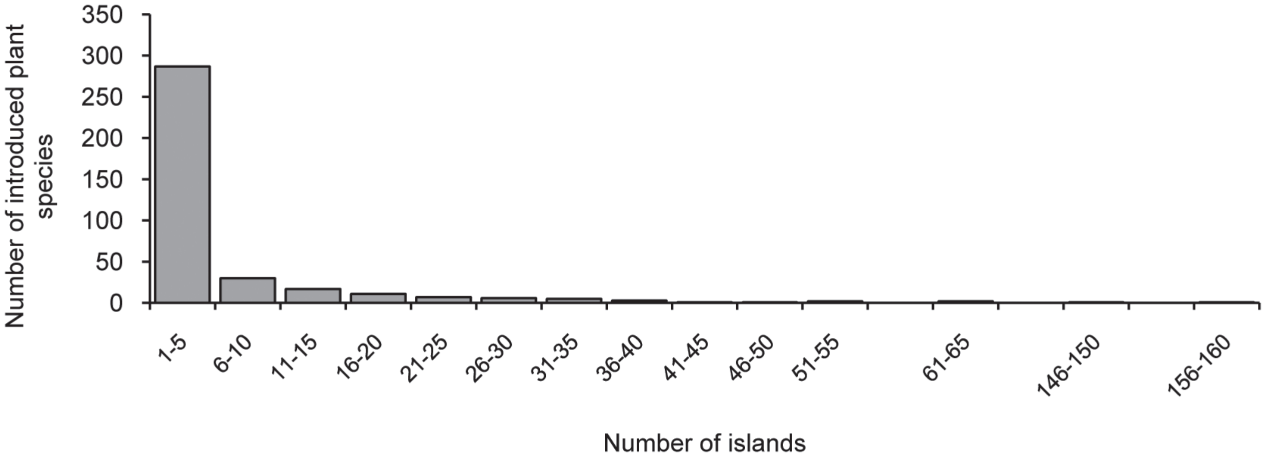



*Figure. 19. Occurrence of introduced plant species on WA islands.*

In Houtman Abrolhos, introduced species comprise 40% of the flora (JM Harvey et al. 2001). The presence of introduced plant species is particularly prevalent on those islands with occupied buildings and those mined for guano (Fig. 20). On Rat Island (Houtman Abrolhos), 47% of the flora is introduced (Dunlop 2013). In 1897, Helms (1898) noted the occurrence of common sowthistle *Sonchus oleraceus*, pimpernel *Lysimachia arvensis* and nettle-leaf goosefoot *Chenopodium murale* on islands mined for guano since 1884. These introductions were attributed to the importation of chaff to feed a horse kept for conveying the guano to a jetty.

Storr (unpubl.) attributed the paucity of exotic plant species (<10%) on seven islands in Jurien Bay to the lack of farming on the adjacent mainland. When these islands were sampled 25 years later, this proportion had increased to 25–50% (G Keighery et al. 2002), doubtless caused by an increase in illegal holiday shacks along

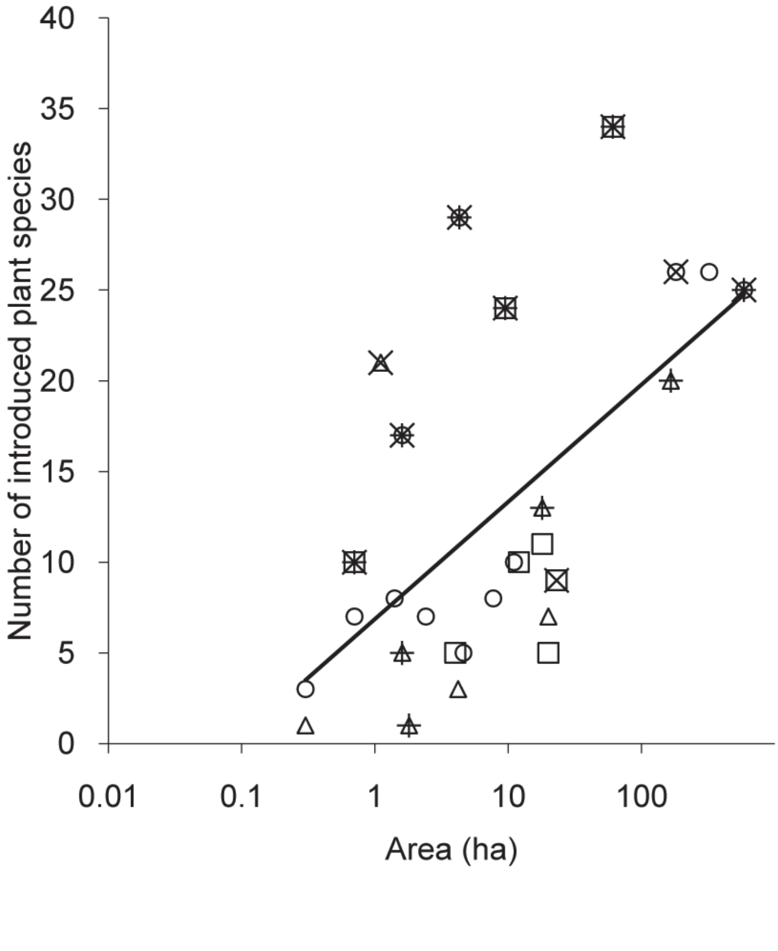



*Figure 20. The number of introduced plant species versus island area for islands in Houtman Abrolhos (data from JM Harvey et al. 2001): Easter Group (□); Pelsaert Group (△); Wallabi Group (○); islands with occupied buildings (x); islands with guano mining (+). No. species = 6.46($Log_{10}$ Area) + 6.87, $R^2$ = 0.37, n = 28, $p < 0.001$.*

the coast and greater use of boats by holiday-makers based at Jurien and Lancelin. Gillham (1963) also drew attention to the high proportion of exotic plant species (41%) on Seal Island near Cape Leeuwin.

In contrast, the larger islands in Shark Bay have unexpectedly low proportions of exotic plant species present: Dorre Island, 8%; Bernier Island, 10%; Faure Island, 13%; Dirk Hartog Island, 14% (AA Burbidge & George 1978; Claymore & Markey 1999; G Keighery & Muir 2008). The 34 smallest islands (<162 ha in area) have a greater proportion of exotic plant species (20%, G Keighery et al. 2006). This may be linked with the presence of breeding colonies of seabirds.

Islands in Shark Bay that have not been mined for guano show the expected increase in plant species richness with island area, whereas those so mined do not show this relationship (Fig. 21). It appears that mining on the larger islands has not reduced the number of native plant species, whereas on small islands it has increased the number of both native and introduced plant species.

Islands in tropical WA have relatively few introduced plant species present. Barrow Island, WA's second largest island, has only 4% of its flora introduced (Buckley 1983). This island was only briefly exposed to grazing by sheep (*The West Australian* 6 January 1882: 2) and has never experienced grazing by goats or cattle, and had no jetty until recently. A large part of the island has been a large oil field since the 1960s, with strict quarantine provisions in place (Butler 1983, 1987). Doole and Roberts islands (Exmouth Gulf) and Depuch Island (Pilbara region) have also been little visited by Europeans, and have only 2–3% of their floras introduced (Royce 1964; Start & McKenzie 1992). Varanus and Bridled islands (Lowendal Group) are used for industrial purposes but unexpectedly have only 2%

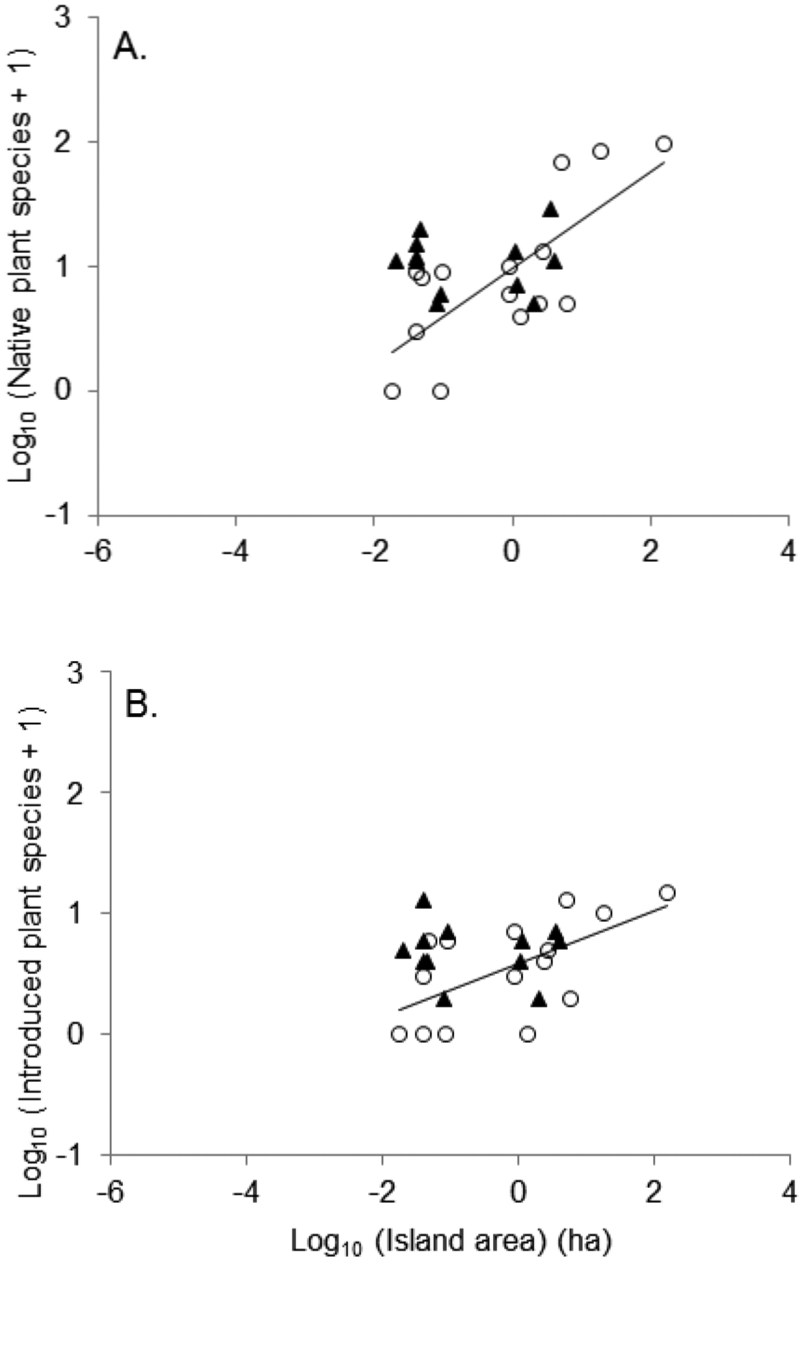



*Figure 21. The number of (A) native and (B) introduced plant species versus island area for small islands mined (▲) or not mined (○) for guano in Shark Bay (data from GJ Keighery et al. 2006). Unmined islands: $Log_{10}$(Native plant species) = 0.39($Log_{10}$ Area) + 0.98, $R^2 = 0.55$, $n = 15$, $p < 0.002$; $Log_{10}$(Introduced plant species) = 0.22($Log_{10}$ Area) + 0.58 $R^2 = 0.37$, $n = 15$, $p < 0.02$.*

and 3.4% of their floras introduced (V and C Semeniuk Research Group 1989). Thevenard Island has been used for several decades for recreation and oil production but introduced species comprise only 3% of its flora (WAPET 1991). Legendre Island has 3.5% of its flora introduced (J Richardson et al. 2007). In contrast, Koolan Island was mined for iron ore for 28 years and supported a population of 850 people. With this high level of disturbance, introduced plant species comprise 15% of this island's flora (G Keighery et al. 1995). Sunday Island, a mission station for nearly 70 years, has 22 introduced plant species (Lyons et al. 2014), constituting 18% of its flora (M Lyons pers. comm.). This contrasts with 23 other islands studied in the Kimberley region (0.3–4.0%), and reinforces the linkage with gross, unmanaged disturbance associated with European activities.

Most of the plant species so far introduced to WA islands have an innocuous impact on island ecology (G Keighery 1996; MT Lohr & Keighery 2014, 2016; Table 13). The most deleterious species are buffel grass (*Cenchrus ciliaris*) on some Pilbara islands, African boxthorn (*Lycium ferocissimum*) on the Beagle Islands, and ice plant (*Mesembryanthemum crystallinum*) on many islands. Some species that have major impacts on coastal mainland sites (e.g. bridal creeper *Asparagus asparagoides*, marram grass *Ammophila arenaria*, lupin *Lupinus* spp.) so far have been seldom recorded on WA islands. One species (arum lily *Zantedeschia aethiopica*) has been subject to intensive control with herbicide on Garden Island (Wykes 1997). On Rottnest Island, >200 species of exotic herbs have been cultivated within the settlement region but very few of these have spread from gardens (G Keighery 1986). Up to 1998, 122 introduced plant species (54% of the flora) had been recorded from Garden Island (G Keighery 1998). This includes several records of previously unrecorded species (*Mesembryanthemum crystallinum, Lycium ferocissimum*). Large increases in frequency of occurrence of *Trachyandra divaricata* were recorded between 1990 and 1996 on Garden Island (McArthur 1998). Introduced species comprise about 40% of the flora of Rottnest Island (Rippey et al. 2003).

Kikuyu grass (*Cenchrus clandestinus*), common in parts of mainland south-west WA, has been recorded on only one WA island (Garden Island). On islands of NSW, kikuyu grass forms dense mats that restrict the construction of burrows by seabirds (RM Cooper et al. 2014). On Big Five Island, the species formed a mattress c. 1 m thick (Gibson 1976). On Montagu Island it has spread greatly, covering 16% of the island in 1990 and 37% by 2000, and causing entanglement of little penguins and avoidance of dense swards by them for nesting (Weerheim et al. 2003). This expansion of kikiuyu grass followed the removal of goats (Heyligers & Adams 2004).

## Sampling completeness and comparability

Similarity in the degree of exploration and search effort of islands is the basis of all valid numerical analyses involving number of species (Remsen 1994; Solem 1990). It has long been recognised (at least since 1768) as a significant factor, 'that district produces the greatest variety which is the most examined' (G White 1789: 55). Recent examples include the increase in bird species recorded on islands in Torres Strait from 150 in 1983 to 252 in 2012 (Lavery et al. 2012), the increase in the number of bird species originally present on a Tongan island with sampling intensity measured by the number of fossil bones identified (Franklin & Steadman 2008), and the discovery of species following improved survey effort, particularly on islands without an airstrip or on remote parts of large islands (Steadman 2006). Equally important are differences in the season of examination, with the dry season yielding fewer plant species than the wet season on the same island (Forster 1778: 172). Butterflies may have short and variable periods when adults are flying. Consequently, on short surveys species are often overlooked (N Davies & Smith 1997). While it is implicit in publications that islands with incomplete or suspect lists of species are excluded from consideration, this is not often stated (e.g. Forster 1778; Reed 1981).

Seldom disclosed in the global scientific literature is how lists of species on islands have been derived, particularly the dates and duration of study, the number of trap nights, and the extent to which parts of large islands were left unexamined or unsampled. Laudable examples of the provision of this information are Wollaston (1865); LA Smith et al. (1978), who report on bird species found on many large islands (1–180 km$^2$); Dueser et al. (1979); Chaloupka and Domm (1985); Adler and Wilson (1985); Boomsma et al. (1987); Woinarski et al. (1999b, 2001); How et al. (2006); Foufopoulos and Mayer (2007); and Greenslade (2008a). Small islands are more likely to be censused completely, whereas bias due to incomplete sampling or collecting increases on larger islands (EO Wilson 1961; van der Werff 1983; Willerslev et al. 2002; WR Turner & Tjørve 2005). However, even small islands (<1 ha) that were searched for plant species only one week apart resulted in different totals being recorded (SG Nilsson & Nilsson 1983).

Studies of invertebrates often result in the collection of large numbers of specimens, especially if pitfall traps are used. It is necessary to eliminate the bias of sample size between sites by constructing rarefaction curves (Valovirta 1984; Niemelä et al. 1985).

Detection of some plant species is hampered when introduced herbivores are present. Following the extirpation of goats on Guadalupe Island (Mexico) in 2005, several native plant species presumed extinct were found again (Garcillán et al. 2008).

Islands that have been visited more often by observers or collectors should have more species recorded than those less often visited (Connor & Simberloff 1978; Noske & Brennan 2002). Duration of the visit is also likely to influence the number of species recorded, with longer visits likely to result in the discovery of more species (Willerslev et al. 2002). For example, plant specimens were collected on Middle

Island (Archipelago of the Recherche) during two days in January 1802 (Vallance et al. 2001), yielding 47 plant species (Weston 1985). In 1950 one day's collection yielded 136 species (JH Willis 1953). Extended visits from 1973 to 1981 have resulted in c. 235 plant species being recorded (Weston 1985; Hopkins & Harvey 1989). Six plant species (*Alyogyne hakeifolia, A. huegelii, Gyrostemon sheathii, Scaevola aemula, Ornduffia parnassifolia, Solanum symonii*), now known to be fire ephemerals, were collected on Middle Island in 1802 but were not collected again until after the 1972–73 fire. This indicates that seeds of these species had lain dormant (with no plants above ground) for >170 years. Without the 1802 collection, these species would have been falsely assumed to represent immigrations (Weston 1985; Hopkins & Harvey 1989).

In contrast, JH Willis (1953) was unable to find *Chorizema ilicifolia* and *Lobelia heterophylla* in the Archipelago of the Recherche, last collected there in 1792. However, both species were recollected there in the 1970s (Western Australian Herbarium 1998-). The flora of Woody Island has also been increased. One day's collecting in 1950 yielded 87 species (JH Willis 1953), nine days' collecting in 1975 yielded 121 species (Goodsell et al. 1976), and collecting in December 2002 and October 2003 yielded 137 species (E Rippey in Western Australian Herbarium 1998-). This reinforces the concept that the number of visits and time spent during each visit to the same island are very important factors.

Timing of visits needs to relate to the phenology of the taxon under study. Thus, a visit in late summer in south-west WA would likely overlook any annual plant species, as these die by early summer (cf. Gillham 1961c; Norman & Brown 1979). A late-summer survey of terrestrial isopods on islets around Rottnest Island yielded few records compared to sampling during autumn and winter (Bunn 1980). Visits to the same island at different seasons may also lead to invalid conclusions about the breeding of seabirds (LA Smith et al. 1978).

Collecting of reptiles in the Montebello Islands in 2000 resulted in numerous new records of species. These were attributed to serendipity, time of the year, high rainfall in the previous two years, and reduced predation pressure from rats and cats (J Richardson et al. 2006).

Adequacy of sampling is difficult to achieve on large islands, and is most influenced by the taxon studied. As an example, discovery of all plant species on three small satellite islands of Rottnest Island, WA was complete after 15 minutes of searching (Fig. 22). In contrast, lists of the plant species present on the islands of the Galápagos remain incomplete, leading one to question the validity of statistical study that aims to predict species richness from island area, elevation etc. (MP Johnson & Raven 1973; Connor & Simberloff 1978; van der Werff 1983).

Even conspicuous plant species can be present but overlooked, as seems to have been the case with *Exocarpos aphyllus* and *Hardenbergia comptoniana* on Penguin Island. Neither species was recorded by Storr (1961) but they were discovered in 1972 (Hussey 1973).

On occasion inadequate sampling of the mainland adjacent to islands has led to incorrect inferences. Alexander (1922) deduced from the presence of various bird species on Houtman Abrolhos that were absent from the adjacent mainland that the avifauna of these islands have a south-western character. Subsequent fieldwork has revealed, however, that these bird species actually do occur on the adjacent mainland (J Ford 1960; Storr 1965d).

On large islands, such as the 25,000 ha Guadalupe Island (Mexico), the access route of different collecting

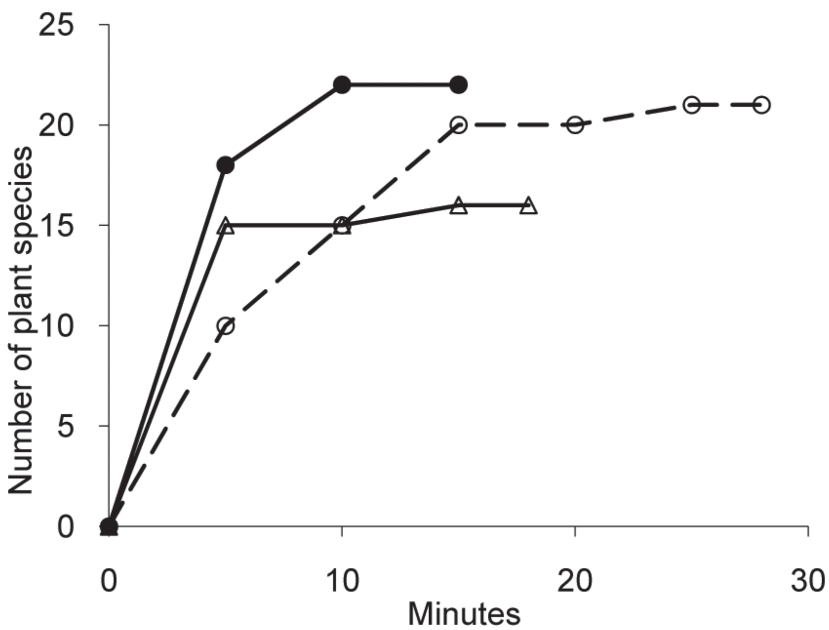



*Figure 22. Accumulation of plant species in relation to search time on three islets adjacent to Rottnest Island (I Abbott unpublished): Green Island (○), Parakeet Island (△) and Rock S end Geordie Bay (●).*

expeditions may have influenced the plant species collected (Garcillán et al. 2008). As well as implicating rarity and patchy distributions in explaining the accumulation of species with sampling effort, it seems that the preferences of collectors for species judged to be more interesting for research are important. Plant species that are rare or difficult to find are over-represented in herbaria, in contrast to exotic weeds, which are common on the island and under-represented in collections.

Finally, even frequently visited islands of moderate size defy the attainment of certainty about the status of some species. For example, Naturalists Island (170 ha, Kimberley region) was visited 21 times during the period 1984–2007, resulting in 80 bird species being recorded (Coate 2008a). However, the status (i.e. whether resident, regular visitor or vagrant) of most species remains unresolved.

## Ecological interactions

As in all ecosystems, there is a complex interplay between species, with some interactions overriding or overwhelming others. It remains uncertain, however, if island ecosystems constitute a unified community of species and resemble a closely woven web, which touched at any point, trembles in all its parts. Alternatively, is the ecosystem a fragile cohesion of species or merely an assemblage of species that occur together only because their geographical ranges overlap but with limited interaction of species?

Some types of interactions (e.g. interspecific competition) have been well studied and perhaps overstated, whereas others remain either little studied or possibly overlooked or underestimated. Competition between species, predation by native species on prey species, pollination of plant species by animal species, over consumption of palatable plant species by herbivores, and the dispersal of fruits of native plants by frugivorous animal species can be significant processes on islands, and are well documented globally (e.g. Burns 2005b; Carlquist 1974; Crowell 1961; Grant 1970; Lack 1971; Thornton 1996; Wardle et al. 2001).

Interspecific competition has often been invoked to explain the reduced size of island avifaunas and the failure of potential colonists to establish (e.g. Darwin 1859; Lack & Southern 1949; EO Wilson 1961; Lack 1966, 1976). This is because isolation affords 'effective protection against the entrance of competitors' (Allee & Schmidt 1951: 627). Experimental study has confirmed the operation of interspecific competition, in the form of aggressive interactions (Reed 1982; Cole 1983). The resources for which competition is assumed include food (i.e. species of animals and the species of plants they eat) and habitat (dominant plant species and their structure). Interspecific competition is presumed to have occurred soon after isolation and to have continued until equilibrium was reached in terms of the niches available. The general ecological poverty on islands favours the evolution of generalist species, which continue to prevent the establishment of specialist species that reach the island (MacArthur 1972; Lack 1976). On islands in Torres Strait, the yellow-spotted honeyeater (*Meliphaga notata*) and varied honeyeater (*Lichenostomus versicolor*) do not coexist as residents. Nor do the brown honeyeater (*Lichmera indistincta*) and dusky honeyeater (*Myzomela obscura*; Draffan et al. 1983). This 'mosaic' or 'chequerboard' pattern of distribution may indicate the strong operation of interspecific competition (EO Wilson 1959, 1961; Diamond 1975), although such an explanation is disputed by Simberloff (1978). Other non-random patterns of distribution are suggestive of the operation of interspecific competition (Alatalo 1982). However, without the rigorous elimination of other potential factors, such patterns may be little more than interesting coincidences.

An unusually detailed quantitative study of populations of landbirds on 44 Finnish islands found little evidence suggestive of interspecific competition excluding species from these islands (Haila et al. 1983). A study of the occurrence of six woody plant species on 27 islands in British Columbia failed to demonstrate non-random co-occurrence for five of them (Burns 2007). Deterministic processes such as interspecific competition therefore do not shape the distribution of most of these plant species.

Sometimes the extent of species impoverishment on islands is misleading. On Corsica, for example, the avifauna comprises c. 70% of the species present on an equivalent mainland area. This species impoverishment is, however, unevenly distributed among the different habitats (J-L Martin 1992). In matorral shrubland the species richness of birds is greater than in this habitat on the mainland, as a result of bird species restricted to forest on the mainland occurring also in matorral on Corsica. The interspecific competition paradigm instead predicts that habitat expansion on Corsica should be from matorral to forest.

As previously indicated ('Species characteristic of WA islands', above), competitive interactions (or absence thereof) have been invoked to explain changes in beak dimensions of birds, body size, abundance, habitat, foraging methods, etc. The extent to which this explanation is based on competition (the dominant paradigm of ecology during the period 1950–1980) or on a careful and detailed evaluation of other relevant factors remains uncertain. The study by Yeaton and Cody (1974) measured the abundance of insects and quantified the vegetation profile on 19 islands off Washington State, USA. It found strong evidence for competitive release in density of song sparrows (*Melospiza melodia*). A similar comparison of a large island off California demonstrated competitive release of four bird species (Yeaton 1974). There are, however, other studies that have failed to demonstrate or confirm interspecific competition as the cause of these insular phenomena (e.g. Wiens 1977a; Dunham et al. 1978; Emlen 1979; Connor & Simberloff 1979; Vassallo & Rice 1982). Furthermore, many of the studies advocating an important role for interspecific competition have themselves been criticised (e.g. Vuilleumier 1977).

Analysis of trophic structure, a measure of functional integrity, of arthropod communities on small islands has resulted in divergent explanations. One emphasises the role of interspecific competition in determining the proportion of species of herbivores, scavengers etc. (Heatwole & Levins 1972). The other emphasises species characteristics such as dispersal ability and microhabitat requirements (Simberloff 1976a).

Assessment of the operation of interspecific competition on WA islands has been limited and largely inferential (Serventy 1951; AR Main 1961a; J Ford 1963). Storr (1966) invoked competition for the same habitat (beaches and dunes) between the Australian pipit and red-capped plover (*Charadrius ruficapillus*) to explain the occurrence in Houtman Abrolhos of the former species on North Island and the latter in the nearby Wallabi Group. However, AA Burbidge (pers. comm.) considers this pattern to have resulted from chance—both species were present on North Island in 2006 and the pipit was absent in 2013 (Blyth et al. 2014). The potential role of competitive exclusion between landbird species was assessed by Abbott (1981b), but no convincing examples were found. Explanations involving climatic change or differences in vegetation have instead been emphasised (Serventy 1951; AR Main 1961a). However, on those small islands near Fremantle with only two species of plant present, *Nitraria billardierei* and *Threlkeldia diffusa* never occur together, suggestive of competitive exclusion (Abbott 1977a).

The skink *Menetia greyii* is common and widespread on mainland WA but is absent from Barrow Island. A similar species of skink, *Proablepharus reginae*, is rare on the mainland but abundant on Barrow Island (LA Smith 1976; Heatwole & Butler 1981). This complementary distribution and abundance is suggestive of interspecific competition (LA Smith 1976). An alternative explanation is geological. Barrow Island is an extension of North West Cape and not the Pilbara mainland (AA Burbidge pers. comm.). On the smaller islands in the Dampier Archipelago, the geckoes *Gehyra* spp. (four species) and Bynoe's gecko (*Heteronotia binoei*) tend to occur on different islands, which may have resulted from interspecific competition (Connell 1983).

As in all populations, competition between conspecifics can be intense, and is ultimately linked to a shortage of nutrients, particularly nitrogen, in the environment (TCR White 1993). This is well illustrated by the tammar on Garden Island. On fertilised and irrigated lawns these wallabies occur at twice the density as in natural bushland (2.45 versus 1.27 ha$^{-1}$), and have higher reproductive success (BK Chambers & Bencini 2010). The tree *Melaleuca lanceolata* on Garden Island attains a height of 10 m and a diameter (at breast height) of 30 cm at the edge of groves, compared to only 6–8 m and 10–15 cm respectively within groves (McArthur 1996a).

Predation of seabird eggs by reptiles has been documented (J Gilbert 1843 in Gould 1865; Warham 1956a, 1958; JAK Lane 1978; Wooller & Dunlop 1979, 1990; Meathrel & Klomp 1990). Western ravens also prey on seabird eggs and their young (Johnstone et al. 1990a). The white-bellied sea-eagle (*Haliaeetus leucogaster*) nests on many islands (Johnstone & Storr 1998), and preys on seabirds and wallabies (Whitlock 1919; Storr 1965d, 1966; Surman & Nicholson 2009). Other raptors, often recorded on WA islands (Dunlop et al. 1988; Johnstone & Storr 1998; Table 14), are presumably visiting and are likely to have less impact on breeding seabirds. On Barrow Island, the perentie (*Varanus giganteus*) preys on hatchlings and eggs of the green turtle (B Green et al. 1986). However, no comparative studies of the impact of predators on prey species on WA islands, by contrasting islands with or without predator species, have been published.

Predator/prey interactions on islands sometimes involve threatened species, as on Dorre Island (boodies eating hatchling loggerhead turtles, ND Thomas 2003) and Barrow Island (golden bandicoots consuming eggs of green turtles, KD Morris 1987). Such examples demonstrate that human intervention needs to be careful and restrained.

The absence of predators from many islands may allow the development of hyperabundant populations of herbivores, with pronounced demographic impacts on plant populations (Terborgh et al. 2006; Spiller & Schoener 2007). The absence of top predators (such as lizards) can result in the presence of more species of mesopredators (such as spiders), as well as very high densities of spiders (TW Schoener & Toft 1983; Spiller & Schoener 1998). However, not all potential prey species exhibit greater densities on islands (TL George 1987). Comparable studies on WA islands are yet to be undertaken.

The introduction of predators to islands may also have telling unforeseen impacts. On Menorca Island, a frugivorous endemic species of lizard became extinct, and this disrupted seed dispersal of an endemic plant species (Traveset & Riera 2005). There have been no similar studies on WA islands. Nonetheless, the re-introduction of bandicoots to Hermite Island should impact on ground-nesting birds. When black rats colonised Penguin Island in 2012, they caused almost complete failure in breeding success of bridled terns (as would be predicted), as well as injuring King's skinks and ringbarking vegetation, apparently in quest of water (Bettink 2015).

Published records of butterflies and birds feeding at flowers on WA islands are limited (Abbott 1982; Abbott & Black 1978; Keast 1975; NL McKenzie et al. 1995; Sedgwick 1978; Söderberg 1918; Storr 1965c; Warham 1957; AAE Williams 1997). The extent to which pollination of populations of plant species in the genera *Bossiaea, Calothamnus, Chorilaena, Eucalyptus, Grevillea, Hakea, Kunzea, Leptospermum, Melaleuca, Paraserianthes* and *Templetonia* on islands is dependent on the presence of particular bird and insect species remains unstudied (cf. PA Cox & Elmqvist 2000; Thornton 1996). There are numerous islands along the south-western coast of WA,

**Table 14**

Landbird species recorded as vagrant (not of regular occurrence) on islands of Western Australia. Non-Australian species are excluded. Two measures of isolation are provided for islands that lie closer to a larger island than to the mainland: Distance to the potential stepping stone island, and distance to the mainland.

| Species | Island (distance to closest presumed source area, km) | Reference |
|---|---|---|
| Unidentified species of quail | Browse (175), Adele (85) | LA Smith et al. 1978, J Walker 1892 |
| *Coturnix pectoralis* | Barrow (55), Faure (6), North (60) [sp. uncertain], Pelsaert (60) [sp. uncertain], Lancelin (0.5), Garden (2), North Twin Peak (8) | Blyth et al. 2007, MG Brooker et al. 1995b, Dell & Cherriman 2008, N Dunlop pers. comm., Fuller & Burbidge 1981, Mather 2015, AN Start pers. comm., WABN No. 135: 25 |
| *Coturnix ypsilophora* | Hermite (20), Trimouille (4), Barrow (55), Varanus (10), Legendre (3), Thevenard (20), Faure (6), Woody (7), Sandy Hook (8), MacKenzie (13/20), Mondrain (11), Middle (Recherche) (9), Daw (32) | Abbott & Black 1978, Andrews 1959, AA Burbidge 1971, AA Burbidge & Prince 1972, AA Burbidge et al. 2000, Dinara Pty Ltd 1988, Goodsell et al. 1976, Kenneally et al. 2000, Kinghorn 1927, Mather 2015, J Richardson et al. 2007, Sedgwick 1978; Serventy 1947, 1952; LA Smith et al. 2005, Storr MSb, Tingay & Tingay MS, WABN No. 85: 8, WAPET 1993 |
| *Threskiornis moluccus* | Koolan (1), Penguin (0.7) | WA database, NL McKenzie et al. 1995 |
| *Threskiornis spinicollis* | Koolan (1) | NL McKenzie et al. 1995 |
| *Elanus caeruleus* | Koolan (1), Hermite (20) and other unidentified islands in Montebello group, Barrow (55), Varanus (10), Thevenard (20), Faure (6), Whitlock (<1), Rottnest (18), Carnac (8), Garden (2), Penguin (0.7) | I Abbott unpubl., MG Brooker et al. 1995b, AA Burbidge et al. 2000, Dell & Cherriman 2008, Dinara Pty Ltd 1986–1993; Mather 2009, 2015; NL McKenzie et al. 1995, Sedgwick 1978, Wykes et al. 1999, Saunders & Rebeira 2009, *The Naturalist News* November 1980: 9-10; WABN No. 93: 4, 102: 14–15, 106: 27; WAPET 1993, Wykes et al. 1999 |
| *Elanus scriptus* | Adele (85) | Abbott 1982, Serventy 1953 |
| *Hamirostra isura* | Barrow (55), N Fisherman (5), Garden (2) | MG Brooker et al. 1995b, R Johnstone pers. comm., Sedgwick 1978 |
| *Hamirostra melanosternon* | Trimouille (4) and unidentified island in Montebello Group, Barrow (55), Varanus (10), Faure (6) | AA Burbidge 1971, AA Burbidge et al. 2000, Dinara Pty Ltd 1986-1993, Mather 2015, Sedgwick 1978 |
| *Hieraaetus morphnoides* | Dirk Hartog (1), Faure (6), Rottnest (18), Garden (2), Penguin (0.7) | MG Brooker et al. 1995b, Dell & Cherriman 2008; Mather 2009, 2011, 2015; Saunders & Rebeira 2009; WABN No. 98: 7, 102: 14-15, 105: 4, 145: 38; BA Wells & Wells 1974, Wykes et al. 1999 |
| *Aquila audax* | Barrow (55), Bernier (39), Garden (2), Bald (1), Woody (7), Mondrain (11), Middle (Recherche) (9) | I Abbott unpubl., Andrews 1959, C Napier 1996 unpubl., Sedgwick 1978, V Serventy 1952, GT Smith 1977, Storr 1965a, Wykes et al. 1999 |
| *Accipiter fasciatus* | Dirk Hartog (1), Faure (6), Rottnest (18), Garden (2), Eclipse (6), Coffin (0.25), Woody (7), Charley (5), Sandy Hook (8), Goose (1) | I Abbott unpubl., Abbott & Black 1978, Anon. 1989, Carter 1917, Dell & Cherriman 2008, Fullagar & van Tets 1976, Goodsell et al. 1976; Mather 2009, 2015; LE Sedgwick MS, Storr 1965c, Saunders & Rebeira 2009, V Serventy 1952, GT Smith 1977, T Stoneman 1995 unpubl., Tingay & Tingay MS; WABN No. 101: 3, 102: 15; Whitlock 1921a, Wykes et al. 1999 |
| *Accipiter cirrocephalus* | Varanus (10), Dirk Hartog (1), Faure (6), Rottnest (18), Carnac (8), Garden (2), Breaksea (5), Michaelmas (2), Bald (1) | Abbott 1978a,1980e; Anon. 1989; MG Brooker et al. 1995b, Carter 1917, Dell & Cherriman 2008, Dinara Pty Ltd 1986-1993, Mather 2015, LE Sedgwick MS, WABN No. 44: 4, JAL Watson pers. comm., Whitlock 1921a, Wykes et al. 1999 |
| *Circus approximans* | Hermite (20) and other unidentified islands in Montebello Group, Faure (6), Pelsaert (60), Lancelin (0.5), Rottnest (18), Garden (2), Eclipse (6), Middle Doubtful (3), Woody (7), Middle | I Abbott unpubl., MG Brooker et al. 1995b, AA Burbidge et al. 2000, Dell & Cherriman 2008, Fuller & Burbidge 1981, Goodsell et al. 1976; Mather 2011, 2015; Tingay & Tingay MS, WABN No. 145: 40, Warham 1955 |

| Species | Island (distance to closest presumed source area, km) | Reference |
|---|---|---|
| *Circus assimils* | Koolan (1), unidentified island in Montebello Group, Varanus (10), Bernier (39), Dorre (52), Dirk Hartog (1), Faure (6), N Fisherman (5), Rottnest (18), Penguin (0.7) | AA Burbidge 1971, AA Burbidge et al. 2000, Carter 1917, Dell & Cherriman 2008; Dinara Pty Ltd 1986-1993, R Johnstone pers. comm., Lipfert 1912, Mather 2015, NL McKenzie et al. 1995, Ogilvie-Grant 1910, Saunders & Rebeira 2009, LE Sedgwick MS; WABN No. 27: 4, 32: 8, 43: 2, 148: 6, 150: 5, 157: 12; Whitlock 1921a |
| *Haliastur sphenurus* | Unnamed island in Montebello Group, Barrow (55), Varanus (10), Legendre (3), Rottnest (18), Carnac (8), Penguin (0.7) | BirdLife WA database, AA Burbidge 1971, Dinara Pty Ltd 1986-1993, J Richardson et al. 2007, Sedgwick 1978, Storr 1965c, JAL Watson 1956 |
| *Ardeotis australis* | Barrow (55), Rottnest (18) | Sedgwick 1978, *The Perth Gazette* 20.8.1842: 3 |
| #*Gallirallus philippensis* | Lacepede (20-30), Dirk Hartog (1), West Wallabi 60), Pelsaert (60), Lancelin (0.5), Rottnest (18), Daw (32), Anvil (10) | I Abbott unpubl., Anon. 1989, AJ Campbell 1890, Carter 1923b, Fuller & Burbidge 1981, Garstone 1978, Helms 1898, V Serventy 1952, LA Smith et al. 2005, Storr MSb, Tarr 1948; WABN No. 84: 25, 101: 3, 103: 17, 145: 28-29 |
| #*Porzana tabuensis* | Unidentified island near Rat (Houtman Abrolhos), Beacon (6.5), N Fisherman (5), Rottnest (18), Eclipse (6), Beaumont (15), Wickham [Stanley] | P Collins 1990 unpubl., J Ford 1965, LA Smith et al. 2005, *The West Australian* 7.12.1907: 5; WABN No. 46: 8, 130: 5, 134: 28; Warham 1955 |
| ^*Pedionomus torquatus* | Pelsaert (60+) | AA Burbidge pers. comm. |
| *Turnix varius* | Dirk Hartog (1), Mondrain (11) | SJJF Davies & Chapman 1974, V Serventy 1952 |
| *Turnix pyrrhothorax* | Koolan (1) | NL McKenzie et al. 1995 |
| *Turnix velox* | Faure (6) | Dell & Cherriman 2008, Mather 2015 |
| *Burhinus grallarius* | Koolan (1), Barrow (55), Bernier (39), Dorre (52), Garden (2) | Cale 1992, source unknown (incorrectly attributed to Abbott 1980f by MG Brooker et al. 1995b), NL McKenzie et al. 1995, Ogilvie-Grant 1910, WABN No. 135: 25 |
| *Vanellus tricolor* | Faure (6), North (Abrolhos) (22/60), unidentified islands in Easter Group, Eclipse (6), Middle (Recherche) (9) | Mather 2015, Serventy 1952, Storr et al. 1986, Warham 1955 |
| •*Columbia livia* | Varanus (10), Dirk Hartog (1), West Wallabi (60), Rottnest (18), Carnac (8) | DCLM file 014447F3201, Dinara Pty Ltd 1986-1993, Saunders & Rebeira 2009, Storr 1965d, BA Wells & Wells 1974 |
| •*Streptopelia chinensis* | Garden (2) | Abbott 1980f, MG Brooker et al. 1995b, K Buller 1949, Calderwood 1953; Sedgwick 1940, 1958; Serventy 1938, Storr MSb |
| •*Streptopelia senegalensis* | Bernier (39), Garden (2), Penguin (0.7) | Alexander 1921b, BirdLife WA database, K Morris et al. 1994 |
| *Phaps chalcoptera* | Dirk Hartog (1), Faure (6), Garden (2) | SJJF Davies 1980, SJJF Davies & Chapman 1974, Dell & Cherriman 2008, Mather 2015; *The Naturalist News* November 1980: 9-10, May 1982: 16; BA Wells & Wells 1974 |
| *Phaps elegans* | Mistaken (<0.1), Woody (7), Remark (1.7/11), MacKenzie (13/20), Goose (1) | Abbott & Black 1978, Anon. 1989, Goodsell et al. 1976, Hull 1922, SG Lane 1982l, SG Lane unpubl., Serventy 1947, 1952, WABN No. 85: 8 |
| *Geopelia cuneata* | Koolan (1), Varanus (10), Dirk Hartog (1) | Carter 1917, 1923b; Dinara Pty Ltd 1986–1993, NL McKenzie et al. 1995 |
| *Geopelia striata* | Barrow (55), Rottnest (18) – aviary escapee? | Sedgwick 1978, WABN No. 155: 11 |
| *Geopelia humeralis* | Legendre (3) | J Richardson et al. 2007 |
| Unidentified species of pigeon | Bernier (39), Dorre (52) | Mees 1962 |
| *Eudynamys orientalis* | Koolan (1) | NL McKenzie et al. 1995 |
| *Chrysococcyx basalis* | Koolan (1), unnamed island in Montebello Group, Trimouille (3), Hermite (20), Varanus (10), Thevenard (20), Bernier (39), Faure (6), West Wallabi (60), East Wallabi (2/55), Rat (28/80), Rottnest (18) | I Abbott unpubl., AA Burbidge et al. 2000, DCLM 2000a, Dell & Cherriman 2008, Dinara Pty Ltd 1988, Kenneally et al. 2000, Mather 2015, NL McKenzie et al. 1995, Saunders & Rebeira 2009; Storr 1965cd, 1966; Storr et al. 1986, WABN No. 103: 5, WAPET 1993 |

| **Species** | **Island (distance to closest presumed source area, km)** | **Reference** |
|---|---|---|
| *Chrysococcyx osculans* | Koolan (1), Barrow (55), Dorre (52), Faure (6) | Dell & Cherriman 2008, Mather 2015, NL McKenzie et al. 1995, Sedgwick 1978, WABN No. 55: 2 |
| *Chrysococcyx lucidus* | Rottnest (18), Garden (2), Hamelin (<1), Michaelmas (2), Bald (1) | Abbott 1980e, unpubl.; K Buller 1949, Glauert 1928, Mather 2011, GT Smith 1977, Storr 1965c |
| *Cacomantis pallidus* | Koolan (1), Hermite (20), Barrow (55), Bernier (39), Faure (6), Dirk Hartog (1), Rottnest (18), Garden (2), Sandy Hook (8) | Abbott 1977c, 1980f; Alexander 1921b, AA Burbidge et al. 2000, Dell & Cherriman 2008, Mather 2015, NL McKenzie et al. 1995, Saunders & Rebeira 2009, Sedgwick 1978, V Serventy 1952, Storr 1965c; WABN No. 42: 3, 102: 3; Wykes et al. 1999 |
| *Cacomantis flabelliformis* | Rottnest (18), Garden (2), Bald (1), Woody (7), Mondrain (11), North Twin Peak (8), Middle (Recherche) (9) | Abbott 1980ef, unpubl.; Abbott & Black 1978, BirdLife WA database, MG Brooker et al. 1995b, SJJF Davies 1980, S Mather pers. comm., GT Smith 1977, AN Start pers. comm., Storr 1965a, Tingay & Tingay MS, JAL Watson pers. comm., Wykes et al. 1999 |
| *Cacomantis variolosus* | Koolan (1) | NL McKenzie et al. 1995 |
| *Cacomantis optatus* | Koolan (1) | NL McKenzie et al. 1995 |
| *Tyto alba* | Barrow (55), Legendre (3), Dorre (52), Faure (6), Beacon (8), Boullanger [Long] (<2), Rottnest (18), Carnac (8), Garden (2), Michaelmas (2), Figure of Eight (13), Lion (3), Sandy Hook (8), Hood (12), Woody (7), North Twin Peak (8), Daw (32) | Abbott 1978a, 1980e; Abbott & Black 1978, Dell & Cherriman 2008, Dickman et al. 1991, J Ford 1965, Goodsell et al. 1976, B Haberley 1990 unpubl., Hull 1922, P Lambert 1991 unpubl., Mather 2015, Mees 1962, J Richardson et al. 2007, Saunders & Rebeira 2009, Sedgwick 1978, V Serventy 1952, LA Smith et al. 2005, AN Start pers. comm., Storr et al. 1986, JAL Watson 1956, Wykes et al. 1999 |
| *Ninox connivens* | Koolan (1) | NL McKenzie et al. 1995 |
| *Ninox boobook* | Adele (85), Hermite (20) [species uncertain], Barrow (55), Dirk Hartog (1), Faure (6), Favourite (3), Rottnest (18), Carnac (8), Garden (2), Hamelin (<1) | Abbott 1978a, MG Brooker et al. 1995b; AA Burbidge 1971; Coate et al. 1994, 2011; J Ford 1965, Glauert 1928, S Mather unpubl., Onton & Webb 2009, Saunders & Rebeira 2009, Sedgwick 1978; Storr 1965c, MSb; JAL Watson pers. comm., Whitlock 1921a, Wykes et al. 1999, |
| *Podargus strigoides* | Bernier (39), Carnac (8) | Abbott 1978a, Lipfert 1912 |
| *Eurostopodus argus* | Bernier (39), Dirk Hartog (1), Faure (6), Garden (2) | MG Brooker et al. 1995b, Carter 1917, 1923b; Dell & Cherriman 2008, Ogilvie-Grant 1910, Storr MSb |
| *Aegotheles cristatus* | Koolan (1) | NL McKenzie et al. 1995 |
| *Eurystomus orientalis* | Koolan (1), Faure (6) | NL McKenzie et al. 1995, WABN No. 155: 13 |
| *******Dacelo novaeguineae* | Garden (2), Chatham (1), Eclipse (6), Breaksea (5), Michaelmas (2), Bald (1) | Abbott 1980e, Abbott & Watson 1978, Fullagar & van Tets 1976, Serventy 1938, AN Start pers. comm., Storr MSb, Warham 1955 |
| *Todiramphus chloris* | North Turtle (15), Hermite (20) | Kolichis 1977, Montague 1914 |
| *Todiramphus sanctus* | Adele (85), East Lacepede (20), unidentified islands in Montebello Group, Varanus (10), Legendre (3), Thevenard (20), Faure (6), West Wallabi (60), Pelsaert (60), Escape (3), Lancelin (0.5), Carnac (8), Garden (2), Bird (0.5), Seal (Shoalwater Bay) (1), Middle Shag (0.9), Penguin (0.7), Hamelin (<1), Eclipse (6), Woody (7), North Twin Peak (8), Middle (Recherche) (9) | Abbott 1978a,1980f, 1982, unpubl.; BirdLife WA database, MG Brooker et al. 1995b, AA Burbidge & Prince 1972, AA Burbidge et al. 2000, Calderwood 1953, SJJF Davies 1980, Dell & Cherriman 2008, Dinara Pty Ltd 1986-1993, Hall 1902, Mather 2015, Montague 1914, J Richardson et al. 2007, Sedgwick 1940, Serventy 1938, V Serventy 1952, Serventy & White 1943, AN Start pers. comm., Storr MSb, Storr et al. 1986; *The Naturalist News* November 1980, May 1982; WAPET 1993, Warham 1955, JAL Watson 1956, Wykes et al. 1999 |

| Species | Island (distance to closest presumed source area, km) | Reference |
|---|---|---|
| *Todiramphus pyrrhopygius* | Koolan (1), Barrow (55), Varanus (10), Faure (6) | Dinara Pty Ltd 1988, Mather 2015, NL McKenzie et al. 1995, WABN No. 135: 25 |
| *Merops ornatus* | Barrow (55), Varanus (10) | Dinara Pty Ltd 1986-1993, WABN No. 135: 25 |
| *Falco cenchroides* | Browse (175), Adele (85), West Lacepede (30), Bedout (35), Elphick Nob (1), Hermite (20), Alpha (<1), Trimouille (3) and other unidentified islands in Montebello Group, North (Abrolhos) (22/60), West Wallabi (60), East Wallabi (2/55), Pelsaert (60), Favourite (4), Boullanger (<2), Whitlock (<1), Escape (3), Lancelin (0.5), Edward (0.1), Carnac (8), Penguin (0.7), Hamelin (<1), Chatham (1), Eclipse (6), Michaelmas (2), Bald (1), Figure of Eight (13), Lion (3), Woody (7), Hastings (12), Mondrain (11), Middle (Recherche) (9), Salisbury (45), Daw (32) | Abbott 1978a,1980e, 1982, unpubl.; Abbott & Black 1978; Abbott & Watson 1978, Alexander 1921b, 1922; AA Burbidge 1971, AA Burbidge et al. 1982, 2000; Coate et al. 1994, 2011; P Collins 1990 unpubl., Dickman et al. 1991, Fullagar & van Tets 1976, Fuller & Burbidge 1981, Goodsell et al. 1976, Kenneally et al. 2000, Kolichis 1977, P Lambert pers. comm. 1989, SG Lane 1978, SG Lane 1982l, SG Lane unpubl., Lindgren 1956, D Perry 1982, Sedgwick 1940; Serventy 1938, 1952; Serventy & White 1943, GT Smith 1977; LA Smith et al. 1978, 2005; Storr 1965ad, 1966, MSb; Tarr 1949, Tingay & Tingay MS, WABN No. 71: 2, Warham 1955, JAL Watson 1956 |
| *Falco longipennis* | Ah Chong (3), Barrow (55), Varanus (10), Bernier (39), Faure (6), Dirk Hartog (1), Lancelin (0.5), Rottnest (18), Garden (2) | Abbott 1977c, AA Burbidge et al. 2000, Dell & Cherriman 2008, Dinara Pty Ltd 1988, J Ford 1965, Howard 1978, Mather 2015, Saunders & Rebeira 2009, Sedgwick 1978; WABN No. 31: 4, 50: 2, 56: 9, 145: 24-25; Wykes et al. 1999 |
| *Falco berigora* | Adele (85), Barrow (55), Varanus (10), Dirk Hartog (1), Faure (6), Rottnest (18), Garden (2), Hamelin (<1), Sandy (3), Chatham (1), Eclipse (6), Breaksea (5), Bald (1), Charley (5), Woody (7), Middle (Recherche) (9) | Abbott 1980e, I Abbott unpubl., BirdLife WA database, Carter 1917, Coate et al. 1994, Dell & Cherriman 2008, Dinara Pty Ltd 1988-1993, Hull 1922, P Lambert 1989 unpubl., SG Lane 1982 pers. comm., Mather 2015, Sedgwick 1978, Storr 1965c, Tingay & Tingay MS, WABN No. 147: 6, Warham 1955, Whitlock 1921a, Wykes et al. 1999 |
| *Falco hypoleucos* | Koolan (1) | NL McKenzie et al. 1995 |
| *Falco peregrinus* | Koolan (1), Ah Chong (3), Varanus (10), Barrow (55), Penguin (0.7), St Alouarn (6), Chatham (1) – species uncertain, Bald (1), Mondrain (11), Middle (Recherche) (9) | Abbott & Black 1978, Abbott & Watson 1978, BirdLife WA database, AA Burbidge et al. 2000, Dinara Pty Ltd 1986-1993, B Haberley 1989 unpubl., JAK Lane 1978, SG Lane 1978, NL McKenzie et al. 1995, GT Smith 1977, Storr 1965a, WABN No. 135: 25 |
| *Calyptorhynchus latirostris* | Rottnest (18), Garden (2) | Errington 2012, Saunders & Rebeira 2009, Storr 1965c, WABN No. 50: 3, Winnett 1989, Wykes et al. 1999 |
| *Cacatua leadbeateri* | Dirk Hartog (1) (after cyclone in 1921) | Whitley 1971 |
| *Cacatua roseicapilla* | Barrow (55), Dirk Hartog (1), Faure (6), West Wallabi (60), unidentified islands in Wallabi Group, Rottnest (18), Garden (2), Penguin (0.7) | BirdLife WA database, MG Brooker et al. 1995b, Carter 1923b, Dell & Cherriman 2008; Mather 2009, 2015; Sedgwick 1978, Saunders & Rebeira 2009; Storr 1965cd, 1966; Storr et al. 1986; WABN No. 68: 2, 94: 2, 102: 15, 103: 5; Wykes et al. 1999 |
| *Cacatua sanguinea* | Barrow (55), Varanus (10), Thevenard (20), Dirk Hartog (1) (after cyclone in 1921), unidentified islands in Wallabi Group & Pelsaert Group, Penguin (0.7) | BirdLife WA database, Carter 1923b, Dinara Pty Ltd 1988, Sedgwick 1978, Storr et al. 1986, WAPET 1993, Whitley 1971 |
| *Nymphicus hollandicus* | Dirk Hartog (1), Faure (6) | AA Burbidge & George 1978, Dell & Cherriman 2008, Mather 2015 |
| ••*Trichoglossus moluccanus* | Rottnest (18) | Blythman & Sansom 2015; Mather 2009, 2011; *Post* 5.9.2009: 76, Saunders & de Rebeira 2009 |
| *Parvipsitta porphyrocephala* | Rottnest (18), Bald (1), Marts (3), Middle (Recherche) (9) | Abbott 1980e, unpubl.; Saunders & de Rebeira 2009, Serventy 1947, Storr 1965a, Tingay & Tingay MS; WABN No. 78: 4, 154: 8 |

| Species | Island (distance to closest presumed source area, km) | Reference |
|---|---|---|
| *Platycercus spurius* | Garden (2) | MG Brooker et al. 1995b, SJJF Davies 1980, Wykes et al. 1999 |
| *Platycercus zonarius* | Rottnest (18), Garden (2) | MG Brooker et al. 1995b, SJJF Davies 1980, Saunders & Rebeira 2009; Storr 1965c, MSb; WABN No. 102: 14, Wykes et al. 1999 |
| *Neophema petrophila* | Dirk Hartog (1), Faure (6), Carnac (8), Garden (2), Chatham (1), Eclipse (6), Lion (3), Remark (1.7/11) | Abbott 1980f, Carter 1917, Dell & Cherriman 2008, Fullagar & van Tets 1976, Hull 1922; P Lambert unpubl., Mather 2015, Serventy 1947, 1952; Warham 1955, JAL Watson 1956, Whitlock 1921a, Wykes et al. 1999 |
| *Melopsittacus undulatus* | Barrow (55), Varanus (10), Legendre (3), Dirk Hartog (1) (after cyclone in 1921) | Abbott 1982, Carter 1923b, Dinara Pty Ltd 1988, 1993; J Richardson et al. 2007, Sedgwick 1978, Whitley 1971 |
| *Malurus splendens?* | Garden (2) | Storr MSb |
| *Malurus leucopterus* | Trimouille (30) | Sheard 1950 |
| *Certhionyx variegatus* | Faure (6) | Dell & Cherriman 2008, Mather 2015 |
| *Glyciphila melanops* | Middle Doubtful (3) | I Abbott unpubl. |
| *Lichmera indistincta* | Varanus (10), Dirk Hartog (1), Garden (2), Penguin (0.7), Sandy (3), Middle Doubtful (3), Woody (7) | I Abbott unpubl., Ashby 1929, BirdLife WA database, Dinara Pty Ltd 1986-1991, LE Sedgwick MS, *The Naturalist News* May 1982: 16, Whitlock 1921a |
| *Phylidonyris novaehollandiae* | Coffin (0.25), Lion (3) | Lindgren 1956, GT Smith & Kolichis 1980 |
| *Melithreptus chloropsis* | Bald (1) | I Abbott unpubl. |
| *Epthianura tricolor* | Hermite (20), Barrow (55), Varanus (10), Thevenard (20), Serrurier [Long] (19), Dirk Hartog (1), Faure (6) | AA Burbidge et al. 2000, Carter 1917, DCLM 2000a, Dell & Cherriman 2008, Dinara Pty Ltd 1986-1993, Kenneally et al. 2000, Mather 2015, Montague 1914, Sedgwick 1978, WAPET 1993 |
| *Epthianura aurifrons* | Faure (6) | Mather 2015 |
| *Epthianura albifrons* | Barrow (55), Favourite (3), North Cervantes (<2), Garden (2) | Alexander 1921b, SJJF Davies 1980, J Ford 1965, Sedgwick 1978, Serventy 1943 |
| *Acanthagenys rufogularis* | Barrow (55), Thevenard (20) | Sedgwick 1978, WAPET 1993, Whitlock 1918 |
| *Anthochaera lunulata* | Garden (2) | MG Brooker et al. 1995b, Wykes et al. 1999 |
| *Anthochaera carunculata* | Rottnest (18), Garden (2), Middle (Recherche) (9), Anvil (10) | V Serventy 1952, LA Smith et al. 2005, Storr 1965c, Wykes et al. 1999 |
| *Manorina flavigula* | Legendre (3), Garden (2) | MG Brooker et al. 1995b, J Richardson et al. 2007 |
| *Purnella albifrons* | Varanus (10), Faure (6) | Dinara Pty Ltd 1986-1993, Mather 2015 |
| *Gavicalis virescens* | Hermite (20), Varanus (10), Wedge (<1), Favourite (4), Whitlock (<1), Lancelin (0.5), Carnac (8), Bird (0.5), Seal (Shoalwater Bay) (1), Middle Shag (0.9), Penguin (0.7) | Abbott 1978a, unpubl.; DCLM 2000a, Dinara Pty Ltd 1986-1993, J Ford 1965, Johnstone & Storr 2004, Kenneally et al. 2000, Sedgwick 1940, Serventy & Marshall 1964, Serventy & White 1943, Storr MSb |
| *Pardalotus punctatus* | Rottnest (18), Woody (7), Mondrain (11) | Abbott & Black 1978, J Ford 1987; Mather 2009, 2011; Saunders & Rebeira 2009, WABN No. 85: 8, 145: 24 [possible breeding attempt] |
| *Pardalotus striatus* | Faure (6), Rottnest (18), Garden (2), Michaelmas (2), High [Duke of Orleans Bay] (joined to mainland by tombolo) | Abbott 1980e, MG Brooker et al. 1995b, Dell & Cherriman 2008, J Ford 1987, JR Ford 1970 pers. comm.; Mather 2009, 2011, 2015; Saunders & Rebeira 2009, Storr 1965c, Wykes et al. 1999, |
| *Calamanthus campestris* | Faure (6) | Mather 2015 |
| *Sericornis frontalis* | Woody (7) | BirdLife WA database |
| *Smicrornis brevirostris* | Rottnest (18) | Mather 2011 |

| Species | Island (distance to closest presumed source area, km) | Reference |
|---|---|---|
| *Gerygone fusca* | Barrow (55), Carnac (2), Michaelmas (2) | Abbott 1978a,1980e; WABN No. 135: 25 |
| *Acanthiza apicalis* | Hamelin (<1), *Mistaken (<0.1) | Abbott 1980e, unpubl.; Carter 1910 |
| *Acanthiza uropygialis* | Enderby (14) | AA Burbidge & Prince 1972, R Johnstone pers. comm. |
| *Acanthiza chrysorrhoa* | Dirk Hartog (1), Garden (2) | MG Brooker et al. 1995b, Carter 1921, SJJF Davies 1980, *The Naturalist News* November 1980: 9-10 |
| *Psophodes occidentalis* | Faure (6) | Dell & Cherriman 2008 |
| *Artamus leucorhynchus* | Varanus (10) | Dinara Pty Ltd, 1986-1993, Serventy & Marshall 1964 |
| *Artamus personatus* 1999 | Barrow (55), Faure (6), Garden (2) | Mather 2015, Sedgwick 1978, Wykes et al. |
| *Artamus cinereus* | Koolan (1), Barrow (55) | NL McKenzie et al. 1995, Sedgwick 1978 |
| *Artamus cyanopterus* | Rottnest (18), Garden (2) | WABN No. 33: 9, Wykes et al. 1999 |
| *Artamus minor* | Dirk Hartog (1) | Carter 1917, Whitlock 1921a |
| *Cracticus torquatus* | Rottnest (18), Observatory (1), Woody (7) | SG Lane 1982l, Mather 2011, Serventy 1947 |
| *Cracticus nigrogularis* | Legendre (3), Faure (6) | Mather 2015, J Richardson et al. 2007 |
| *Cracticus tibicen* | Rottnest (18), Penguin (0.7) | Mather 2009, 2011; Serventy & White 1943, Saunders & Rebeira 2009, Storr 1965c, WABN No. 48: 3 |
| *Strepera versicolor* | *Michaelmas (2), *Mistaken (<0.1) | Abbott 1980e, Hull 1922, SG Lane 1982 pers. comm. |
| *Coracina maxima* | Garden (2) | MG Brooker et al. 1995b |
| *Coracina novaehollandiae* | Varanus (10), Thevenard (20), Dirk Hartog (1), Faure (6), North (Abrolhos) (22/60), West Wallabi (60), East Wallabi (2/55), Rottnest (18), Garden (2), Figure of Eight (13), Woody (7), Mondrain (11) | Abbott 1977c, Abbott & Black 1978, MG Brooker et al. 1995b, Carter 1917, Dinara Pty Ltd 1986-1988, Glauert 1928, SG Lane 1982l, SG Lane 1982 pers. comm.; Mather 2009, 2011, 2015; Saunders & Rebeira 2009, LE Sedgwick MS, AN Start pers. comm.; Storr 1965cd, 1966; Storr et al. 1986; *The Naturalist News* November 1980, May 1982; WABN No. 71: 2, 102: 3; WAPET 1993, Whitlock 1921a, Wykes et al. 1999 |
| *Lalage tricolor* | Unnamed island in Montebello Group, Barrow (55), Varanus (10), Legendre (3), Rottnest (18) | I Abbott unpubl., AA Burbidge et al. 2000, Dinara Pty Ltd 1988, Glauert 1928, Saunders & Rebeira 2009, J Richardson et al. 2007, Sedgwick 1978, Storr 1965c, |
| *Pachycephala occidentalis* | Breaksea (5) | Abbott 1980e |
| *Pachycephala rufiventris* | Unidentified island in Montebello Group, West Wallabi (60), Garden (2) | MG Brooker et al. 1995b, AA Burbidge et al. 2000, SJJF Davies 1980, Montague 1914, Storr et al. 1986; *The Naturalist News* November 1980: 9-10, May 1982: 16 |
| *Colluricincla harmonica* | Faure (6), Rottnest (18), Garden (2), Woody (7) | MG Brooker et al. 1995b, Dell & Cherriman 2008, Mather 2009, T Stoneman 1995 unpubl., *The Naturalist News* November 1980: 9-10 |
| *Oriolus flavocinctus* | Koolan (1) | NL McKenzie et al. 1995 |
| *Rhipidura leucophrys* | Barrow (55), unidentified island in Montebello Group, Varanus (10), Thevenard (20), Faure (6), North (Abrolhos) (22/60), Beacon (8), Sandland (<1), North Cervantes (<2), Wedge (<1), Lancelin (0.5), Rottnest (18), Carnac (8), Bird (0.5), Penguin (0.7) | Abbott 1978a, I Abbott pers. obs. 1976, BirdLife WA database, AA Burbidge et al. 2000, Dell & Cherriman 2008, Dinara Pty Ltd 1986-1993, N Dunlop pers. comm., J Ford 1965, Mather 2015, Saunders & Rebeira 2009, Serventy 1938, Serventy & White 1943; Storr 1965c, MSb; Storr et al. 1986, *The Naturalist News* March 2013; WABN No. 31: 4, 35: 8, 71: 3, 135: 25; WAPET 1993 |

| Species | Island (distance to closest presumed source area, km) | Reference |
|---|---|---|
| *Rhipidura albiscapa* | Varanus (10), Faure (6), Rottnest (18) | Dell & Cherriman 2008, Dinara Pty Ltd 1988; Mather 2009, 2015; Saunders & Rebeira 2009, Storr 1965c, WABN No. 31: 4 |
| *Grallina cyanoleuca* | Adele (85), Browse (175), unnamed island in Montebello Group, Barrow (55), Varanus (10), Thevenard (20), Dirk Hartog (1), North (Abrolhos) (22/60), Whitlock (<1), Rottnest (18), Garden (2), Penguin (0.7) | Abbott 1982, unpubl.; BirdLife WA database, AA Burbidge et al. 2000, Carter 1917, Coate et al. 1994, SJJF Davies 1980, Dinara Pty Ltd 1986-1993, J Ford 1965, Glauert 1928, Saunders & Rebeira 2009, Sedgwick 1978, Storr 1965c; WABN No. 33: 9, 34: 8, 71: 3; WAPET 1993 |
| @*Corvus splendens* | Rottnest (18) | *Fremantle Gazette* 13.6.2006: 12 |
| *Corvus bennetti* | Barrow (55), Varanus (10), Thevenard (20) | Dinara Pty Ltd 1986-1993, Sedgwick 1978, WAPET 1993 |
| *Corvus perplexus* | Burton (55), North Fisherman (5), Boullanger [Long] (<2), Escape (3), Carnac (8), Penguin (0.7), Sandy (3), Michaelmas (2), Bald (1), Middle Doubtful (3), Figure of Eight (13), Sandy Hook (8), Long (1.3/12.5), Remark (1.7/11), MacKenzie (13/20), Middle (Recherche) (9), Salisbury (45), Daw (32) | Abbott 1978a, 1980e, unpubl.; BirdLife WA database, AA Burbidge et al. 1982, M Chambers 2005, J Ford 1965, B Haberley 1986 & 1989 unpubl., RE Johnstone pers. comm., SG Lane 1982f, Sedgwick 1940; Serventy 1938, 1952; Serventy & White 1943, LA Smith et al. 2005, Storr MSb, Storr et al. 1986, Tingay & Tingay MS, WABN No. 145: 38 |
| *Eopsaltria australis* | Carnac (8) | JAL Watson 1956 |
| *Eopsaltria georgiana* | Hamelin (<1), *Mistaken (<0.1) | Abbott 1980e, Carter 1910, Onton & Webb 2009 |
| *Petroica boodang* | Chatham (1) | Abbott & Watson 1978 |
| *Petroica goodenovii* | Dirk Hartog (1), Faure (6), Pelsaert (60) | Abbott 1977c, Dell & Cherriman 2008, Hall 1902, BA Wells & Wells 1974, Whitlock 1921a |
| *Cheramoeca leucosterna* | Dirk Hartog (1), North (Abrolhos – attempted nesting) (22/60), Rottnest (18) | AA Burbidge & George 1978, Storr et al. 1986, Wykes 1987 |
| @*Hirundo rustica* | Koolan (1) | NL McKenzie et al. 1995 |
| *Hirundo neoxena* | Koolan (1), Thevenard (20), Beacon (6.5), Favourite (4), Escape (3), Edward (0.1), Middle Shag (0.9), Sandy (3) | I Abbott unpubl., SG Lane 1982f, NL McKenzie et al. 1995, Sedgwick 1940, WABN No. 46: 8, WAPET 1993 |
| *Petrochelidon ariel* | Browse (175), Barrow (55), Thevenard (20), Faure (6), Garden (2) | Abbott 1982, MG Brooker et al. 1995b, Chevron Australia 2000, Mather 2015, Sedgwick 1978 |
| *Petrochelidon nigricans* | East Lacepede (20), Hermite (20), North West (1) and other unidentified islands in Montebello Group, Varanus (10), Legendre (3), Thevenard (20), Dirk Hartog (1), Rottnest (18), Carnac (8), Garden (2), Penguin (0.7), Hamelin (<1), Sandy (3), Middle Doubtful (3), Woody (7), North Twin Peak (8) | Abbott 1978a, 1982, unpubl.; Abbott & Black 1978, BirdLife WA database, MG Brooker et al. 1995b, AA Burbidge 1971, AA Burbidge et al. 2000, Calderwood 1953, SJJF Davies 1980, Dinara Pty Ltd 1986-1993, Glauert 1928, Mather 2009, Onton & Webb 2009, J Richardson et al. 2007, LE Sedgwick MS, Serventy 1938, V Serventy 1952, Storr 1965c, *The Naturalist News* May 1982, WABN No. 34: 7, WAPET 1993, JAL Watson 1956, Whitlock 1921a, Wykes et al. 1999 |
| *Megalurus mathewsi* | Barrow (55), Varanus (10), Pelsaert (60) | Dinara Pty Ltd 1988, Fuller & Burbidge 1981, Hall 1902, WABN No. 135: 25 |
| *Megalurus cruralis* | Barrow (55), Dirk Hartog (1), Dorre (52), Faure (6), North (Abrolhos) (22/60) | Dell & Cherriman 2008, Mather 2015, Sedgwick 1978, LE Sedgwick MS, Storr 1960, 1966; Storr et al. 1986, WABN No. 55: 2, Whitlock 1921a |
| *Megalurus gramineus* | Pelsaert (60) | Fuller & Burbidge 1981, Storr et al. 1986 |
| *Cisticola exilis* | Varanus (10) | Dinara Pty Ltd 1986-1993 |
| *Zosterops lateralis* | Bernier (39), Faure (6), Beacon (6.5), North Fisherman (5), Green [near Rottnest] (0.1), Flat Rock [near Carnac] (0.1), Penguin (0.7), Hamelin (<1), Middle Doubtful (3), Sandy Hook (8) | Abbott 1977cd, unpubl.; BirdLife WA database, Dell & Cherriman 2008, R Johnstone pers. comm., P Lambert pers. comm., Lipfert 1912, Mather 2015, Mees 1962, Onton & Webb 2009, Storr MSb, Tingay & Tingay MS, WABN No. 46: 8 |
| •*Sturnus vulgaris* | Garden (2) | Storr & Johnstone 1988 |

| Species | Island (distance to closest presumed source area, km) | Reference |
|---|---|---|
| *Dicaeum hirundinaceum* | Dirk Hartog (1), Faure (6) | Carter 1917, Dell & Cherriman 2008, Mather 2015, Whitlock 1921a |
| *Emblema pictum* | Depuch (2), Barrow (55) | Sedgwick 1978, Stokes 1846 Vol. 2: 175, Storr 1964d |
| *Stagonopleura oculata* | Coffin (0.25), Middle (Recherche) (9) | B Haberley 1989 unpubl., V Serventy 1952, GT Smith & Kolichis 1980, Tingay & Tingay MS |
| *Neochmia ruficauda* | Barrow (55) | WABN No. 135: 25 |
| *Taeniopygia guttata* | Trimouille (4), South East [Montebello Group] (1), Hermite (20), Varanus (10), Thevenard (20) | AA Burbidge 1971, AA Burbidge et al. 2000, DCLM 2000a, Dinara Pty Ltd 1986-1993, Serventy & Marshall 1964, WAPET 1993 |
| *Erythrura gouldiae* | Koolan (1) | NL McKenzie et al. 1995 |
| *Anthus australis* | East Wallabi (2/55), Gun (12), Whitlock (<1), Carnac (8), Eclipse (6), Bald (1), Middle Doubtful (3), Figure of Eight (13), Sandy Hook (8), Long (1.3/12.5) | Abbott 1978a, unpubl.; P Collins 1990 unpubl., J Ford 1965, Fullagar & van Tets 1976, Helms 1898, SG Lane 1982l, GT Smith 1977, Storr et al. 1986, Tingay & Tingay MS, Warham 1955, JAL Watson pers. comm. |

• Self-introduced exotic species
•• Native species introduced to mainland WA
@ Exotic species not yet established in WA
^ Native Australian species not otherwise known from mainland WA
# This species acts like a landbird on WA islands
* Treated (probably incorrectly) as extinctions by Abbott (1980e)

and many of these offer considerable scope for comparative studies of fruit production based on the presence/absence of the New Holland and singing honeyeaters. Similarly, *Leucopogon* is the sole genus in the family Ericaceae that is widely represented on the south-western islands of WA. Flowers are pollinated by bees, moths, butterflies and flies (G Keighery 1996). Comparisons between islands and mainland of the same species in terms of seed output are yet to be undertaken.

When herbivorous mammals such as rabbits and goats are introduced to islands, much of the vegetation is eaten off, exposing large areas of soil to erosion (Gillham 1960, 1962; Turbott 1963). Rabbits leave only unpalatable plant species and cause palatable species to become restricted to less accessible parts (cliffs and crevices). They also expose seabird burrows to elevated temperatures. Rabbit Island near Wilson's Promontory, Victoria is the best-studied island in Australia of the suppressive effects of rabbits (Norman 1967, 1970, 1988; Norman & Harris 1981; Norman et al. 2010). Rabbits were present on this island from 1836 to 1965. Without the rabbits, condition of the vegetation improved, the number of plant species increased, eroded areas became vegetated, and the distribution of shearwaters increased as vegetative cover expanded. Sedgwick (1940) attributed the sparseness of the vegetation on Penguin Island (WA) in 1939 to the numerous rabbits present. Comparable information is also available for Carnac Island (Abbott 1980d; Abbott et al. 2000).

Grazing and browsing of palatable plant species by indigenous herbivorous mammals can alter vegetation dynamics, particularly after a fire in summer (Storr 1963). This prevents the regeneration of dominant plant species (AR Main 1967; Hesp et al. 1983; Rippey & Hobbs 2003). On Rottnest Island the plant species *Acacia rostellifera, Eremophila glabra, Lepidosperma pubisquameum, Olearia axillaris* and *Rhagodia baccata* were eaten to local extinction by the quokka, whereas the exotic *Trachyandra divaricata* and the native species *Carex preissii, Conostylis candicans* and *Guichenotia ledifolia* evidently are unpalatable and increased in cover and frequency (Rippey & Hobbs 2003). *Acanthocarpus preissii* is also unpalatable (AR Main 1967). On Garden Island the tammar exerts strong grazing pressure on several plant species, including *Acanthocarpus preissii, Rhagodia baccata* and *Austrostipa flavescens*, seedlings of the dominant tree species (*Callitris preissii*), and the weeds *Asparagus asparagoides* and *Geranium molle* (Bell et al. 1987; GIEAC 1997; McArthur 1996b; McArthur & Bartle 1981). Unpalatable species such as *Parietaria debilis* have consequently increased in cover (McAthur & Bartle 1981). It appears that some plant species are either absent from, or rare on, Barrow Island as a result of selective grazing by marsupials (Buckley 1983). Heavy browsing of several plant species on the Wallabi Islands (Houtman Abrolhos) by tammars (Storr 1965d) is likely to have had similar consequences.

From time to time the occasional judicious application of fire at meso-scales is necessary to rejuvenate senescing vegetation dominated by *Melaleuca huegelii* and *Acacia rostellifera* (McArthur 1996a). However, if performed at too small a scale there is a risk of herbivorous marsupials browsing palatable germinants to local extinction (McArthur 1996b, 1998).

The ash-bed effect of fire also stimulates growth of plant species. On Garden Island, the dominant tree species *Callitris preissii* and *Melaleuca lanceolata* had attained a height of 8 m and a bole diameter (at breast height) of 15 cm 33 years after wildfire (McArthur 1996a). After fire on Garden Island, there is short-term proliferation of the opportunist *Solanum symonii* (McArthur 1996b), a species with abundant fruits that are eaten by the rare brush bronzewing (Abbott 1980f).

Seed dispersal can influence the occurrence of plant species on islands. On the mainland of British Columbia, both dry-fruited and fleshy-fruited species occur commonly, but the latter predominate on islands as a consequence of bird species flying from the mainland to them (Burns 2005b). Two bird species, the singing honeyeater and grey-breasted white-eye, occur widely on the islands of south-west WA (Abbott 1981b). Both eat the soft fruits of *Rhagodia* spp., *Threlkeldia diffusa* and *Enchylaena tomentosa*, which are common plant species on most islands (even small ones) and may aid the dispersal of these species between islands. The singing honeyeater also disperses the seed of *Pittosporum ligustrifolium* on Rottnest Island, with passage through the gut breaking the dormancy of the seeds and increasing their viability (Dunlop & Galloway 1984). The grey-breasted white-eye spreads the seed of the introduced arum lily *Zantedeschia aethiopica* on Garden Island (GIEAC 1998) and that of *Lycium ferocissimum* to other islands. The role of rainforest birds in dispersing seeds within and between these habitat patches on islands and adjacent mainland of the Kimberley region is likely to be important (Johnstone & Burbidge 1991), but studies have yet to be conducted.

One intriguing interaction is the apparent extinction of the introduced black rat (*Rattus rattus*) on Sunday Island (R Palmer et al. 2013c). These rats were probably introduced by pearling luggers in the 1880s. The native species of rodent there (grassland melomys) is thought to have outcompeted the black rats once the mission station on the island closed in 1962 (cf. KD Taylor 1975). A rich guild of native predator species may also have prevented introduced black rats from establishing on more than a small part of Barrow Island (KD Morris 2002).

On small islands, increasing populations of nesting seabirds can destroy native vegetation and permit the invasion of weeds and other exotic plants, which further displace native plants (Wooller & Dunlop 1981; Rippey et al. 1998; Bancroft et al. 2005b). Conversely, changes in the extent, height and density of vegetation may be detrimental to surface-nesting seabirds. For example, colonies of bridled terns moved from Low Rocks to Sterna Island in c. 2000 for this reason (Coate et al. 2004). Dieback of the canopy of mangrove trees on Morley, Wooded and Pelsaert islands affected the breeding of lesser noddies (*Anous tenuirostris*). On Wooded Island the die-off of mangrove canopy partly resulted from a nesting population of pied cormorants (*Phalacrocorax varius*; Surman & Nicholson 2009).

An outbreak of a scale insect (*Pulvinaria urbicola*) on Tryon Island, Great Barrier Reef, possibly stimulated by a drought, led to a marked impact on the *Pisonia* forest. This then allowed the expansion of other plant species, including weeds (Batianoff et al. 2009a). On Coringa Cay (Coral Sea), *Pisonia grandis* became nearly extinct before a coccinellid (*Cryptolaemus montrouzieri*) was introduced and successfully controlled the scale insect (Greenslade 2008b).

An unexpected interaction is the benefit supplied to some native species by species that have been introduced to islands. For example, on Rottnest Island caterpillars of the native butterfly species *Vanessa itea* and *V. kershawi* feed on the weed species *Urtica urens* and *Arctotheca calendula* respectively (Powell 1993; AAE Williams & Powell 2000) Two other butterfly species (*Trapezites argenteoornus*, *Geitoneura klugii*) have been recorded feeding at the flowers of plant species introduced to the islands (AAE Williams 1997). Larvae of *Danaus plexippus* feed on the introduced plant *Gomphocarpus fruticosus* (Rippey & Rowland 1995). Host plant species for other butterfly species are listed by Dixon (2011). In the Montebello Islands the bungarra (*Varanus gouldii*) has used black rats as a source of food for c. 100 years (AA Burbidge et al. 2000), but did not depend on them as the goanna has persisted following the eradication of the rats (AA Burbidge pers. comm.).

One of the most unusual ecological interactions so far detected on a WA island is that between a species of seabird (silver gull) and a species of snake (tiger snake). On Carnac Island, gulls protect their nests by pecking at snakes, blinding them in one or both eyes (Aubret et al. 2005). Blind snakes can only feed on slow-moving, helpless prey (gull chicks), whereas normal-sighted snakes can also consume fast-moving prey (lizards and mice).

Another interesting interaction between human modification of an island and the introduction of a wallaby species has been documented on North (Abrolhos) Island. Five tammars were introduced in 1985 by fishers, who now live seasonally on the island in 30–40 huts. This settlement provides additional shelter, food and water for these wallabies. The wallabies increased to hundreds within 20 years and have severely grazed vegetation along an airstrip (constructed in 1979) and in an area regenerating from fire. By 2003, *Myoporum insulare* showed evidence of ringbarking, foliage of *Scaevola crassifolia* was heavily browsed, and there were no seedlings present in unfenced quadrats (K Morris et al. 2003). The painted button-quail no longer occurs (Blyth et al. 2014). More than 1100 tammars were culled in the period 2007–2008 (A Desmond n.d. and pers. comm.).

Some ecological interactions on islands are quite surprising in their ramifications. In the Tokelau Islands (Pacific Ocean), the introduced rats gnaw holes in the growing coconut fruits. When these fall to the ground, mosquitoes use the fluids in these fruits to breed. These mosquitoes are the main vectors of filariasis among the Polynesian residents (Laird 1963). In Hawai'i, the introduction of Pacific rats by Polynesians is believed to have destroyed the lowland forest (Athens 2009). The introduction of mosquitoes has also impacted on the distribution and abundance of honeycreepers (Warner 1968; Van Riper et al. 2002).

### *Coups de foudre*

'Coups de foudre'—accidental incidents, extraordinary incidents, and recurrent catastrophic events (the so-called 'black swans'; Taleb 2007)—have affected many islands during the millennia since their formation. MacArthur (1972) referred to 'capricious history'. Examples of such changes in circumstances include the devastation caused by a mega tsunami (Playford 2014), a volcanic eruption (Brattstrom 1963; Harrison & Hendrickson 1963; Thornton 1996), a landslide (F Marchant 2003), a cyclone (Spiller & Schoener 2007; Stoddart 1962), a prolonged drought (Halse et al. 1995; Heatwole et al. 1981; J Short et al. 1997), a deluge of rain very much exceeding the daily average (likely to cause erosion), an intense heatwave (AA Burbidge et al. 1993; Gillham 1962), an intense summer fire (Pearson et al. 2004; Pen & Green 1983; Whitley 1944), a shipwreck that resulted in the introduction of cats or rats, an oil spill from a shipwreck, the arrival of a salt water crocodile (*Crocodylus porosus*; Coate et al. 2004), the presence of a single carnivore (IAW MacDonald & Cooper 1995), the introduction of plant or animal disease, or occupation by humans who prey on edible species to the point of local extinction.

The passage of two cyclones in 1988 and 1989 caused defoliation, breakage of branches, uprooting of trees, and washing away of small individuals of the mangrove *Avicennia marina* on Varanus Island (LeProvost Semeniuk & Chalmer 1989). In the Archipelago of the Recherche, fires caused by lightning have been recorded on 13 islands during the period 1972–1998 (CALM file 034467F3102, Vol. 6). The impact of these natural fires on island-ecosystem properties, including litter recycling and supply rates of nutrients, is likely to be important (cf. Wardle & Zackrisson 2005).

Some of these unexpected setbacks are avoidable. Unauthorised landings, consumption of species, arson, and the introduction of predators and diseases can be minimised by frequent patrols and education. Lightning-caused fire could, if desired, be contained on larger islands (e.g. Barrow, Dirk Hartog, Rottnest, Garden) by the creation of a system of well-maintained firebreaks that allows access by fire-fighting crews, and by deployment of 'water bombing' aircraft.

Larger island area was considered by Van Balgooy (1969) to provide a buffer against local disasters. This would be correct for a tsunami and possibly for a cyclone and wildfire, but not for drought, pluvial deluge, heatwave or the introduction of pest animals. The successful translocation of marsupial herbivores or fungivores such as *Petrogale*, *Macropus*, *Bettongia* and *Potorous* species to islands of Australia (T Robinson et al. 1996; Woinarski et al. 2014b) implicates mishap and not insufficient resources or interspecific competition as a cause of the natural absence of these species from these islands.

Finally, the converse of the detrimental impacts described above consists of those incidents involving fortuity. These, however, are few (or possibly not well documented). Cats and house mice were recorded on Bernier Island in 1906 but both species had apparently become extinct there by 1959 (Ride & Tyndale-Biscoe 1962) and definitely so by the 1980s when the islands began to experience regular monitoring by ecologists (see Table 1). House mice have also apparently disappeared from Faure Island, and black rats have disappeared from Cockatoo and Sunday islands (R Palmer et al. 2013c; R Palmer pers. comm.). A mass introduction by silver gulls of olive fruits on Penguin Island in 2014 fortunately resulted in only three germinants, all of which died (Brown & Paczkowska 2016).

## LINKAGES BETWEEN THE 15 FACTORS

It can be difficult to disentangle the individual roles of highly correlated factors (Kohn & Walsh 1994; Ricklefs & Lovette 1999). For example, cays with vegetation in the Bahamas are larger, higher and closer to mainland islands than are unvegetated cays (Morrison 1997). Non-obvious factors may compound the effects of obvious factors, and there may be an intricate network of factors that are integrated almost to the point of indivisibility.

Quail Island in Westernport Bay (Victoria) is 480 ha in area, separated from the mainland by only a narrow channel, is well protected from wave action, and is vegetated with scrub and forest (Hyett & Gottsch 1963). It has many bird species unknown from similar-sized (and sometimes larger) islands in Bass Strait, including common bronzewing (*Phaps chalcoptera*), eastern rosella (*Platycercus eximius*), superb fairy-wren (*Malurus cyaneus*), southern emu-wren (*Stipiturus malachurus*), noisy miner (*Manorina melanocephala*), white-browed scrubwren (*Sericornis frontalis*), brown thornbill (*Acanthiza pusilla*), Australian magpie (*Cracticus tibicen*), grey shrike-thrush (*Colluricincla harmonica*), and eastern yellow robin (*Eopsaltria australis*).

Rotamah Island (280 ha), situated <100 m from mainland Victoria, has eucalypt forest and woodland present (EK Turner 1985). Many bird species unknown from islands of similar (and sometimes larger) area elsewhere in Victoria and Bass Strait occur frequently or breed on this island (AH Burbidge 1985; Mitchell & Moss 2000), for example emu (*Dromaius novaehollandiae*), yellow-tailed black cockatoo (*Calyptorhynchus funereus*), crimson rosella (*Platycercus elegans*), eastern rosella, white-throated treecreeper (*Cormobates leucophaea*), superb fairy-wren, noisy miner, white-browed scrubwren, brown thornbill, eastern whipbird (*Psophodes olivaceus*), grey butcherbird, Australian magpie, grey currawong (*Strepera versicolor*), rufous whistler (*Pachycephala rufiventris*), grey shrike-thrush and eastern yellow robin.

Similarly, the large Kooragang Island (2560 ha) situated in the Hunter River (NSW) supports small populations of superb fairy-wren, white-browed scrubwren, brown thornbill, grey butcherbird, Australian magpie, rufous whistler, grey shrike-thrush, magpie-lark (*Grallina cyanoleucai*), and formerly the variegated wren (*Malurus lamberti*) (AD Stuart 2002; van Gessel & Kendall 1972). These occurrences hint at a primary role on these islands of the extent of isolation (both in terms of distance from the mainland and the short period of time since separation) combined with the retention of suitable habitat protected from ocean swell with its ongoing direct deposition of salt spray.

Linkages between factors may not be additive but synergistic, and their operation may depend on exceeding a threshold. For example, cats stranded on a small island after shipwreck might starve because the island lacks adequate prey, whereas on a larger island a population of cats might establish and eventually cause the local extinction of some prey species.

Correlations between some factors make it difficult to attribute definitively either the presence or absence of a species or a particular vegetation type to a single factor. Deltaic islands, and islands in small coastal lakes, are informative on this point as they have retained a mainland type of flora. Islands in the Murray River (WA) delta, separated from the mainland by river channels <100 m wide, support the plant species *Banksia littoralis*, *Eucalyptus rudis*, *Jacksonia* (two species), *Macrozamia riedlei*, and *Melaleuca cuticularis* and *M. rhaphiophylla* (Serventy 1970; Hussey et al. 1992; G Keighery & Muir 2010). These species are absent from all offshore islands of WA. Remarkably, karri *Eucalyptus diversicolor* occurs on Honeymoon Island in Wilson Inlet, near Denmark (G Keighery 2015). The factors most relevant in explaining this persistence are proximity to the mainland and protection from ocean waves and the consequent reduction in seaspray.

The red wattlebird (*Anthochaera carunculata*), broad-tailed thornbill (*Acanthiza apicalis*), grey butcherbird, Australian magpie, rufous whistler, grey fantail (*Rhipidura albiscapa*) and scarlet robin (*Petroica boodang*) have been recorded regularly on some of the Murray River (WA) delta islands (Serventy 1970; Keast 1975). Also present is the quenda (southern brown bandicoot, *Isoodon obesulus*; Lintern & Roe 1993). We thus disagree with the claim that islands separated from the mainland only by a creek are of 'no intrinsic biological interest' (Moreau 1940: 48).

On a small island (c. 250 m from the mainland) in Lake Clifton with *Melaleuca cuticularis* thickets present, an unexpected diversity of landbird species has been recorded (Ireland 1983), including splendid fairy-wren (*Malurus splendens*), red wattlebird, striated pardalote (*Pardalotus striatus*), western gerygone and scarlet robin. Similarly, a bird list for an (unidentifiable) island in Lake Preston included Australian ringneck (*Platycercus zonarius*), broad-tailed thornbill, grey butcherbird, Australian magpie, rufous whistler, grey fantail and magpie-lark. The common bronzewing (*Phaps chalcoptera*), red-tailed black cockatoo (*Calyptorhynchus banksii*), Baudin's cockatoo (*C. baudinii*), Australian ringneck, red-winged fairy-wren (*Malurus elegans*), splendid fairy-wren, southern emu-wren (*Stipiturus malachurus*), western spinebill (*Acanthorhynchus superciliosus*), brown honeyeater, New Holland honeyeater, red wattlebird, white-browed scrubwren, western gerygone, broad-tailed thornbill, western thornbill (*Acanthiza inornata*), Australian magpie, varied sittella (*Daphoenositta chrysoptera*), western golden whistler, grey fantail, white-breasted robin (*Eopsaltria georgiana*), and scarlet robin have been recorded on Molloy Island, a forested island (140 ha) at the confluence of the Scott and Blackwood rivers and only c. 50 m from the adjacent mainland (WABN 1943–2016 No. 57: 2; C Wilder pers. comm.). Although most of these records are doubtless of vagrant individuals, they again indicate the relevance of distance (accessibility) and absence of seaspray (allowing retention of suitable habitat).

A more extreme circumstance, when an island is joined by an isthmus to the mainland, should provide additional insights into the influence of interrelationships between distance, area, lessened deposition of salt spray and habitat variety on vegetation and biota. Many inshore islands along the eastern Australian coast now form capes, headlands, promontories and bluffs along the mainland coast. At Port Stephens (NSW), the tied islands Yacaaba and Tomaree Heads, and Shark 'Island', should offer rewarding comparisons with the nearby Cabbage Tree and Boodelbah islands. In eastern Tasmania, Maria and Bruny islands (both comprised of two tied islands) and Schouten Island invite comparison with islands tied to Tasmania *sensu stricto*, namely Tasman, Forestier and Freycinet peninsulas. Some of the examples listed in 'Concepts and definitions' above for WA should also be suitable for study.

Detailed descriptive study of the Dongara–Lancelin islands has revealed extensive interrelationships between islands' shape, area, topography, maximum elevation, substrate and vegetation type, and the numbers of species of birds and reptiles present (J Ford 1963, 1965). No one factor predominates. Sometimes a deficiency in one factor can be compensated for by other factors.

Botanical studies of islands of Victoria have indicated that guano and sea salt have parallel effects on vegetation (Gillham 1960). Edaphic modifications by nesting seabirds are detrimental to heath vegetation. Drought in summer (an effectively rainless period in south-west WA) combined with high rates of evaporation results in toxic concentrations of guano in soil, but by destroying existing plants and manuring the soil, seabirds produce an 'arable' habitat well suited to weeds (Gillham 1960).

Abbott and Black (1978) proposed a conceptual framework to explain the development of plant communities on islands. This involved three factors: Exposure to salt-laden winds; density of breeding seabirds; and type of rock and soil present. Islands or portions of islands with limited exposure to salt spray and with breeding seabirds either absent or present only at low density support the most speciose plant communities (as recorded on Bald, Mondrain and Sandy Hook islands). The number of exotic grass species recorded on islands of south-west WA correlates with island area and a habitat disturbance index (Abbott 1992). It is likely that large islands have experienced more human visits and disturbance to sites.

Despite a sophisticated numerical study of the plants and mammals in an archipelago adjacent to Arnhem Land, Northern Territory (Woinarski et al. 1999b, 2000), the analyses found it difficult to disentangle the role of the various factors examined in explaining inter-island differences. The implication of this detailed and exemplary study is that the search for a single factor as an explanation should be abandoned.

One potentially important, but largely neglected, factor is the size of the species pool on the adjacent mainland (or large island). The number of butterfly species recorded on islands around Britain is positively correlated with the number of butterfly species within a 25 km radius of the nearest mainland-point (Hockin 1981; Dennis & Shreeve 1997). Butterfly species with wide geographical ranges tend to be mobile, use a broad variety of host plants, have long flight periods, and are often multi-brooded. These species are more likely to occur on islands than species with narrow geographic ranges (Dennis et al. 2000b).

## THE TRANSITION FROM MAINLAND TO ISLAND: KNOWNS; KNOWN UNKNOWNS; AND UNKNOWN UNKNOWNS

No one knows precisely the sequence and chronology of the biological processes that operate as an area of mainland coast gradually transforms into a peninsula or promontory and then an island. This is partly because the composition of the biota present at the time on the mainland is not exactly known (some species may have been absent at the time and only established subsequently on the mainland coast). Also of unknown significance is the relative extent of extrinsic, intrinsic, determinative, and chance factors (Karr 1982a; Fig. 23). Knowledge of how this transformation to a depauperate biota occurs therefore remains inferential.

The conceptual model proposed in Figure 23 outlines plausible pathways to the equivalent outcomes of failure to establish (for a species arriving on a continental island) and failure to persist (for a species present on a continental island newly isolated from the mainland). For the former class of species, the primary issue is the frequency of dispersal, with the secondary filters comprising how many individuals arrive and the suitability of the island for establishment to occur. For the second class of species, the primary issues are subsequent changes in climate during the several millennia following isolation and increased exposure to salt-laden winds, particularly on islands with small area. These changes result in further ecological changes, involving habitat suitability and other resources, increased or decreased interspecific competition, increased or decreased predation, and increased predation following the arrival of humans.

What follows is a plausible explanation but it may not be the only possible one. It is reasonable to assume that the species present and the condition of the vegetation at a particular time represent equilibria between all operating factors. Several of these factors, including small area, remoteness, reduced diversity of habitats, and low species richness of plants and insects, mutually reinforce one another and deplete the numbers of species of reptiles, landbirds and mammals present. As each species becomes locally extinct, the biota adjusts to a new equilibrium, at first by rapid change and then progressively by slower alteration, during which residual effects of the factor are slowly effaced (Poore & Robertson 1949).

Abbott (1980e) compared and contrasted the plant and landbird species found on headlands, capes, promontories, peninsulas and adjacent islands that varied in area. Even small coastal segments of the mainland have more species present than on similarly-sized islands, which have been isolated for c. 7 ka. This implies that immigration of species into coastal mainland sites is a recurrent and important process that effectively ceases once these sites become insularised. The ending of this process may be the chief disruptive factor that shapes the biota developing on the newly formed island.

The numerous studies of fragmented landscapes published since the 1980s reinforce the correctness of this deduction. For example, a 140,000 km$^2$ area in WA of native vegetation in 1830 had been reduced to 13% of this area by 1987, forming a wheatbelt (Saunders 1989). Only 6.7% of the original area, comprising 639 remnants (nature reserves) with a median area of 114 ha, is formally protected from further clearing. The process of clearing native vegetation did not, however, begin to impact on bird species until after 1900. Comparison of two nearly adjacent districts that differ in time of clearing shows that 15 species had disappeared from the older district in a period of c. 80 years and only four species from the other district within c. 50 years. Smaller remnants of native vegetation have experienced more rapid loss of species. For example, a 81 ha remnant that became isolated in the 1920s had only 20 native vegetation-dependent bird species 50 years later; a further 20 years later another four species had become extinct (Saunders 1989).

Studies of newly formed islands in lakes also indicate that loss of many species occurs rapidly. Barro Colorado Island (1560 ha) was formed by the creation of the Panama Canal in 1914 and set aside as a reserve in 1923. By the 1970s it had lost at least 45–60 bird species (EO Willis 1974; Karr 1982a), some 20–30% of the

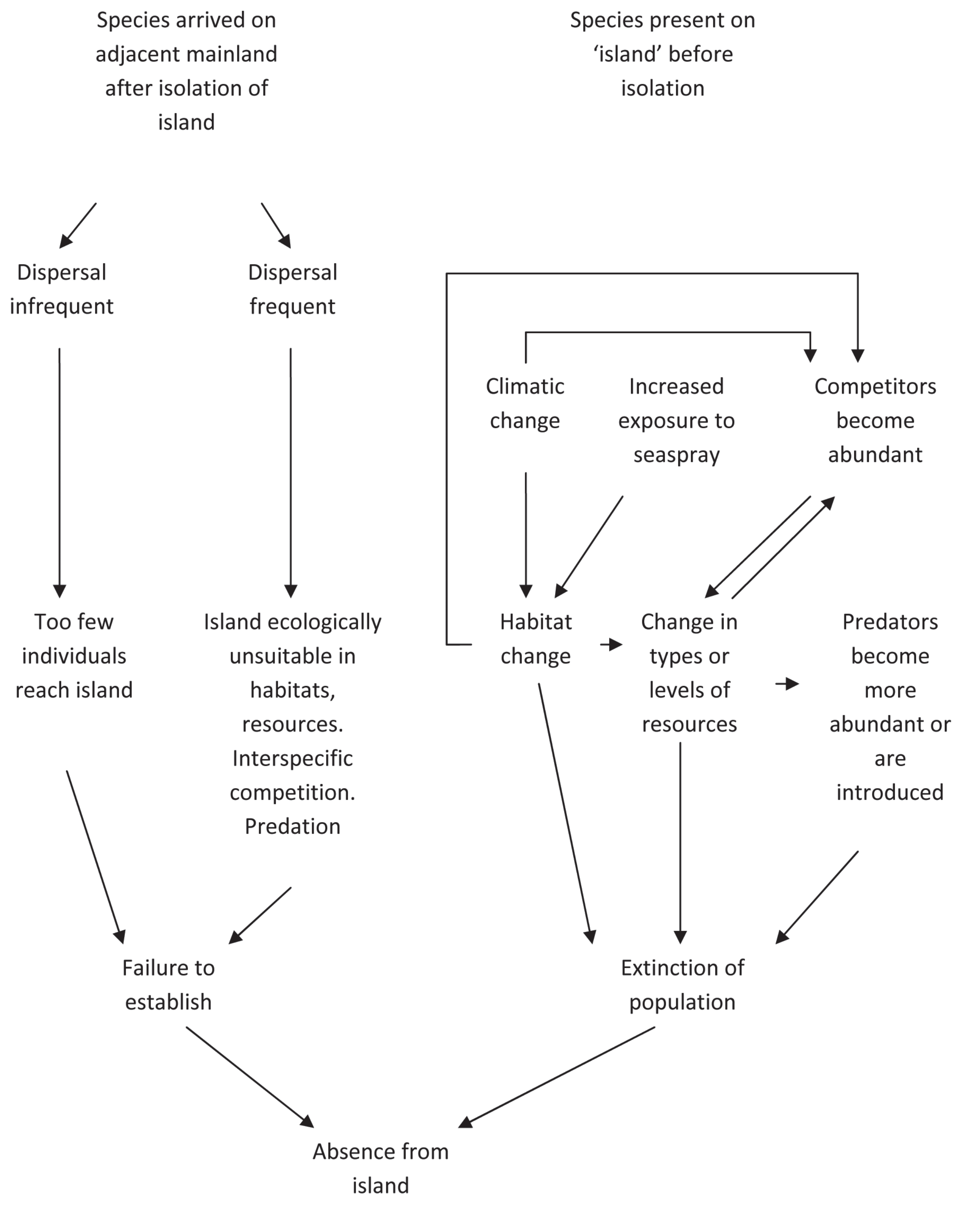



*Figure 23. Diagram of processes potentially involved in preventing species from immigrating to islands or establishing on islands, and of processes involved in species becoming extinct on islands (based on Abbott 1980b).*

original number of breeding species of birds. Smaller islands in lakes have experienced even faster loss of species (Terborgh et al. 2001; L Gibson et al. 2013). Mayr (1942: 225) regarded remote islands as 'evolutionary traps, which in due time kill one species after another that settles on them'. JM Diamond (1972) referred to the process of loss of species as 'relaxation', a term borrowed from physics where it signifies a gradual return of a system to equilibrium. Ecological degradation or ecosystem decay seem more apt and less euphemistic designations, and terms such as disassembly or disruptive repercussions seem preferable on the grounds of (neutral) language that does not presuppose equilibrium.

There are numerous mechanisms that could amplify feedbacks and potentially combine to accelerate population decline and eventual loss of species. Some mechanisms appear to operate in a hierarchy. Those species that are tightly networked with other species and thus exhibit a high level of co-dependence should be at higher risk of extinction if other species in this network become extinct or decline. For most species, surprisingly little is known about the factors limiting establishment of immigrant species and restricting persistence of populations already present. Although this point was clearly made nearly 50 years ago (Udvardy 1969), it remains valid. What follows is a reconstruction of the likely sequence of events and the critical turning points:

1. Species in ecological assemblages in a defined area always conform to a pattern of a few abundant species and many rare species (a lognormal frequency distribution). Most individuals are apportioned (inequitably) to only a few species. Large organisms are likely to be rarer than small ones. Some species will be stenotopic, with low vagility (Udvardy 1969). The long right-sided tail of the lognormal frequency distribution for the newly insularised island would soon truncate through loss of species with small population size. These species then become more vulnerable to breeding failure resulting from stochastic events, so-called 'demographic accidents' (Pimm et al. 1993). Thus, even on the large Kangaroo Island (South Australia, 4500 km$^2$), about one-third of the 58 landbird species recorded by Carpenter and Horton (1999) occurred at <10% of the 108 sites surveyed, and four species contributed >25% of all records.
2. As the environment of the newly separated island changes, species should vary in their 'trajectories of response' to isolation (to use the term of Lugo 2008). Some species will be unaffected, some will become extinct, and some will readjust ecologically to new opportunities (e.g. changes in habitat selection).
3. Species with low mean annual survival rates are prone to extinction (Karr 1990).
4. Species with a low coefficient of variation of abundance on islands are more likely to persist than species with population size highly variable from year to year (SJ Wright & Hubbell 1983).
5. Large or heavy species have a lower intrinsic rate of natural increase relative to those with small body mass (Fenchel 1974). Populations of large species may take longer to recover from disturbance and should therefore be at higher risk of extinction.
6. The sequence of extinction of species on continental islands should be the converse of the sequence of arrival on oceanic islands (the latter detailed by Thornton 1996). For continental islands this should be as follows: Predators first, then parasites, herbivores, omnivores, detritivores and plants. The biomass of predators varies with that of their prey (Hatton et al. 2015); small islands should have less of the latter than larger islands.
7. Species on coastal mainland sites are linked, either via metapopulations or through proximity to other conspecific populations (species that are abundant on the nearby mainland have the potential to experience increased opportunities for dispersal to islands). Upon isolation, dispersal either ceases or is much reduced, so that extinctions of island populations cannot readily be compensated.
8. Species lose ecological functionality, despite persisting, because their population density decreases to below an effective size (Säterberg et al. 2013).
9. The number of species and the total number of individuals present are highly correlated (Abbott 1975a). A newly isolated island will hold fewer individuals than a similar-sized coastal mainland area.
10. Increased exposure to salt spray and strong winds, particularly on smaller islands, initiates successional changes that affect the extent of habitats, and may eliminate the structure of the habitat required by some species. The loss of species of *Eucalyptus*, *Xanthorrhoea* and *Pimelea,* and *Allocasuarina fraseriana* and *Casuarina obesa* from Rottnest Island (Backhouse 1993) may be linked to this factor. Exposure may limit the quality and quantity of food and cover for animal species (Crowell 1983).
11. Major disturbances, such as extended drought, tsunami or an intense and extensive fire generated by lightning strike, may reduce populations of some species so much that they become prone to extinction from other factors. However, if such disturbances affect abundant species more than rare species, species richness may be stabilised (Paine 1966). Through the disruption of competitive exclusion, decline in species richness that normally accompanies isolation may be moderated or retarded.
12. If an island is accessible to Aboriginal people, their activities on the island may severely reduce

populations of species that are highly prized as food, particularly the larger species of birds and mammals. Aborigines may also increase the frequency of fire on islands and this may favour some species and disfavour others. Aborigines may also have brought dingoes as companion animals, and some may have escaped and had longer-term impacts on prey species, before themselves becoming extinct on these islands.

13. The absence of Aboriginal people during a period of 5–10 ka obviously removes anthropogenic burning (Abbott 2003), leading to change in vegetation and floristics. This in turn is likely to disfavour some bird species (as on Kangaroo Island, South Australia; HA Ford 2013). Persistence of such species is prevented by successionally-imposed habitat restriction (Thornton 1996). Plant species dependent on frequent fire should become non-observable above ground (RP Russell & Parsons 1978).
14. Extinction of a species 'will certainly affect other species which it either preyed upon, or competed with, or served for food; while the increase of any one animal [species] may soon lead to the extinction of some other to which it was inimical' (Wallace 1881: 215).
15. Large animals usually have larger home ranges than small animals and thus occur at lower density (Harestad & Bunnell 1979). Part of the reason for this is that population density varies inversely with body mass (Damuth 1981). Large species are thus more vulnerable to local extinction. The extinction of large predators (*Dasyurus*, snakes, varanids, owls, raptors) may in turn result in trophic cascades, with smaller predator species (e.g. spiders) becoming more abundant, so-called mesopredator release. Such changes may have irreversible knock-on effects for other species (Estes et al. 2011), including plants (Terborgh et al. 2006).
16. Isolation will restrict dispersal of many species, increasing their population density and thus intensifying intraspecific and interspecific competition. These processes may lead to habitat segregation or habitat expansion (Crowell 1983).
17. Herbivores are more abundant than carnivores (Peters & Raelson 1984) and thus are more likely to persist. They may become more common once their predators become extinct (Crowell 1983), and may reduce the population size of browsed or grazed plant species. However, the loss of some herbivorous species should lead to a decline in species richness of plants because moderate levels of grazing maximise the species richness of plants (Zeevalking & Fresco 1977). Plant community production varies with total foliage biomass (Hatton et al. 2015); small islands should support less of the latter than larger islands, and thus should support a lower biomass of herbivores.
18. Extinction of honeyeater and other pollinator species should affect seed production and ultimately the persistence of some plant species (Anderson et al. 2011).
19. Reduced abundance of plant species that act as hosts for insect species should result in decreased abundance and even the extinction of herbivorous species (e.g. butterflies), depending on their degree of polyphagy.
20. Establishment of breeding seabirds will increase local soil fertility, which should alter the species composition of plant communities and the soil biota.
21. Shortages of resources, or altered availability of resources, on islands may provide a competitive advantage to some species and disfavour others (Abbott 1975b).
22. Insufficient food supply can cause stress and mortality, as occurred in August 2011 when a rocky headland in Lake Argyle became isolated by floods, temporarily marooning c. 700 wallabies.
23. Species restricted to one habitat type are vulnerable should that habitat transform via ecological succession into a different type or decrease in size. For example, most of the species of epigeal arthropods established on One Tree Island, Great Barrier Reef, are restricted to only one of the five habitats present (Heatwole et al. 1981).
24. In response to the changes outlined, there will be ecosystem-level change and ongoing readjustment of the ecological traits of all remaining species (Cushman 1995).

Even on large islands it is difficult to account for the absence of most species, despite monographic analysis (e.g. Noske & Brennan 2002). Discussion of the reasons offered invariably involves comparison of a number of factors between source area and island, with no definitive conclusion attained.

## SPECIES TURNOVER

The clearest natural demonstration of the two ingredients of species turnover—colonisation and extinction—is when a new island forms. Surtsey resulted from a volcanic eruption in 1963 in the ocean c. 30 km from the coast of Iceland. Its formation provided an unparalleled modern opportunity to record colonisation by mosses and vascular plants, the dispersal mechanisms involved, and the development of habitat. Invertebrates and birds have also reached the island (Fridriksson 1975, 1989). Motmot Island was formed in 1968 by a volcanic eruption in a lake on Long Island, New Guinea. Relatively close to its source area (4 km), it has been colonised rapidly by plant, invertebrate and bird species (Ball & Glucksman 1975). Regrettably, such direct evidence is not available in WA. A tsunami striking a low island is the disturbance in

WA most likely to produce a tabula rasa (blank canvas), and such natural experiments are 'too rare not to be fully exploited by island ecologists' (Schipper et al. 2001: 1351).

Landfalls (accidental or deliberate) on WA islands by Dutch, French and English navigators (including F Pelsaert, S Volkersen, W de Vlamingh, W Dampier, G Vancouver, N Baudin, M Flinders, P King, D d'Urville, L Stokes and H Denham) and their collectors (J Labillardière, A Menzies, F Péron, R Brown, A Cunningham, J Quoy, J Gaimard, B Bynoe and F Rayner) produced the earliest natural history records (1629–1858) for these islands (Alexander 1914, 1916, 1918; AS George 1971, Serventy 1979, Whittell 1954a, 1945b; JH Willis 1959). Remarked upon were the flora and fauna of more than 20 islands: Adolphus, Bat, Kater, Valentine, Bedout, Depuch, East Lewis, Enderby, Bernier, Dirk Hartog, West Wallabi, Pelsaert, Gun, Rottnest, Carnac, Garden, Seal (King George Sound), Fly (Geake Point), Green (Oyster Harbour), Observatory, Mondrain, Goose and Middle (Archipelago of the Recherche). Indeed, the first records of Australian mammal and bird species were made on a WA island in 1629. Although this casually acquired information is of limited scientific value, it does help provide a baseline of the historical presence or abundance of some of the more conspicuous species of fauna and flora.

The detection of faunal and floral change on islands depends on an adequate baseline. Most of the early observers and collectors listed above were short-term visitors to WA islands (Abbott 2006) and thus did not usually record all species present. Baseline surveys did not commence until 1843 (Abbott 2008; Table 15). The first complete island lists of landbirds and seabirds were compiled in 1843 and 1889 (Houtman Abrolhos; J Gilbert in Whittell 1942; AJ Campbell 1890b), followed by 1891 (Adele Island; J Walker 1892), 1903 (Rottnest Island; Lawson 1905), and 1910 (Bernier and Dorre islands; Lipfert 1912). The first list of mammal species on an island was published in 1906 (Bernier Island; O Thomas 1906). The results of extensive collecting on Dorre Island, Barrow Island and islands in the Archipelago of the Recherche in the period 1899–1914 by J Tunney were, however, never published (Kitchener & Vicker 1981). Island plant lists were not produced until much later, namely 20 islands in the Archipelago of the Recherche (JH Willis 1953); Rottnest, Garden and Carnac islands (McArthur 1957, Storr 1962); Shoalwater Bay islands (Storr 1961); and North Island and the Wallabi Group, Houtman Abrolhos (Storr 1960, 1965d). The earliest insular lists for butterflies were published only recently (Koolan Island, LE Koch & van Ingen 1969; Barrow and adjacent islands, Smithers & Butler 1983). Since the 1960s there has been a rapid increase in the production of comprehensive species lists for many islands (Table 1).

Species turnover refers to changes in species composition on islands over time. A minimum of two surveys is required to detect species turnover. The pattern *species recorded/species not recorded* indicates species' extinction, and the pattern *species not recorded/species recorded* indicates species' immigration. With three or more surveys, confidence increases, although this is tempered by the differing observational abilities of those undertaking the surveys, the time spent on the island, and whether the entire island was traversed. The patterns *recorded/not recorded/recorded* and *not recorded/recorded/not recorded* may indicate respectively extinction followed by re-immigration and immigration followed by extinction. Alternatively, for both mobile and sedentary species, these patterns may signify pseudoturnover.

Recognition of species turnover is thus not always straightforward, and requires assessment of the sedentariness/mobility of the species, its pattern of occurrence on other islands, and the degree of thoroughness of each survey (in terms of time spent on the island and the coverage of all habitats present).

The natural dynamism of WA island biotas (at least since observations by Europeans commenced) depends largely on the taxonomic component investigated. Wallabies, seabirds and landbirds are the most completely known of the vertebrate fauna. Therefore these taxa provide the best (although still imperfect) means of detecting species turnover.

Most species turnover for mammals is linked to human-caused factors (Abbott 1980c; Table 16). There have been few immigrations and extinctions caused by natural factors, with all but one extinction attributable to factors linked with humans, and c. 10 immigrations not caused by humans. There have also been few extinctions or immigrations of reptiles and frogs on WA islands caused by natural factors (Table 16). For landbirds, instances of species establishing or becoming locally extinct on islands are more frequent (Abbott 1973; 1974a, 1974d; 1978a, 1980b; Table 17). Because some bird species (e.g. black-faced cuckoo-shrike *Coracina novaehollandiae*, tree martin *Petrochelidon nigricans*) occur on Rottnest Island in increasingly large numbers (Saunders & de Rebeira 2009) but have not yet established, a distance effect appears unlikely and unsuitability of habitat has to be invoked.

## Landbird species

Although the occurrence of landbird species has been documented for many WA islands, few thorough or repeated surveys were undertaken until the 1970s (Table 15). Abbott and Grant (1976) found only one island in WA suitable for examining species turnover of landbirds. This island (Rottnest) satisfied the essential requirements of at least two surveys, as well as the criteria of reliability, efficiency and validity (see 'Assumptions', above, for full explanation of these terms). After several years of field work in WA, Abbott (1978a) was in a position to include a further 12 islands. For other islands, doubts remained about the thoroughness of some surveys (whether only small parts of large islands were surveyed) and the reliability of identification of species. Many other islands are yet to be revisited a second time.

**Table 15**

The number of breeding native species of landbird recorded on the same WA island but on different occasions. Islands are listed from north to south, and then from west to east. Landbird species on these islands potentially include quail, pigeons, raptors (excluding osprey *Pandion haliaetus*, brahminy kite *Haliastur indus*, and white-bellied sea-eagle *Haliaeetus leucogaster*), buff-banded rail, Australian bustard, bush stone-curlew, banded lapwing, button-quail, cockatoos, parrots, cuckoos, owls, kingfishers, bee-eater and all passerines. Native species that have established or have become extinct on islands are identified in Table 17, and native species that have been recorded as vagrant are identified in Table 14. The column 'No. species adjusted' corrects the previous column for pseudoturnover of species that are likely to have been overlooked rather than assuming that species became extinct and re-immigrated.

| Island | Year | No. species recorded | No. species adjusted (if deemed necessary) | Reference(s) |
|---|---|---|---|---|
| Adele | 1891 | 1 | 1 | J Walker 1892 |
| | 1949 | 1 | 1 | D Serventy 1952 |
| | 1978 | 1 | 1 | LA Smith et al. 1978 |
| | 1978 | 1 | 1 | Abbott 1982 |
| | 1989 | 1 | 1 | Coate et al. 1994 |
| | 1990 | 1 | 1 | Coate et al. 1994, 2011 |
| | 1993 | 1 | 1 | WABN No. 67: 3 |
| Browse | 1949 | 0 | 0 | D Serventy 1952 |
| | 1972 | 0 | 0 | AA Burbidge in LA Smith et al. 1978 |
| | 1978 | 0 | 0 | Abbott 1982 |
| East Lacepede | 1949 | 0 | 0 | D Serventy 1952 |
| | 1978 | 0 | 0 | Abbott 1982 |
| Bedout | 1901 | 0 | 0 | Tunney 1902 |
| | 1949 | 0 | 0 | D Serventy 1952 |
| | 1968 | 0 | 0 | Fletcher 1980 |
| | 1972 | 0 | 0 | TE Bush & Lodge 1977 |
| | 1975 | 0 | 0 | Kolichis 1977 |
| | 1978 | 0 | 0 | Abbott 1982 |
| Hermite | 1912 | 6 | 6 | Montague 1914 |
| | 1958 | 6 | 6 | Serventy & Marshall 1964 |
| | 1970, 1971 | 6 | 6 | AA Burbidge 1971 |
| | 2000 | 5 | 6 | Kenneally et al. 2000 |
| North West [Montebello Group] | 1978 | 2 | 2 | I Abbott unpubl. |
| | 1994–5 | 2 | 2 | AA Burbidge unpubl., AA Burbidge et al. 2000 |
| | 1999 | 2 | 2 | AA Burbidge unpubl., AA Burbidge et al. 2000 |
| Trimouille | 1912 | 4 | 4 | Montague 1914 |
| | 1994 | 5 | 5 | AA Burbidge et al. 2000, AA Burbidge pers. comm. |
| | 2000 | 6 | 6 | Kenneally et al. 2000 |
| Varanus | 1958 | 4 | 4 | Serventy & Marshall 1964 |
| | 1985 | 5 | 5 | Dinara Pty Ltd 1986 |
| | 1986 | 5 | 5 | Dinara Pty Ltd 1986 |
| | 1987 | 5 | 5 | Dinara Pty Ltd 1986 |
| | 1988 | 5 | 5 | Dinara Pty Ltd 1986 |
| | 1990 | 5 | 5 | Dinara Pty Ltd 1986 |
| | 1991 | 5 | 5 | Dinara Pty Ltd 1986 |
| | 1992 | 5 | 5 | Dinara Pty Ltd 1986 |
| | 1993 | 5 | 5 | Dinara Pty Ltd 1986 |
| Barrow | 1917, 1918 | 12 | 12 | Whitlock 1918, 1919 |
| | 1958 | 9 | 9 | Serventy & Marshall 1964 |
| | 1964–75 | 15 | 15 | Butler 1970, 1975 |
| | 1976 | 15 | 15 | Sedgwick 1978 |
| North Sandy | 1978 | 3 | 3 | Abbott 1982 |
| | 1997 | 3 | 3 | F Stanley unpubl. |
| Airlie | 1978 | 6 | 6 | Abbott 1982 |
| | 1997 | 6 | 6 | T Vigilante unpubl. |

| Island | Year | No. species recorded | No. species adjusted (if deemed necessary) | Reference(s) |
|---|---|---|---|---|
| Thevenard | 1989 | 7 | 7 | WAPET 1993 |
| | 1990 | 7 | 7 | WAPET 1993 |
| | 1991 | 7 | 7 | WAPET 1993 |
| | 1992 | 7 | 7 | WAPET 1993 |
| Bessieres [Anchor] | 1978 | 4 | 4 | Abbott 1982 |
| | 1997 | 4 | 4 | F Stanley unpubl. |
| Bernier | 1906 | 6 | 6 | Ogilvie-Grant 1909, 1910 |
| | 1910 | 6 | 6 | Lipfert 1912 |
| | 1959 | 8 | 8 | Mees 1962 |
| | 1963 | 6 | 6 | Storr MS |
| | 1976 | 8 | 8 | I Abbott unpubl. |
| | 1977 | 5 | 5 | Howard 1978 |
| Dorre | 1910 | 8 | 8 | Lipfert 1912 |
| | 1959 | 9 | 9 | Mees 1962 |
| | 1988 | 8 | 8 | Cale 1992 |
| Dirk Hartog | 1916 | 23 | 23 | Carter 1917 |
| | 1918, 1920 | 22 | 22 | Whitlock 1921ab |
| | 1972, 1974, 1976 | 20 | 21 | AA Burbidge & George 1978 |
| | 1973 | 19 | 21 | BA Wells & Wells 1974 |
| | 1976 | 18 | 21 | I Abbott unpubl. |
| | 2013, 2014 | 21 | 21 | AH Burbidge pers. comm. |
| Faure | 2000 | 17 | 17 | Dell & Cherriman 2008 |
| | 2005 | 19 | 19 | Dell & Cherriman 2008 |
| | 2008 | 17 | 18 | S Mather unpubl. |
| | 2009 | 19 | 19 | S Mather unpubl. |
| | 2010 | 19 | 19 | S Mather unpubl. |
| | 2012 | 17 | 19 | S Mather unpubl. |
| | 2013 | 18 | 19 | S Mather unpubl. |
| | 2014 | 16 | 19 | S Mather unpubl. |
| North (Houtman Abrolhos) | 1913 | 5 | 5 | Alexander 1922 |
| | 1959 | 3 | 3 | Storr 1960 |
| | 2006 | 5 | 5 | Blyth et al. 2007 |
| | 2013 | 3 | 4 | Blyth et al. 2014 |
| West Wallabi | 1843 | 4 | 5 | J Gilbert 1843 (in Whittell 1942; GC Sauer 1999) |
| | 1897 | 4 | 5 | Helms 1898 |
| | 1899 | 4 | 5 | Hall 1902 |
| | 1913 | 5 | 5 | Alexander 1922 |
| | 1959-60 | 5 | 5 | Storr 1965d |
| East Wallabi | 1843 | 5 | 5 | J Gilbert 1843 [in Whittell 1942, GC Sauer 1999], *The Inquirer* 19.4.1843 |
| | 1907 | 4 | 5 | CG Gibson 1908, *The West Australian* 7.12.1905: 5 |
| | 1913 | 5 | 5 | Alexander 1922 |
| | 1959–60 | 5 | 5 | Storr 1965d |
| | 1975 | 4 | 4 | I Abbott unpubl. |
| | 2006 | 5 | 5 | Blyth et al. 2007 |
| Pigeon | 1913 | 3 | 3 | Alexander 1922 |
| | 1959–60 | 3 | 3 | Storr 1965d |
| Pelsaert | 1843 | 2 | 2 | J Gilbert 1843 [in Whittell 1942, GC Sauer 1999], *The Inquirer* 19.4.1843 |
| | 1889 | 2 | 2 | AJ Campbell 1890b |
| | 1897 | 2 | 2 | Helms 1898 |
| | 1899 | 1 | 2 | Hall 1902 |
| | 1913 | 2 | 2 | Alexander 1922 |
| | 1948 | 3 | 3 | Tarr 1948 |
| | 1975 | 2 | 2 | I Abbott unpubl. |
| | 1977 | 2 | 2 | Garstone 1978 |
| | 1977–81 | 2 | 2 | Fuller & Burbidge 1981 |
| | 1982 | 1 | 2 | WABN No. 26: 11 |

| Island | Year | No. species recorded | No. species adjusted (if deemed necessary) | Reference(s) |
|---|---|---|---|---|
| North Fisherman | 1961 | 1 | 2 | J Ford 1965 |
| | 1971 | 1 | 2 | R Johnstone pers. comm. |
| | 1973 | 2 | 2 | R Johnstone pers. comm. |
| | 1974 | 2 | 2 | R Johnstone pers. comm. |
| | 1975 | 2 | 2 | R Johnstone pers. comm. |
| | 1976 | 2 | 2 | R Johnstone pers. comm. |
| | 1989 | 2 | 2 | P Lambert pers. comm. |
| Favourite | 1961 | 1 | 1 | J Ford 1965 |
| | 1976 | 1 | 1 | I Abbott unpubl. |
| Boullanger | 1961 | 4 | 4 | J Ford 1965 |
| | 1976 | 4 | 4 | I Abbott unpubl. |
| Tern | 1961 | 1 | 1 | J Ford 1965 |
| | 1976 | 1 | 1 | I Abbott unpubl. |
| Whitlock | 1961 | 4 | 4 | J Ford 1965 |
| | 1976 | 4 | 4 | I Abbott unpub. |
| Escape | 1961 | 2 | 2 | J Ford 1965 |
| | 1976 | 2 | 2 | I Abbott unpubl. |
| Lancelin | 1959 | 2 | 2 | J Ford 1965, Storr MSb |
| | 1976 | 2 | 2 | I Abbott unpubl. |
| | 1981 | 2 | 2 | *The Naturalist News* Jan/Feb 1982: 10-13 |
| | 1997 | 1 | 2 | WABN No. 84: 24–25 |
| Rottnest | 1903 | 12 | 12 | Lawson 1905 |
| | 1927–28 | 11 | 11 | Glauert 1928 |
| | 1931–32 | 8 | 11 | Kilpatrick 1932 |
| | <1938 | 12 | 12 | Serventy 1938 |
| | 1955 | 13 | 13 | Storr MSb |
| | 1956 | 13 | 13 | Storr MSb |
| | 1957 | 12 | 13 | Storr MSb |
| | 1958 | 13 | 13 | Storr MSb |
| | 1959 | 12 | 13 | Storr MSb |
| | 1962 | 12 | 13 | Storr MSb |
| | 1974 | 11 | 13 | I Abbott unpubl. |
| | 1975–76 | 9 | 13 | I Abbott unpubl. |
| | 1980–92 | 16 | 16 | Saunders & de Rebeira 2009 |
| | 1982 | 16 | 16 | Saunders & de Rebeira 1983 |
| | 1983 | 16 | 16 | Saunders & de Rebeira 1983 |
| | 1983 | 14 | 16 | B & K McRoberts unpubl. |
| | 1984 | 15 | 16 | B & K McRoberts unpubl. |
| | 1985 | 15 | 16 | B & K McRoberts unpubl. |
| | 1986 | 15 | 16 | B & K McRoberts unpubl. |
| | 1987 | 15 | 16 | B & K McRoberts unpubl. |
| | 1989 | 13 | 16 | B & K McRoberts unpubl. |
| | 1990 | 11 | 16 | B & K McRoberts unpubl. |
| | 1993 | 14 | 16 | B & K McRoberts unpubl. |
| | 1996 | 14 | 16 | B & K McRoberts unpubl. |
| | 1998–2007 | 19 | 19 | Saunders & de Rebeira 2009 |
| | 2009 | 16 | 19 | S Mather unpubl. |
| | 2011 | 17 | 19 | S Mather unpubl. |
| | 2013 | 15 | 19 | S Mather unpubl. |
| Carnac | 1934–77 | 1 | 1 | summary in Abbott 1978a |
| Garden | 1937? | 8 | 12 | Serventy 1938 |
| | 1937–39 | 10 | 12 | Sedgwick 1940 |
| | 1948 | 10 | 12 | K Buller 1949 |
| | 1953 | 10 | 12 | Calderwood 1953 |
| | 1959 | 12 | 12 | Storr MSb |
| | 1974 | 11 | 12 | Abbott 1980f & unpubl. |
| | 1975 | 12 | 12 | Abbott 1980f & unpubl. |
| | 1978 | 12 | 12 | Abbott 1980f & unpubl. |

| Island | Year | No. species recorded | No. species adjusted (if deemed necessary) | Reference(s) |
|---|---|---|---|---|
| | 1979 | 14 | 14 | SJJF Davies 1980 |
| | 1980 | 10 | 14 | *The Naturalist News* November 1980: 9-10 |
| | 1982 | 12 | 14 | *The Naturalist News* May 1982: 16, WABN No. 22: unpaginated |
| | 1991 | 17 | 17 | MG Brooker et al. 1995ab, 1996 |
| | 1993 | 12 | 17 | BirdLife WA database |
| | 1995–97 | 16 | 17 | Wykes et al. 1999 |
| | 1996 | 14 | 18 | BirdLife WA database; WABN No. 78: 22–23 |
| | 2005 | 12 | 18 | BirdLife WA database |
| Bird | 1940–42 | 1 | 1 | Serventy & White 1943 |
| | 1959 | 1 | 1 | Storr MSb |
| | 1975 | 1 | 1 | I Abbott unpubl. |
| Seal (Shoalwater Bay) | 1937–38–39? | 1 | 1 | Sedgwick 1940 |
| | 1940–42 | 1 | 1 | Serventy & White 1943 |
| | 1955 | 1 | 1 | Storr MSb |
| | 1959 | 1 | 1 | Storr MSb |
| | 1974 | 1 | 1 | I Abbott unpubl. |
| Penguin | 1937–39? | 2 | 2 | Sedgwick 1940 |
| | 1940–42 | 2 | 2 | Serventy & White 1943 |
| | 1941 | 2 | 2 | E Sedgwick pers. comm. |
| | 1947 | 2 | 2 | E Sedgwick pers. comm. |
| | 1955 | 2 | 2 | Storr MSb |
| | 1959 | 2 | 2 | Storr MSb |
| | 1975 | 2 | 2 | I Abbott unpubl. |
| | 2009 | 3 | 3 | BirdLife WA database |
| | 2011 | 3 | 3 | BirdLife WA database |
| | 2013 | 3 | 3 | BirdLife WA database |
| | 2015 | 3 | 3 | BirdLife WA database |
| Sandy | 1976 | 2 | 2 | I Abbott unpubl. |
| | 1981 | 2 | 2 | SG Lane 1982f |
| Chatham | 1975 | 2 | 2 | Abbott & Watson 1978 |
| | 1989 | 2 | 2 | P Lambert unpubl. |
| Eclipse | 1954 | 2 | 2 | Warham 1955 |
| | 1973 | 2 | 2 | Fullagar & van Tets 1976 |
| | 1975 | 2 | 2 | Abbott 1980e & unpubl. |
| Coffin | 1976 | 4 | 4 | SG Lane unpubl. |
| | 1976 | 4 | 4 | I Abbott unpubl. |
| | 1976-79 | 4 | 4 | GT Smith & Kolichis 1980 |
| Bald | 1959 | 12 | 12 | Storr 1965a |
| | 1971 | 12 | 12 | GT Smith 1977 |
| | 1976 | 12 | 12 | GT Smith 1977 |
| | 1976 | 12 | 12 | Abbott 1980e |
| Figure of Eight | 1950 | 3 | 3 | V Serventy 1952 |
| | 1981 | 4 | 4 | SG Lane 1982l |
| Lion | 1921 | 2 | 2 | Hull 1922 |
| | 1944 | 3 | 3 | Serventy 1947 |
| | 1956 | 3 | 3 | Lindgren 1956 |
| Woody | 1975 | 7 | 7 | Goodsell et al. 1976 |
| | 1976 | 7 | 7 | Abbott & Black 1978 |
| | 1995 | 8 | 8 | BirdLife WA database [1.2.1995] |
| | 1996 | 8 | 8 | BirdLife WA database [28.1.1996] |
| | 2011 | 8 | 8 | BirdLife WA database [22.4.2011 & 24.4.2011] |
| Sandy Hook | 1950 | 7 | 7 | V Serventy 1952 |
| | 1976 | 7 | 7 | Tingay & Tingay MS |
| Long | 1950 | 4 | 4 | V Serventy 1952 |
| | 1981 | 4 | 4 | SG Lane 1982l |

| Island | Year | No. species recorded | No. species adjusted (if deemed necessary) | Reference(s) |
|---|---|---|---|---|
| Remark | 1950 | 4 | 4 | V Serventy 1952 |
| | 1981 | 4 | 4 | SG Lane 1982l |
| MacKenzie [Round] | 1950 | 3 | 3 | V Serventy 1952 |
| | 1981 | 3 | 3 | SG Lane 1982l |
| Mondrain | 1950 | 8 | 8 | V Serventy 1952 |
| | 1976 | 8 | 8 | Abbott & Black 1978 |
| | 1977 | 7 | 8 | I Abbott unpubl. |
| Middle (Archipelago of the Recherche) | 1950 | 8 | 8 | V Serventy 1952 |
| | 1977 | 8 | 8 | Tingay & Tingay MS |
| | 1988 | 7 | 7 | Anon. 1989 |
| Salisbury | 1950 | 3 | 3 | V Serventy 1952 |
| | 1977 | 2 | 3 | Abbott & Black 1978 |
| | 1982 | 3 | 3 | AA Burbidge et al. 1982 |
| Daw | 1950 | 3 | 4 | V Serventy 1952 |
| | 1986 | 4 | 4 | Smith et al. 2005 |
| | 1988 | 4 | 4 | Anon. 1989 |
| | 1991 | 4 | 4 | LA Smith et al. 2005 |

For this review we have located satisfactory data for 51 islands (Tables 11 and 13). Most (32) islands for which adequate records exist demonstrate no extinctions or immigrations of landbird species. This is evidence of an equilibrium, but not of a dynamic kind.
Another eight islands at face value show extinctions and/or immigrations, but these instances are interpreted parsimoniously by us as pseudo-extinctions and/or pseudo-immigrations. The most compelling examples where reasonable adjustment has been made are:

1. Migratory species (seasonal breeding visitors) not detected because the survey was performed during the time of year when such species are absent. Examples include Horsfield's bronze cuckoo (*Chrysococcyx basalis*) and the rainbow bee-eater (*Merops ornatus*).
2. Highly mobile species suspected to form a metapopulation with mainland or other island populations. Examples include the grey-breasted white-eye (Sansom & Blythman 2015), brush bronzewing (WABN 1943–2016 No. 35: 8), rock parrot, welcome swallow (WABN 1943–2016 No. 70: 9), and some raptors. The welcome swallow has sometimes not been recorded on islands in Houtman Abrolhos (Table 15). We regard this as pseudoturnover because this species is highly mobile and is known to fly over a gap of ocean of 18 km (Storr MSb). In one paper about the avifauna of several localities (including an island) in south-west WA, this widespread species was not listed at all (Hall 1902), surely as a consequence of inadvertence. The little corella (*Cacatua sanguinea*) was recorded in April 1984 as a flock of 15–20 birds at an oil drilling rig some 45 km west of Barrow Island (WABN 1943–2016 No. 32: 9).
3. Highly sedentary and secretive species suspected to have been overlooked. Examples include the white-browed scrubwren, rufous fieldwren (*Calamanthus campestris*) and southern emu-wren.
4. On very frequently visited islands, conspicuous species recorded on most visits but not on a small number of visits are assumed to have been overlooked. For some very well-studied islands (Barrow, Rottnest), occurrences of some species are of the *recorded/not recorded/recorded* pattern. We suspect, based on the ecology of the species involved, that these also represent spurious extinctions and immigrations. Examples include the banded lapwing (*Vanellus tricolor*), fan-tailed cuckoo (*Cacomantis flabelliformis*), sacred kingfisher (*Todiramphus sanctus*), red-capped robin, grey-breasted white-eye and Australian pipit on Rottnest Island during the period 1986–1996.

Therefore, in the interest of transparency, we have presented in Table 15 separate columns for the number of species actually recorded and the number of species adjusted to eliminate what we consider to be pseudo-extinction and pseudo-immigration.

What we consider to be genuine local extinctions and immigrations are listed in Table 17. Immigrations (32) exceed extinctions (13) of native landbird species, with Rottnest (10 versus 3), Garden (6 versus 1), Faure (3 versus 0), Barrow (2 versus 0) and Trimouille (2 versus 0) islands showing strong evidence of non-equilibrium

**Table 16**

Species turnover of native species of mammals, frogs and reptiles on islands of Western Australia.

| Species | Island (area in ha) | Year of extinction (E) or immigration (I) | Comments about likely cause(s) | Reference |
|---|---|---|---|---|
| **Monotremes** | | | | |
| *Tachyglossus aculeatus* | Faure (5100) | **I** (1930s, 1990s) | 1 individual introduced by island lessees on each occasion; tracks seen in 2000 | Baynes 2008 |
| **Macropodoids** | | | | |
| *Bettongia lesueur* | Dirk Hartog (58,600) | **E** (>1890, 1913?) | Predation by feral cats; disease | *The Sunday Times* 4.6.1933: S27, JJ Walker 1897 |
| *Bettongia lesueur* | Boodie (730) | **E** (1985) | Accidental poisoning (later reintroduced from Barrow Island) | KD Morris 2002, J Short & Turner 1993 |
| *Bettongia penicillata* | Faure (5100) | **E** (<1930s) | Linked to pastoral occupation in 1873 via predation by feral cats? | Aplin et al. 2008, Baynes 2008, Schmitz & Richards 2008 |
| *Lagorchestes conspicillatus* | Hermite (1020) | **E** (between 1912 and 1950) | Predation by feral cats | Montague 1914 |
| *Lagorchestes conspicillatus* | Trimouille (520) | **E** (between 1840 and 1912) | Predation by feral cats? | AA Burbidge et al. 2000, Montague 1914, Stokes 1846 |
| *Macropus fuliginosus* | Boullanger (34) | **I** (by 1985) | One animal only; absent by 1991 | Abbott & Burbidge 1995 |
| *Macropus fuliginosus* | Ballee (19) | **I** (by 1986) | Swimming to island | Browne Cooper et al. 1989 |
| *Macropus fuliginosus* | Culeenup (51) | **I** (by 1986) | Swimming to island | Browne Cooper et al. 1989 |
| *Macropus fuliginosus* | Jeegarnyeelip (15) | **I** (by 1986) | Swimming to island | Browne Cooper et al. 1989 |
| *Macropus fuliginosus* | Yunderup (8) | **I** (by 1986) | Swimming to island | Browne Cooper et al. 1989 |
| *Macropus fuliginosus* | Worallgarook (8) | **I** (by 1986) | Swimming to island | Browne Cooper et al. 1989 |
| *Macropus fuliginosus* | Woody (188) | **I** (by 1975) | At least 2 animals in 1975 and 1976; suspected to have been placed there after tourism activities commenced in 1973 | Abbott & Black 1978, Goodsell et al. 1976 |
| *Macropus robustus* | Dixon (495) | **I** (by 1970s) | Island accessible at low tide | K Palmer 1975 |
| *Macropus robustus* | East Intercourse (300) | **I** (before causeway constructed) | Colonised by swimming? | Abbott & Burbidge 1995 |
| *Macropus robustus* | Carey (63) | **I** (<2000) | Colonised by swimming? | F Stanley pers. comm. |
| *Macropus robustus* | Potter (150) | **I** (<2000) | Crossing at low tide and swimming across channels? | F Stanley pers. comm. |
| *Macropus robustus* | Simpson (78) | **I?** (by 1992) | Colonised by swimming? | Start & McKenzie 1992 |
| *Macropus eugenii* | North (Abrolhos) (176) | **I** (<1928) but **E** by 1959; then **I** 1983 (unsuccessful) & **I** 1985 (5 animals) from West Wallabi | Released by fishermen | AA Burbidge in Poole et al. 1991: 628, A Desmond pers. comm., Miller et al. 2011, K Morris et al. 2003, Storr 1960 |
| *Petrogale lateralis* | Depuch (1100) | **E** (between 1962 and 1982) | Predation by foxes, despite comment by WDL Ride that 'there is no evidence' that this population is threatened by the fox | Haouchar et al. 2013, JE Kinnear et al. 2002, Ride 1964b |
| *Setonix brachyurus* | Breaksea (100) | **E** (between 1881 & 1889) | Shooting for sport? | Abbott 2006, AJ Campbell 1890a; Dalton 1886: 458, 462; Kitchener & Vicker 1981: 75 |

| Species | Island (area in ha) | Year of extinction (E) or immigration (I) | Comments about likely cause(s) | Reference |
|---|---|---|---|---|
| **Other marsupials** | | | | |
| *Isoodon auratus* | Hermite (1020) | **E** (<1912) | Predation by feral cats | AA Burbidge 1971, Montague 1914 |
| **Rodents** | | | | |
| *Hydromys chrysogaster* | Hermite (1020) | **E** (>1971) | Predation by feral cats | AA Burbidge 1971, 2004b |
| *Hydromys chrysogaster* | Trimouille (520) | **E** (>1966) | Predation by feral cats | AA Burbidge 1971, 2004b |
| *Hydromys chrysogaster* | Alpha (120) | **E** (>1983) | Predation by feral cats | AA Burbidge 1971, 2004b |
| *Hydromys chrysogaster* | Bernier (4300) | **I** (1987?) | If natural immigration, this would require a 39 km crossing of ocean from mainland WA | Friend & Thomas 1990 |
| *Rattus fuscipes* | East Wallabi (307) | **E** (>1967) | No obvious cause | I Abbott pers. obs. 1975, NK Cooper & How 2006; O'Loughlin 1965, 1966 |
| **Pinnipeds** | | | | |
| *Neophoca cinerea* | Rottnest (1700) | **E** (between 1803 and 1829: no subsequent breeding) | Slaughtered by sealers | Abbott 1979 |
| *Neophoca cinerea* | Garden (1200) | **E** (between 1803 and 1829: no subsequent breeding) | Slaughtered by sealers | Abbott 1979 |
| *Neophoca cinerea* | Carnac (16) | **E** (between 1803 and 1829: no subsequent breeding) | Slaughtered by sealers | Abbott 1979 |
| *Neophoca cinerea* | Daw (212) | **E** (between 1950 and c. 1990) | Disturbed by fishermen (anchorage) | Gales et al. 1994 |
| **Frogs** | | | | |
| *Litoria moorei* | Garden (1200) | **I** (1982?) | Presumed to represent an introduction as the island originally lacked standing water | Wykes et al. 1999 |
| **Reptiles** | | | | |
| *Egernia stokesii* | Rat (56) | **E** (between 1889 & 2003) | Predation by cats and rats | Alexander 1922, AJ Campbell 1890b, Dunlop 2013, How et al. 2004 |
| *Crenodactylus ocellatus*, *Lerista distinguenda*, *Menetia greyii* | Rat (56) | **E?** (<2012) | Attributed to predation by feral cats, black rats, and great increase in abundance of house mice following the eradication of the black rats in 1991 | Dunlop 2013 |
| *Morelia spilota* | North [Abrolhos] (176) | **E** (<1959) | Linked to the presence of fishing camps? | Storr 1960 |
| *Morelia spilota* | East Wallabi (307) | **E** (2006?) | No obvious cause | Maryan et al. 2009 |
| *Lerista lineata* | Rottnest (1700) | **E?** (after 1986) | No obvious cause | GM Storr in Rottnest Island Management Maryan et al. 2015, GM Storr in Rottnest Island Management Planning Group 1985c: 24-25 |
| *Egernia napoleonis* | Rottnest (1700) | **E?** (after 1959) | No obvious cause | B Bush et al. 2010 |

(immigrations exceeding extinctions). There are 11 instances of species becoming locally extinct followed by re-immigration to the same island. There are two instances of immigration followed by extinction. There is one instance for each of the sequences *extinction–immigration–extinction* and *immigration–extinction–immigration*.

Concerning foreign landbird species (introduced to mainland WA), three species of pigeons have self-introduced to nine islands adjacent to metropolitan Perth (Table 17). Finally, all but one of six introductions to WA islands are now extinct, and most of these are a result of persecution by humans.

Our review of the literature has documented the casual occurrence of landbird species on WA islands, namely 128 species native to WA, six foreign species (non-Australian or non-Western Australian), two Australian species, and one Australian (but not Western Australian mainland) species (Table 14). Most of these occurrences are of single birds.

Two WA islands have received so much attention that it is possible to examine in great detail the frequency and numbers recorded of vagrant landbird species. Storr (1964a, 1965b, 1965c) visited Rottnest Island 62 times (275 days) during the period 1953–1962; and Saunders and de Rebeira (1983) visited 26 times (130 days) between 1981 and 1983. Abbott (1978a) visited Carnac Island 10 times (70 days) between 1974 and 1977. On WA islands, particularly the frequently surveyed Carnac and Rottnest islands, most vagrant landbird species have been recorded on each occasion as single birds (Storr 1965c; Abbott 1978a; Saunders & de Rebeira 1985, 2009; Table 14). On Rottnest Island there have been 70 sightings of 23 non-marine, non-passerine birds between 1903 and 1983, representing 38% of the potential immigrant species occurring on the adjacent mainland, and 39 sightings of seven passerine species, representing 23% of potential immigrant species (Saunders & de Rebeira 1983). Saunders and de Rebeira (1983) noted that of the 109 sightings of vagrants, only one species had individuals present in sufficient numbers during the breeding season to establish a breeding population. Furthermore, of the 115 species present on the adjacent mainland, 54% have never been recorded on Rottnest Island. In conclusion, these data indicate that the colonising ability of most bird species present on the mainland coast of WA is low.

It may therefore be useful to recognise a spectrum, determined by the extent of casual occurrence of landbird species on WA islands. At one extreme are species that comprise a metapopulation with mainland populations (e.g. grey-breasted white-eye, western raven, various raptors), moving freely between inshore islands and mainland. At the other extreme are species that are unable or unwilling to cross a broad expanse of ocean (e.g. white-browed scrubwren, singing honeyeater, western golden whistler). In the centre of this spectrum are species that show a blurred distinction between sedentariness and mobility.

## Seabird species

More than 60 instances of turnover of seabird species have been recorded in WA (Table 17), with immigrations (44) predominating over disappearances (22). Three species re-established on two islands (in Houtman Abrolhos) once the threatening process ceased. Eight species have extended their occupation of WA islands since records by Europeans commenced (Dunlop & Wooller 1990; Johnstone & Storr 1998; Table 17), with numerous examples of range extension of breeding seabirds documented, apparently associated in most cases with increased sea temperature and regular intrusion of the poleward-flowing Leeuwin Current.

An example of a tropical seabird species on the brink of establishing permanent populations on islands of south-west WA is the red-tailed tropicbird (*Phaethon rubricauda*). On Rottnest Island one pair bred in 1959 and 1992 (Saunders & de Rebeira 1993), and one or two individuals have been observed subsequently (WABN 1943–2016 No. 126: 5, No. 149: 8).The breeding population on Sugarloaf Rock ultimately failed (Table 17, Onton & Webb 2009), and breeding on Pelsaert Island has been sporadic (Table 17).

## Waterbird species

Six species of waterbird demonstrate turnover on WA islands (Table 17). There are three local extinctions, four immigrations, and one immigration followed by an extinction, and one extinction followed by an immigration. Some, but not all, of the species turnover is linked to human activity.

## Plant species

Island floras show extensive extinction and immigration of species, although this relies on the (probably incorrect) assumption that absence of plant cover of a species above ground implies that no viable seeds or dormant reproductive propagules are present on the surface of, or within, the soil. This assumption is obviously incorrect for species that rely on fire to initiate germination (Hopkins 1981; Weston 1985). Nonetheless, there are numerous genuine examples of species turnover of plants on WA islands (Abbott 1977a; Abbott & Black 1980; Rippey et al. 1998; Abbott et al. 2000; Rippey et al. 2003), particularly of exotic species reaching islands unassisted by humans and less so of native plant species (Abbott 1992). On the four largest Shoalwater Bay islands, the proportion of introduced plant species varies from 51% to 79% (Rippey et al. 1998). Clearly none of these species was present in 1829, when the nearby mainland began to be settled by Europeans. On well-studied Carnac Island, the proportion of introduced plant species has progressively increased: 34% (1951), 56% (1958–9, 1966–7), 59% (1975–6) and 63% (1995–6) (Abbott et al. 2000).

In a comparison of 20 islands examined in 1956 or 1959 and again in 1975, annual plant species had higher extinction rates than did perennial species, introduced

**Table 17**

Turnover of bird species on islands of Western Australia. Human-assisted immigration (translocation) is excluded (see Table 12), except for foreign species.

| Species | Island(s) | Year of extinction (E) or immigration (I) if known | Comments about likely cause(s) | Reference(s) |
|---|---|---|---|---|
| **Seabirds** | | | | |
| *Eudyptula minor* | Garden | **I** (<2009) | On rockwalls at HMAS Stirling naval base | WABN No. 130: 20 |
| *Pterodroma macroptera* | Mistaken | **E** (between 1911 and 1921) | | Carter 1923a, Hull 1922, Ogilvie-Grant 1910, |
| *Puffinus pacificus* | Rat | **E** (>1945) | Predation by black rats and feral cats | Dunlop 2013, Storr et al. 1986 |
| *Puffinus carneipes* | Green (Oyster Harbour) | **E** (>1827) | Collected for food | Abbott 2001 |
| *Puffinus carneipes* | Mistaken | **E** (between 1906 and 1921) | Bycatch | Hull 1922, Kinghorn 1927, SG Lane 1977, Lavers 2014 |
| *Puffinus carneipes* | Goose (Archipelago of the Recherche) | **E** (>1948) | | Lavers 2014 |
| *Puffinus assimilis* | Rat | **E** (>1945) | Predation by black rats and feral cats | Storr et al. 1986 |
| *Pelagodroma marina* | Mistaken | **E?** (>1921) | Because Ogilvie-Grant 1910 and Carter 1923a do not record this species and Johnstone & Storr 1998 do not list it as a breeding species on this island, this extinction may be spurious | Hull 1922 |
| *Phaethon rubricauda* | Rat | **E** (1890s) | | Storr et al. 1986 |
| *Phaethon rubricauda* | Pelsaert | **E** (1954)<br>**I** (1988) | Probably better treated as an irregular breeder; last recorded breeding in December 2000 | AA Burbidge pers. comm., Coate 1989, Storr et al. 1986, WABN No. 48: 3, 50: 8, 51: 2 |
| *Phaethon rubricauda* | Sugarloaf Rock | **I** (1963/1967?)<br>**E** (2008-2009?) | The population began expanding in 1968 and then declined from c. 1995; now vagrant | Onton & Webb 2009, Serventy 1965, Tarbotton 1968, Tarburton 1971, Watts & Tarbottom 1967; WABN No. 137: 11, 145: 10, 147: 6; K Williams pers. comm. 2014 |
| *Fregata minor* | Adele | **I** (1990) | | Coate et al. 1994, 2011 |
| *Sula sula* | Adele | **I** (1990) | | Coate et al. 1994, 2011 |
| *Anous stolidus* | Bedout | **E** (>1901) | Predation by black rats | Fuller & Burbidge 1998a, Johnstone & Storr 1998 |
| *Anous stolidus* | Rat | **E** (1889–1930s) | Predation by feral cats | Dunlop 2013, Storr et al. 1986 |
| *Anous stolidus* | Lancelin | **I** (c. 1991) | | Dunlop 2009, Dunlop & Goldberg 1999, Dunlop & Mitchell 2001; WABN No. 61: 2, 84: 24-25 |
| *Anous tenuirostris* | Wooded | **I** (1907) | | Storr et al. 1986 |
| *Anous tenuirostris* | Pelsaert | **E** (<1907)<br>**I** (1936) | | Storr et al. 1986 |
| *Larus pacificus* | 6 islands: Lancelin, Rottnest, Carnac, Garden, Seal, Penguin | **E** (>1890s?) | Presumed extinct on these islands, based on the current hiatus in distribution, record of the Noongar name used by the 'Aborigines of Perth', and its occurrence in the 1840s 'along the coast but no where in any considerable numbers'. (This species was recorded as vagrant on Rottnest Island in 2002 & 2009 – WABN No. 102: 3, 130: 5.) | J Ford 1965; J Gilbert n.d. = 1840?, 1843?; Johnstone & Storr 1998, Serventy & White 1943, Storr 1964a, Stranger 2002 |

| Species | Island(s) | Year of extinction (E) or immigration (I) if known | Comments about likely cause(s) | Reference(s) |
|---|---|---|---|---|
| *Sterna bengalensis* | Adele | **E** (between 1891 & 1972) | Still present, but not breeding | Coate 1997, Johnstone & Storr 1998, D Serventy 1952, J Walker 1892 |
| *Sterna anaethetus* | Rat | **E** (>1889)<br>**I** (>1999) | Re-establishment after eradication of feral cats and black rats | Alexander 1922, AA Burbidge & Morris 2002, AJ Campbell 1890b, CG Gibson 1908, Helms 1898, Serventy 1943, Storr et al. 1986 |
| *Sterna anaethetus* | At least 23 islands, from Rottnest to Seal (Cape Leeuwin) | **I** (<1889–1956) | | Johnstone & Storr 1998, Serventy & White 1943 |
| *Sterna anaethetus* | Investigator | **I** (2000s?) | | Dunlop 2009 |
| *Sterna fuscata* | Bedout | **E** (> 1901) | Predation by black rats | Fuller & Burbidge 1998a, KD Morris 1989b |
| *Sterna fuscata* | Rat | **E** (<1945) | Predation by feral cats | Fuller et al. 1994, Storr et al. 1986 |
| *Sterna fuscata* | Lancelin | **I** (< 1998) | | Dunlop 2009, Dunlop & Mitchell 2001 |
| *Sterna dougallii* | At least 11 islands from Beagle to Seal (Shoalwater Bay) | **I** (1950s-1975) | | Dunlop 1979, J Ford 1965, Johnstone & Storr 1998, WABN No. 35: 8 |
| **Waterbirds** | | | | |
| *Cereopsis novaehollandiae* | Bald | **E** (> 1890) | Presumably shot for food | AJ Campbell 1900: 1021 |
| *Cygnus atratus* | Rottnest | **I** (> 1980)<br>**E** (1989) | 1 pair, one of which died and the other was euthanased by a vet | Saunders & de Rebeira 2009 |
| *Nycticorax caledonicus* | Bird | **E** (between 1900 & 1920) | | Alexander 1921b; D Le Souëf 1901: 184, 1902; Sedgwick 1940 |
| *Nycticorax caledonicus* | Lion | **E** (between 1921 & 1944 or 1956) | 'Found breeding in thousands' versus c. 40 nests in 1921 | Hull 1922, Kinghorn 1927, Lindgren 1956, V Serventy 1952 |
| *Pelecanus conspicillatus* | Penguin | **I** (1998) | | Rippey et al. 2002b |
| *Pelecanus conspicillatus* | Green (Oyster Harbour) | **E** (1826)<br>**I** (1985) | **E**: Young birds collected for food.<br>**I**: ?Fed by local fisherman | Abbott 2001, *Albany Advertiser* 14.10.1999: 20 |
| *Phalacrocorax melanoleucos* | Wooded | **I** (1983) | | Storr et al. 1986 |
| *Gallirallus philippensis* [This species behaves like a landbird on islands] | Rottnest | **I** (2002?) | First breeding recorded in November 2003 | WABN No. 109: 4, 110: 14–15, 145: 28–29 |
| *Gallirallus philippensis* | Penguin | **I** (between 1977 and 2004) | | BirdLife WA database, M Chambers 2005; *The Naturalist News* March 2013, Jan–Feb 2015, WABN No. 46: 2, 78: 21, 94: 23–24, 149: 37, 153: 36 |
| **Landbirds** | | | | |
| *Coturnix ypsilophora* | Trimouille | **I** (<1994) | | AA Burbidge et al. 2000, Kenneally et al. 2000 |
| Unidentified species of quail | Garden | **E** (>1829) | | AH Gilbert 1829 |
| Unidentified species of quail | Rottnest | **E** (>1872) | WN Clark recorded 'numerous coveys' during a 9 month residence in 1831 | Lovat 1914: 211, *The Perth Gazette* 20.8.1842: 3 |

| Species | Island(s) | Year of extinction (E) or immigration (I) if known | Comments about likely cause(s) | Reference(s) |
|---|---|---|---|---|
| *Accipiter fasciatus* | Rottnest | **I** (first bred 2011) | Change of status from 2009 | Mather 2009, 2011; WABN No. 145: 24–25 |
| *Circus assimilis* | Barrow | **E** (between 1917 & 1964)<br>**I** (<1964) | | Butler 1970, 1975; Sedgwick 1978, Serventy & Marshall 1964, Whitlock 1918 |
| *Turnix varius* | North (Abrolhos) | **E** (between 1945 and 2006)<br>**I** (by 2006)<br>**E** (by 2013) | | Blyth et al. 2007, 2014 |
| *Turnix varius* | East Wallabi | **E** (between 1960 & 1975)<br>**I** (between 1975 & 2006) | | Blyth et al. 2007 |
| *Turnix varius* | Pigeon | **E** (>1913) | | Alexander 1922, Storr 1965d |
| *Turnix varius* | Rottnest | **I** (c. 2002) | Well established by 2003 | Mather 2009, 2011; Saunders & de Rebeira 2009; WABN No. 101: 3, 102: 14, 103: 5 & 26, 110: 15, 115: 7 |
| *Turnix varius* | Garden | **I** (1985) | | MG Brooker et al. 1995, Wykes et al. 1999 |
| *Vanellus tricolor* | Dirk Hartog | **I** (< c. 1916) | | Carter 1917, Whitlock 1921a |
| *Vanellus tricolor* | Rottnest | **I** (1934) | Uses nesting sites provided by human activity (e.g. runway verges, sand blowouts). Population size in January 1998–2011: 8–41 | Saunders & de Rebeira 1985, Storr 1965b; WABN No. 86: 10, 87: 9, 90: 7, 91: 10–11, 94: 12, 95: 13, 100: 10, 102: 16; 103: 5, 12; 106: 12, 137: 16 |
| *Vanellus tricolor* | Garden | **I** (between 1975 and 1979) | Previously vagrant (1948) | SJJF Davies 1980, WABN No. 87: 9, 91: 11 |
| *Phaps elegans* | North (Abrolhos) | **E** (between 1913 and 1945)<br>**I** (by 2006) | | Blyth et al. 2007, 2014; Storr 1960, 1966 |
| *Phaps elegans* | Pigeon | **E** (>1959)<br>**I** (by 1981) | *Rattus rattus* present in 1965 | O'Loughlin 1966; Storr 1965d, 1966; Storr et al. 1986 |
| *Phaps elegans* | Rottnest | **E** (>1872, possibly 1920s) | Trapped and sold to captains of ships; predation by feral cats?; shooting? | Glauert 1928, Joske et al. 1997, Lovat 1914: 211, Storr 1965c |
| *Phaps elegans* | Breaksea | **E** (between 1820s and 1975, possibly between 1858 and 1881) | Shooting by lighthouse keepers from 1858? | Abbott 1980e, Dalton 1886, Lockyer 1827, Wolfer 2008 |
| *Phaps elegans* | Mistaken | **E** (between 1840s and 1975) | ?Recreational shooting | Abbott 1980e, WN Clark 1841 |
| *Ocyphaps lophotes* | Faure | **I** (1880s) | After installation of watering troughs following development of pastoral station? | Dell & Cherriman 2008 |
| *Geopelia humeralis* | Trimouille | **E** (between 1912 & 2000)<br>**I** (by 2000) | Immigration linked to eradication of black rats? | AA Burbidge pers. comm., AA Burbidge et al. 2000, Kenneally et al. 2000, Montague 1914, Serventy & Marshall 1964 |
| *Chrysococcyx basalis* | Barrow | **I** (<1964) | | Butler 1970, Serventy & Marshall 1964, Whitlock 1918 |
| *Chrysococcyx basalis* | Bernier | **E** (between 1959 and 1976)<br>**I** (by 1976) | | I Abbott unpubl., Howard 1978, Mees 1962, Storr MSb |
| *Chrysococcyx basalis* | Dorre | **I** (by 1959)<br>**E** (by 1988) | | Cale 1992, Mees 1962 |
| *Cacomantis flabelliformis* | Rottnest | **I** (>1960s) | Change of status from uncertain or non-breeding migrant (up to 1962) to uncommon breeding migrant (from 1982) | Mather 2009; Saunders & de Rebeira 1983, 2009; Storr 1965c |

| Species | Island(s) | Year of extinction (E) or immigration (I) if known | Comments about likely cause(s) | Reference(s) |
|---|---|---|---|---|
| *Todiramphus sanctus* | Rottnest | **I** (?1980s) | Change of status from uncertain or non-breeding migrant (up to 1962) to uncommon breeding migrant (from 1982) | Mather 2009, 2011; Saunders & de Rebeira 1983, 2009; Storr 1965c, MSb; WABN No. 27: 4, 55: 9, 103: 5 |
| *Todiramphus chloris* | Hermite | **E** (>1912) | | AA Burbidge et al. 2000 |
| *Merops ornatus* | Rottnest | **I** (1977) | Some 170 birds present during summer 2004; uses nesting sites provided by human activity (e.g. road cuttings, sand pits, golf course fairways) | Abbott et al. 1978, Mather 2009, Saunders & de Rebeira 1985 |
| *Merops ornatus* | Garden | **I** (<1979) | | MG Brooker et al. 1995b, SJJF Davies 1980, Wykes et al. 1999 |
| *Falco cenchroides* | Varanus | **I** (between 1958 and 1985) | | Dinara Pty Ltd 1986, Serventy & Marshall 1964 |
| *Falco cenchroides* | Pelsaert | **I** (1 pair, 1948), apparently **E** thereafter | | Tarr 1949 |
| *Cacatua roseicapilla* | Rottnest | **I** (>1998) | Unknown, but previously vagrant (1953, 1959, 1983, 1993, 1996); 20 birds recorded in summer 2008 | Mather 2009, B & K McRoberts unpubl., Saunders & de Rebeira 2009; Storr 1965c, MSb |
| *Amytornis textilis* | Dirk Hartog | **E** (between 1918 and 1920) | Predation by feral cats | Abbott et al. 2014; Carter 1917, 1923b; Whitlock 1921a |
| *Gerygone fusca* | Rottnest | **I** (1950) | Provision of suitable habitat (*Eucalyptus gomphocephala* woodland) | Storr 1965c |
| *Cracticus torquatus* | Dirk Hartog | **I** (between 1927 and 1967) | | I Abbott pers. obs 1976, Ashby 1929, SJJF Davies & Chapman 1974, Sedgwick 1968, BA Wells & Wells 1974 |
| *Cracticus tibicen* | Garden | **I** (between 1979 and 1991) | Unknown, but previously vagrant/occasional visitor | Abbott 1980f, MG Brooker et al. 1995, K Buller 1949, Calderwood 1953, Sedgwick 1940, Serventy 1938, Storr MSb, Wykes et al. 1999 |
| *Coracina novaehollandiae* | Barrow | **I** (<1964) | | Butler 1970, Serventy & Marshall 1964, Whitlock 1918 |
| *Coracina novaehollandiae* | Garden | **I** (1996) | | Wykes et al. 1999 |
| *Pachycephala rufiventris* | Rottnest | **E** (>1903) | Occasionally vagrant since 1903 | Serventy 1938, Storr 1965c |
| *Grallina cyanoleuca* | Garden | **I** (1996) | Unknown; previously vagrant | SJJF Davies 1980, Wykes et al. 1999 |
| *Corvus bennetti* | Bernier | **E** (between 1959 and 1976) **I** (by 1976) | | I Abbott unpubl., Howard 1978, Mees 1962, Storr MSb |
| *Melanodryas cucullata* | Dirk Hartog | **E** (>1921) | | Carter 1917, Whitlock 1921a |
| *Cheramoeca leucosterna* | Faure | **I** (between 2000 and 2005) | | Dell & Cherriman 2008, Legge et al. 2012 |
| *Hirundo neoxena* | Trimouille | **I** (by 1958) | | AA Burbidge et al. 2000, Kenneally et al. 2000, Serventy & Marshall 1964 |
| *Hirundo neoxena* | Hermite | **I** (by 1958) | | AA Burbidge 1971, Kenneally et al. 2000, Serventy & Marshall 1964 |
| *Hirundo neoxena* | Figure of Eight | **I** (by 1981) | | SG Lane 1982l, Serventy 1952 |
| *Hirundo neoxena* | Lion | **I** (by 1944) | | Hull 1922, Lindgren1956, Serventy 1947 |

| Species | Island(s) | Year of extinction (E) or immigration (I) if known | Comments about likely cause(s) | Reference(s) |
|---|---|---|---|---|
| *Petrochelidon nigricans* | Rottnest | **I** (1983?) | Unknown; previously vagrant. Since c. 1983 it has occurred in large numbers, but it is uncertain if it breeds regularly on the island | Mather 2009, 2011; Saunders & Rebeira 1993; WABN No. 27: 4, 62: 2, 70: 2, 93: 30 |
| *Megalurus gramineus* | Faure | **I** (between 2000 and 2005) **E** (between 2005 and 2008) **I** (between 2008 and 2009) | | Dell & Cherriman 2008, Legge et al. 2012, Mather 2015 |
| *Megalurus gramineus* | Breaksea | **E** (>1889) | | Abbott 1980e, AJ Campbell 1900 |
| *Eremiornis carteri* | Hermite | **E** (between 1912 and 1958) | Predation by feral cat and rats | AA Burbidge 1971, Montague 1914, Serventy & Marshall 1964 |
| *Zosterops luteus* | Hermite | **I** (<1958) | | Serventy & Marshall 1964 |
| *Zosterops luteus* | Barrow | **E** (between 1917 and 1964) **I** (<1964) | | Butler 1970, Serventy & Marshall 1964, Whitlock 1918 |
| *Stagonopleura oculata* [Species identification uncertain] | Middle (Recherche) | **E** (>1890) | | *fide* V Serventy 1952 (We have been unable to find the reference in the copy of Andrews 1959 examined by us) |
| *Stagonopleura oculata* | Woody | **I** (between 1976 and 1995) | | BirdLife WA database; WABN No. 77: 10, 85: 8 |
| *Taeniopygia guttata* | Barrow | **E** (between 1917 and 1964) **I** (<1964) | | Butler 1970, Serventy & Marshall 1964, Whitlock 1919 |
| *Taeniopygia guttata* | Faure | **I** (>1880s?) | ?After installation of watering troughs when pastoral station established | Dell & Cherriman 2008 |
| *Anthus australis* | Hermite | **E** (>1994) **I** (<2000) | Not recorded in 1996 or 1999; immigration probably from Barrow Island after eradication of black rats | AA Burbidge pers. comm., AA Burbidge 1971, AA Burbidge et al. 2000, Kenneally et al. 2000 |
| *Anthus australis* | Barrow | **E** (<1958) **I** (<1964) | | Butler 1970, Sedgwick 1978, Serventy & Marshall 1964; Whitlock 1918, 1919 |
| **Foreign birds (self-introduced)** | | | | |
| *Columbia livia* | Rottnest | **I** (<1890), **E** (1890) | Destroyed because of their polluting rainwater storage | Storr 1965c |
| *Columbia livia* | Garden | **I** (<1953) | Control by shooting & baiting | Calderwood 1953; GIEAC 1998, 1999 |
| *Columbia livia* | Shoalwater Bay islands (Penguin, Seal, Middle Shag, West Shag, East Shag, Gull Rock, Bird) | **I** (between 1975 and 1977) | Attracted by silos present on mainland coast at Rockingham | Rippey et al. 1998, WABN No. 78: 21 |
| *Streptopelia chinensis* | Rottnest | **I** (c.1938) | | Sedgwick 1958, Storr 1965c |
| *Streptopelia senegalensis* | Dirk Hartog | **I** (between 1984 and 2013) | | AH Burbidge pers. comm. |
| *Streptopelia senegalensis* | Rottnest | **I** (c.1930) | | Sedgwick 1958, Storr 1965c |
| *Streptopelia senegalensis* | Garden | **I** (<1940) | | Sedgwick 1958 |

| Species | Island(s) | Year of extinction (E) or immigration (I) if known | Comments about likely cause(s) | Reference(s) |
|---|---|---|---|---|
| **Foreign birds (Introduced by humans)** | | | | |
| *Callipepla californica* | Rottnest | **I** (c. 1877) **E** (1880s?) | | Joske et al. 1997 |
| *Numida meleagris* | Rottnest | **I** (1870s?), **E** (<1904); **I** (<1910) | The 1870s introduction 'wiped out by the native prisoners' | Joske et al. 1997, *The West Australian* 10.1.1910: 2, 10.4.1934: 11 |
| *Pavo cristatus* | Rottnest | **I** <1910), **E** (as a breeding species, 2010) | Culled to 3 males in 2010; one seen September 2011; 3 present in July 2014 | www.sciencewa.net.au/topics/environment-a.../357-rottnest-culls-feral-peacocks [accessed 25.11.2010], Mather 2011, *Post* 12.9.2009: 11, Serventy 1948, Storr 1965c, *The West Australian* 10.1.1910: 2, WABN No. 152: 23 |
| *Gallus gallus* | Middle (Recherche) | **I** (<1891) **E** (<1950) | Possibly penned and not feral | *The Australasian* 22.8.1891: 18 |
| *Phasianus colchicus* | Rottnest | **I** (1877–1880, then 1928) | 1 male and 3 females released ex Perth Zoo | Joske et al. 1997, Serventy 1948, Storr 1965c |
| *Meleagris gallopavo* | Garden | **I** (1946) **E** (1958) | Feral population shot out | Storr & Johnstone 1988 |
| **Native birds (introduced by humans)** | | | | |
| *Leipoa ocellata* | Rottnest | **I** (<1934) | 1 pair released ex Perth Zoo; failed | *The West Australian* 10.4.1934: 11 (originally discussed in *The Sunday Times* 31.3.1929: 12S, 30.6.1929: 7S) |

species had higher extinction rates than did native species, introduced species had higher immigration rates than did native species, and on islands with breeding colonies of silver gulls, plant species had higher immigration rates than on islands without colonies of gulls (Abbott 1977a). Immigration rates were independent of isolation, and extinction rates were independent of island area. This finding is explicable if it is assumed that seabird colonies override the importance usually ascribed to island area and isolation in influencing extinction and immigration rates (Abbott 1977a).

This study was repeated in 1976, 1977 and 1978 on a subset of 76 islands between Rottnest Island and Shoalwater Bay (Abbott & Black 1980). Comparison of the floras present showed that 29 of the islands unvegetated in 1975 gained no immigrant plant species. Thirteen of the vegetated islands had the same plant species (i.e. no immigrations or extinctions). The remaining 34 islands showed evidence of immigrations and/or extinctions (mostly either one or the other). In the period 1975–1977 islets around Rottnest Island experienced more immigrations (21) than extinctions (5), whereas the islets to the south of Rottnest showed the reverse (39 extinctions, 16 immigrations). In contrast, during the period 1977–1978, the islets around Rottnest showed an excess of extinctions (16) over immigrations (9). Note that the islands south of Rottnest were not studied in 1977–78. Most of the plant species that became locally extinct or that immigrated were annuals.

Small islets tend to change little in species richness of plants in comparison to larger islets (Abbott & Black 1980). In this sense small islets have more stable floras than do large islands, probably because of the more severe impact of physical factors on the island environment (salt spray and limited occurrence of soil resulting from erosion caused by wave action).

A census of native plant species on 30 islets around Rottnest Island in December 1982 and 1984 found no change on 15 islands, immigration on three islands, and local extinction on 12 islands (Abbott & Black unpubl.). All of the species that became locally extinct are tolerant of sea spray.

A major limitation of species richness as a metric is that it combines species that differ in habitat, diet and other ecological characteristics. In an effort to minimise this, Abbott (1992) examined species turnover in a subset of closely-allied species, grasses, on 30 islands of south-west WA that had been visited more than once. This data set comprised 82 native species and 93 exotic species. The exotic-grass component was much more dynamic than the native-grass component, with more than twice as many immigrations and extinctions. This difference was ascribed to most of the former being annual and most of the latter being perennial. The aggregate number of immigrations and extinctions was balanced both for native species (11 versus 14) and for exotic species (29 versus 31). Individual islands differed remarkably, with nearly half the immigrations of exotic species occurring on two islands (Pigeon, Pelsaert) and about half the extinctions of exotic species occurring on three islands (Lancelin, Penguin, Woody). In contrast, immigrations and extinctions of native grass species were spread more evenly among islands.

The difficulty involved in determining valid species turnover on a large island is well illustrated by the flora of Rottnest Island (Rippey et al. 2003). The first list, from the 1950s, was assembled by one collector (Storr 1962). The second list (1998–2001) was based on the collective effort of 40 volunteers. The total number of species was similar but apparent immigrations (eight native species, 30 introduced species) and extinctions (19 native species, 24 introduced species) were evident.

Further examples of plant species becoming 'extinct' on WA islands have been documented. Abbott and Black (1980) recorded apparent (i.e. above ground) short-term extinctions, perhaps better described as 'temporary absences', on small islets off Fremantle (discussed below). Weston (1985) was unable to recollect three plant species first collected on Middle (Archipelago of the Recherche) Island in 1802 (JH Willis 1959). Three plant species (*Stipa elegantissima, Phyllanthus calycinus* and *Alyxia buxifolia*) were collected on Carnac Island in 1839 but not since (Abbott 1977a). *Amyema melaleucae* and *Acacia truncata* were collected on Rottnest Island in 1839 but have not been found since (Rippey et al. 2003). The absence of *Malva australiana* from Penguin Island probably signifies genuine local extinction, as this species was recorded recently on nearby islands (Rippey et al. 1998). This species had also presumably disappeared from Rottnest Island before 1962 (Rippey et al. 2003).

## Mammal species

Of the 54 insular populations of wallabies and bettongs (Abbott & Burbidge 1995; LA Gibson and McKenzie 2012b), only 5% have become extinct since the European settlement of WA (Table 16). None of these extinctions is attributable to natural causes (AA Burbidge 1999, AA Burbidge et al. 1997). There have been no natural colonisations of WA islands by wallabies or bettongs, despite the demonstrated swimming ability of some macropodid species (Serventy & Marshall 1964; Browne Cooper et al. 1989). Indeed, almost all immigrations of native species of mammals to WA islands have been human-assisted (Table 16). Some insular populations of *Macropus robustus* (Abbott and Burbidge 1995) occur on islands that are connected at low tide to the mainland and thus are probably not genuinely isolated. These are omitted from consideration in this section.

However, given the occurrence of several tsunamis (perhaps 30 m in height) along the coast of the Pilbara and Kimberley regions during recent millennia (Playford 2014), it is likely that mammal species on small, low or exposed large islands may have become locally extinct (e.g. Maret, Berthier, Northwest, Varanus islands). It is possible that the current occurrence of species of native rodents on Champagny, East Montalivet, Bathurst, Trimouille and Thevenard islands represent natural recolonisations. Molecular analyses of these insular populations and comparison with mainland populations may elucidate this matter.

Twelve species of European or Asian mammal have been introduced either deliberately or indirectly (self-introduced from the mainland) to WA islands (Abbott & Burbidge 1995; I Abbott unpubl.; AA Burbidge pers. comm.): Black rat (40 islands); rabbit (22); house mouse (21); cat (19); fox (18); goat (11); sheep (10); horse (2); pig (1); camel (*Camelus dromedaries*; 1); monkey, possibly *Macaca* sp. (1); red deer (*Cervus elaphus*; 1); and hog deer (*Axis porcinus*; 1). Most of these individual animals or populations have now either been removed or eradicated (Table 12; also discussed below).

## Reptile species

Attempts to exterminate snakes (*Pseudonaja affinis*) on Rottnest Island (AJ Campbell 1890a) were unsuccessful. However, one species of snake did become extinct on North (Abrolhos) and East Wallabi Islands (Table 16). There has been one confirmed extinction of a lizard species on a WA island (Rat Island, Houtman Abrolhos), three other lizard species are suspected to be extinct on this island, and two other lizard species are suspected to be extinct on Rottnest Island (Table 16). Almost all of these extinction events were caused by human activities, which is consistent with the global trend (Case et al. 1992). This trend continues (e.g. Smith et al.2012). Nevertheless, the risk of misclassifying cryptic reptile species as immigrant or extinct is well illustrated by the discovery of *Lerista christinae* on Rottnest Island as late as 1970 (LA Smith 1997) and the rediscovery of the Ningaloo worm lizard (*Aprasia rostrata*) on Hermite Island in 2006 (Maryan & Bush 2007).

In conclusion, the WA island data offer little support for the dynamic equilibrium model proposed 50 years ago by MacArthur and Wilson (1963, 1967). On some islands there is an equilibrium, but it is not dynamic (i.e. no immigrations or extinctions). Many exotic (non-Australian) species of plants and landbirds have become established on islands, and there are more immigrations of native landbird species than there are local extinctions. Before Europeans settled in WA, it appears that species turnover on islands was either non-existent or infrequent.

## Vegetation change

Recognition of the types of vegetation present on islands is based on the combination of floristics (particularly the dominant plant species) and structure (height of these species). Detection of change in vegetation structure on islands (at least from pre-colonial or early colonial times) relies appreciably on casual remarks by early visitors to islands, including M Flinders (Flinders 1814), C Fremantle (Cottesloe 1928), T Wilson (TB Wilson 1835), C von Hügel (D Clark 1994) and J Stirling

(Shoobert 2005). More detailed comparisons only became possible when adequate baseline maps of vegetation types on larger islands were prepared. However, the number of islands with published vegetation maps and hence for which comparisons are possible remains small: Rottnest, Carnac and Garden islands (all near Fremantle), and Bald Island (on the southern coast east of Albany).

The first vegetation map of Garden Island was published in 1974, based on aerial photographs taken in 1963 and ground verification (Garden Island Working Group 1974; McArthur & Bartle 1981). The next map, in colour, was based on 1976 aerial photography and field checking in 1978 (McArthur & Bartle 1981). Setting aside obvious changes as a result of clearing for roads and buildings and the spread of unstable sand (blow outs), evidence exists of vegetation dynamics (based on dominant plant species) in historic times. These changes include the retreat of *Callitris preissii* stands near the northern end of the island, replacement of *Acacia cochlearis* thickets near the southern end by *A. rostellifera* scrub, invasion of grassland at the northern and southern ends by *A. rostellifera*, replacement of *A. rostellifera* scrub on the eastern side by *Melaleuca lanceolata*, and the increase in extent of *C. preissii* and *M. lanceolata* between 1942 and 1976 in the northern interior of Garden Island (McArthur & Bartle 1981).

When this map was updated using 1989 aerial photography, no major change during this 11-year period was evident, except for the loss of A. *rostellifera* as co-dominant in various communities and the senescence of this species in *A. rostellifera* scrub (McArthur 1996a). These changes seem to be caused by the low frequency of fire on the island (McArthur 1998). The establishment in the early 1990s of 24 permanent quadrats (20 m × 20 m) in the major plant communities should allow the detection of further successional change and the determination of the likely causes.

Although Rottnest Island has been settled for much longer than Garden Island, the coverage of the dominant plant species in colonial times remains uncertain. The first vegetation map was not produced until 1974 (Edmiston & White 1974), well after extensive change driven by wildfire and increased density of a marsupial herbivore (Storr 1963). Based on aerial photography in 1941, 1955 and 1978, the forest and scrub vegetation types dominated by *A. rostellifera*, *M. lanceolata*, and *Pittosporum ligustrifolium – Templetonia retusa* have become greatly fragmented (Penn & Green 1983). It seems that *A. rostellifera* scrub covered much of the island in 1903, 1919 and 1928 (Storr 1963).

The island for which vegetation dynamics have been most completely worked out is Carnac Island. A vegetation map was produced in 1951 (McArthur 1957) and again in 1975 (Abbott 1980d), based on aerial photographs and field inspection. Nine vegetation types were recognised in 1975, two more than in 1951, but large differences in the spatial extent of several types were noted. Subsequently, a more detailed retrospective study was undertaken using aerial photographs taken in 1965, 1972, 1984 and 1995, with the latter also checked on the island (Abbott et al. 2000). Dramatic changes occurred throughout the 40-year period, and these were attributed to herbivory by rabbits, drought, chloride toxicity, nesting seabirds, and competition with introduced weed species.

The first vegetation map (partial) of Bald Island resulted from a short visit in 1959 (Storr 1965a), followed by a map for the entire island in 1976 (Abbott 1981a). In contrast to Rottnest, Carnac and Garden islands, Bald Island has experienced little disturbance by Europeans, making it possible to separate anthropogenic factors from natural influences. Little change in vegetation was evident during the 17-year interval.

Many WA islands have now been mapped for their vegetation types (Abbott 1981a; Abbott & Black 1978; Anon. 1975; Apache Energy Pty Ltd 1997; Buckley 1983; Goodsell et al. 1976; JM Harvey et al. 2001; Henson et al. 2014; Hesp et al. 1983; G Keighery et al. 1995, 2002, 2006; G Keighery & Muir 2008, V & C Semeniuk Research Group 1989). These need to be revisited, remapped and assessed for stability of vegetation types. A larger sample of islands should permit generalisation and differentiation between the importance of natural and human factors.

## BIOGEOGRAPHIC POINTS OF INTEREST, SURPRISES AND ANOMALIES: EXAMPLES OF GENERA AND SPECIES UNDER-REPRESENTED OR OVER-REPRESENTED ON WA ISLANDS

Focus on species richness, a popular metric in widespread use in community ecology and biogeography, can be misleading. Species richness aggregates the presence of many species, which may differ in numerous traits. These include minimum population size, below which the species cannot persist; home range; ability and willingness to disperse across water; and flexibility of habitat preference. Therefore it is valuable to examine groups of similar (congeneric) species and identify peculiarities in distribution or discrepancies in patterns of occurrence on islands, and elucidate the processes that have created the patterns. EO Wilson (1959) termed this approach 'biogeography of the species'.

Equally compelling is the insular occurrence of particular species of interest. Lack (1942) commented on the erratic or idiosyncratic distribution of many bird species on small islands around Scotland, despite the occurrence of suitable habitat. This section highlights some of the more enigmatic distributional patterns (particularly discontinuities in the insular range of species and surprising juxtapositions of species) and biogeographic curiosities found on WA islands. Examples for plant species of interest are listed in Table 18. As noted by JH Willis (1953: 5), no two of the 20

**Table 18**

Examples of plant species on Western Australian islands with interesting patterns of occurrence that invite explanation. Islands are listed from north to south, and then from west to east.

| Species (Family) | Coastal mainland range | Island occurrence | Point of interest |
|---|---|---|---|
| *Acacia rostellifera* (Fabaceae) | S of North West Cape to S of Cape Naturaliste, E of Albany to Cape Arid | Salutation, Baudin, Sunday, Rottnest, Garden, Carnac, Penguin, Bird, Middle (Recherche) | Distributional hiatus: not recorded on Houtman Abrolhos |
| *Acrotriche cordata* (Ericaceae) | S of Dongara to E of Cape Arid | Houtman Abrolhos (West Wallabi, East Wallabi, Seagull), Rottnest, Garden, Middle (Recherche) | Distributional hiatus: not recorded on Carnac, Eclipse, Michaelmas, Bald, Mondrain, Salisbury |
| *Alyxia buxifolia* (Apocynaceae) | Shark Bay to S of Dongara, Perth to Cape Naturaliste, E of Cape Arid | Baudin, East Wallabi, Rottnest, Garden, Penguin, Middle (Recherche) | Distributional hiatus: not recorded on Bernier, Dorre, Faure, Dirk Hartog, Carnac, West Wallabi, Mondrain, Salisbury |
| *Andersonia sprengelioides* (Ericaceae) | Cape Leeuwin to E of Cape Arid | Eclipse, Michaelmas, Bald, Woody, Long, Remark, Pasco, Mondrain | Distributional hiatus: not recorded on Middle (Recherche) |
| *Beyeria viscosa* (Euphorbiaceae) | S of Geraldton to W of Cape Arid (discontinuous) | West Wallabi, East Wallabi, Oystercatcher, Rottnest, Garden, Hamelin, Woody, Sandy Hook, Long, Remark, Pasco, Wilson, MacKenzie, Middle (Recherche) | Distributional hiatus: not recorded on Carnac, Penguin, Eclipse, Michaelmas, Bald, Mondrain |
| *Caladenia latifolia* (Orchidaceae) | Geraldton to E of Cape Arid | Rottnest, Garden, Mistaken, Breaksea, Michaelmas, Bald, Figure of Eight, Boxer, Long, Woody, Mondrain, North Twin Peak, South Twin Peak | Distributional hiatus: not recorded on Carnac, Penguin, Eclipse, Middle (Recherche), Salisbury |
| *Callitris preissii* (Cupressaceae) | S of Dongara to E of Cape Arid | Rottnest, Garden, Bald, Sandy Hook, Long, Woody, Mondrain, North Twin Peak, Middle (Recherche) | Distributional hiatus: not recorded on Carnac, Eclipse, Michaelmas, Salisbury |
| *Carex preissii* (Cyperaceae) | N of Perth to W of Cape Arid (discontinuous) | Rottnest, Carnac, Garden, Eclipse, Breaksea, Mistaken, islet next to Mistaken, Michaelmas, Bald | Mostly restricted to large islands |
| *Cassytha racemosa* (Lauraceae) | North West Cape to E of Cape Arid | Boullanger [Long], Garden, Penguin, Mondrain | Distributional hiatus: not recorded on Bernier, Dorre, Dirk Hartog, Faure, Houtman Abrolhos, Rottnest, Carnac & numerous islands of the southern coast |
| *Clematis linearifolia* (Ranunculaceae) | Shark Bay to Cape Leeuwin, E of Bremer Bay to E of Cape Arid | Dirk Hartog, Salutation, Boullanger [Long], Rottnest, Carnac, Garden, Penguin, Boxer, Middle (Recherche), Goose | Distributional hiatus: not recorded on Bernier, Dorre, Faure, Houtman Abrolhos, Woody, Mondrain, Salisbury |
| *Clematis pubescens* (Ranunculaceae) | S of Perth to E of Cape Arid | Hamelin, Breaksea, Michaelmas, Bald, Mondrain, North Twin Peak, Middle (Recherche), Salisbury, Daw [Christmas] | Distributional hiatus: not recorded on Eclipse |
| *Cycas basaltica* (Cycadaceae) | Kimberley | Berthier, Darcy | Distributional hiatus: not recorded on most islands |
| *Daucus glochidiatus* (Apiaceae) | North West Cape to SA border | Bernier, Dorre, Dirk Hartog, Faure, Houtman Abrolhos (8 islands), Boullanger [Long], Wedge, Rottnest, Carnac, Garden, Michaelmas, Bald, Figure of Eight, Boxer, Observatory, Long, Remark, Pasco, Woody, Mondrain, MacKenzie, North Twin Peak, South Twin Peak | Distributional hiatus: absent from Penguin & not recorded on many south coast islands |

| Species (Family) | Coastal mainland range | Island occurrence | Point of interest |
|---|---|---|---|
| *Drosera macrantha* (Droseraceae) | North of Geraldton to W of Cape Arid | Observatory, Sandy Hook, Woody, Mondrain | Distributional hiatus: not recorded on most islands |
| *Exocarpos sparteus* (Santalaceae) | North West Cape to E of Cape Arid | North (Abrolhos), West Wallabi, Boullanger [Long], Lancelin, Garden, Penguin, Hamelin, Mistaken, Sandy Hook, Mondrain | Distributional hiatus: not recorded on East Wallabi, Rottnest, Carnac & most islands of the south coast |
| *Eucalyptus cornuta* (Myrtaceae) | Cape Naturaliste to Cape Arid | Mistaken, Michaelmas, Observatory, Remark, Woody, Mondrain, High, Table, North Twin Peak, Middle (Recherche) | Distributional hiatus: not recorded on Eclipse, Breaksea, Bald |
| *Eucalyptus oraria* (Myrtaceae) | Shark Bay to S of Geraldton | Bernier, Dorre, Dirk Hartog, East Wallabi | Distributional hiatus: not recorded on West Wallabi |
| *Ficinia nodosa* (Cyperaceae) | Shark Bay to E of Cape Arid | North (Houtman Abrolhos), Rottnest, Carnac, Garden, Penguin, Hamelin, Saddle, Eclipse, Breaksea, Mistaken, islet next to Mistaken, Gull Rock, Michaelmas, Coffin, Bald, Middle Doubtful, Figure of Eight, Boxer, Sandy Hook, Remark, Woody, Mondrain, MacKenzie, North Twin Peak, South Twin Peak, Cave, Middle (Recherche), Goose, Douglas, Salisbury, Daw [Christmas] | Distributional hiatus: not recorded on Bernier, Dorre, Dirk Hartog, Faure, Wallabi, Easter or Pelsaert Groups (Houtman Abrolhos) |
| *Gahnia trifida* (Cyperaceae) | N of Geraldton to E of Cape Arid | Rottnest, Bald, Sandy Hook, Woody, Pasco, Mondrain, Middle (Recherche) | Distributional hiatus: not recorded on Houtman Abrolhos, Carnac, Garden, Penguin, Eclipse, Breaksea, Michaelmas |
| *Guichenotia ledifolia* (Malvaceae) | Shark Bay to Cape Naturaliste, E of Albany to E of Cape Arid | Dirk Hartog, Rottnest, Garden | Apparent restriction to large islands of west coast, but absent from Bernier, Dorre, Faure, Salutation, West & East Wallabi (Houtman Abrolhos) |
| *Hardenbergia comptoniana* (Fabaceae) | S of Dongara to E of Albany | Garden, Penguin, Hamelin, Michaelmas | Distributional hiatus: not recorded on Rottnest, Carnac, Eclipse, Breaksea |
| *Isolepis cernua* (Cyperaceae) | Shark Bay to W of Cape Arid | Dirk Hartog, Saddle, Breaksea, Mistaken, Michaelmas, Mondrain, Middle (Recherche) | Distributional hiatus: not recorded on Bernier, Dorre, Faure, Salutation, Houtman Abrolhos, Rottnest |
| *Lepidosperma gladiatum* (Cyperaceae) | S of Dongara to E of Cape Arid | Boullanger [Long], Rottnest, Carnac, Garden, Penguin, Saddle, Eclipse, Breaksea, Mistaken, islet next to Mistaken, Michaelmas, Bald, Boxer, Observatory, Pasco, Mondrain, North Twin Peak, Middle (Recherche), Salisbury, Daw [Christmas] | Distributional hiatus: not recorded on Lancelin & many islands in the Archipelago of the Recherche |
| *Leucopogon insularis* (Ericaceae) | S of Dongara to S of Perth | West Wallabi, East Wallabi, Rottnest, Garden | Apparent restriction to large islands on west coast |
| *Leucopogon parviflorus* (Ericaceae) | S of Dongara to E of Cape Arid | Rottnest, Garden, Hamelin, Michaelmas, Archipelago of the Recherche (Figure of Eight, Boxer, Goose, Middle, Salisbury) | Distributional hiatus: not recorded on several large islands, including Wallabi Group (Houtman Abrolhos), Eclipse, Breaksea, Bald |

| Species (Family) | Coastal mainland range | Island occurrence | Point of interest |
|---|---|---|---|
| *Muehlenbeckia adpressa* (Polygonaceae) | N of Geraldton to E of Cape Arid | Penguin, Hamelin, Archipelago of the Recherche (Figure of Eight, Boxer, Observatory, Woody, Sandy Hook, Long, Remark, MacKenzie, Mondrain, North Twin Peak, South Twin Peak, Kermadec [Wedge], Douglas, Middle, Goose, Salisbury, Daw [Christmas]) | Distributional hiatus: not recorded on Rottnest, Carnac, Garden, Eclipse, Breaksea, Michaelmas, Bald |
| *Paraserianthes lophantha* (Fabaceae) | Busselton to Cape Arid | Michaelmas, Red, Archipelago of the Recherche (Figure of Eight, Boxer, Long, Remark, Sandy Hook, Woody, Pasco, Mondrain, Kermadec, [Wedge], Termination, Taylor, North Twin Peak, South Twin Peak, Douglas, Middle (Recherche), Daw [Christmas] | Distributional hiatus: not recorded on Eclipse, Breaksea, Bald, Salisbury |
| *Phyllanthus calycinus* (Phyllanthaceae) | Shark Bay to E of Cape Arid | Bernier, Dorre, West Wallabi, East Wallabi, Whitlock, Rottnest, Garden, Bald, Boxer, North Twin Peak, Middle (Recherche) | Distributional hiatus: not recorded on Dirk Hartog, Faure, Carnac, Eclipse, Breaksea, Michaelmas |
| *Pimelea gilgiana* (Thymelaeaceae) | Shark Bay to N of Perth | Dirk Hartog, North Cervantes, Escape | Distributional hiatus: not recorded on Bernier, Dorre, Salutation |
| *Pittosporum ligustrifolium* (Pittosporaceae) | N of Geraldton to Cape Naturaliste | Rottnest, Garden, Penguin, Seal (Shoalwater Bay) | Distributional hiatus: not recorded on Houtman Abrolhos, Carnac |
| *Pittosporum phillyreoides* (Pittosporaceae) | Burrup Peninsula to S of Geraldton | Shark Bay (Bernier, Dorre, Dirk Hartog, Three Bays, Salutation, Baudin), Houtman Abrolhos (11 islands) | Distributional hiatus: not recorded on Faure |
| *Santalum acuminatum* (Santalaceae) | S of North West Cape to Cape Naturaliste, E of Cape Arid | Baudin | Distributional hiatus: not recorded on Bernier, Dorre, Dirk Hartog, Faure, Wallabi Group (Houtman Abrolhos), Rottnest |
| *Santalum spicatum* (Santalaceae) | North West Cape to S of Geraldton | Bernier, Dorre, Dirk Hartog, Faure | Apparent restriction to large islands |
| *Solanum symonii* (Solanaceae) | N of Geraldton to Cape Leeuwin, E of Albany to E of Cape Arid | Wallabi Group (5 islands) (Houtman Abrolhos), Rottnest, Carnac, Garden, Breaksea, Mistaken, Michaelmas, Green [Oyster Harbour], Gull Rock, Bald, Boxer, North Twin Peak, Middle (Recherche), Salisbury | Distributional hiatus: not recorded on West Wallabi, Penguin, Eclipse, Mondrain |
| *Spyridium globulosum* (Rhamnaceae) | S of Geraldton to E of Cape Arid | North (Abrolhos), West Wallabi, East Wallabi, Rottnest, Carnac, Garden, Penguin, Michaelmas, Observatory, Sandy Hook, Long, Remark, Woody, North Twin Peak, Middle (Recherche), Salisbury | Apparent restriction to larger islands, though not recorded on Eclipse, Breaksea, Bald, Mondrain |
| *Stylidium adnatum* (Stylidiaceae) | Cape Naturaliste to W of Cape Arid | Eclipse, Breaksea, Mistaken, Michaelmas, Bald, Figure of Eight, Boxer, Woody, Wilson, Mondrain, North Twin Peak, Middle (Recherche), Goose, Daw [Christmas] | Distributional hiatus: not recorded on Chatham |

| Species (Family) | Coastal mainland range | Island occurrence | Point of interest |
|---|---|---|---|
| *Templetonia retusa* (Fabaceae) | Shark Bay to E of Cape Arid | Baudin, Whitlock, Rottnest, Bald, Sandy Hook, Long, Woody, Pasco, Mondrain | Distributional hiatus: not recorded on Bernier, Dorre, Dirk Hartog, Faure, Houtman Abrolhos, Carnac, Garden, Penguin, Eclipse, Breaksea, Michaelmas |
| *Thomasia cognata* (Malvaceae) | N of Perth to E of Cape Leeuwin, E of Bremer Bay to W of Cape Arid (discontinuous) | Rottnest, Garden | Distributional hiatus: not recorded on Carnac, Penguin |
| *Thryptomene saxicola* (Myrtaceae) | Cape Naturaliste to Cape Arid | Eclipse, Breaksea, Michaelmas, Bald, Observatory, High (Duke of Orleans Bay), Middle (Recherche) | Distributional hiatus: not recorded on most islands in the Archipelago of the Recherche |
| *Trachymene coerulea* (Araliaceae) | N of Geraldton to Cape Leeuwin, Albany | Rottnest, Garden | Apparent restriction to large islands |
| *Trachymene pilosa* (Araliaceae) | Shark Bay to E of Cape Arid | Bernier, ?Dirk Hartog, East Wallabi, ?Rottnest, Garden, Michaelmas, Figure of Eight, Boxer, Sandy Hook, Long, Remark, Woody, Pasco, Mondrain, North Twin Peak, South Twin Peak, Middle (Recherche), Daw [Christmas] | Distributional hiatus: not recorded on Dorre, Faure, Salutation, West Wallabi, Eclipse, Breaksea, Bald |
| *Westringia dampieri* (Lamiaceae) | Shark Bay to S of Perth, W of Albany to E of Cape Arid | Bernier, Dorre, Dirk Hartog, West Wallabi, East Wallabi, Rottnest, Garden, Michaelmas, Bald, Boxer, Observatory, Woody, Pasco, Mondrain, Middle (Recherche), Goose | Distributional hiatus: not recorded on Faure, Salutation, Carnac, Penguin, Eclipse, Breaksea, Figure of Eight |

Sources: Abbott 1981a; Abbott & Black 1980; Abbott et al. 2000; AA Burbidge & George 1978; Claymore & Markey 1999; JM Harvey et al. 2001; G Keighery & Muir 2008; Western Australian Herbarium 1998-; Rippey et al. 1998, 2003; JH Willis 1953.

islands in the Archipelago of the Recherche examined by him during a three-week reconnaissance 'were identical floristically, each having an individuality attributable to the composition of the plant communities present, and most islands yielding some species not shared by any others'.

Excluded from consideration in this section are those plant species that are widespread on the mainland coast and are tolerant of salt spray, and thus would be expected to occur on many islands, including small ones (e.g. *Carpobrotus virescens, Threlkeldia diffusa*, *Senecio pinnatifolius*). Also not considered are those species that have limited occurrence on the mainland coast and thus can only be represented on islands adjacent to their geographical range on the mainland. Examples include the plant species *Leptospermum sericeum* and *Cyperus microcephalus*; the bird species thick-billed grasswren (*Amytornis textilis*), spinifexbird (*Eremiornis carteri*), and painted finch (*Emblema pictum*); and the reptile species *Cryptoblepharus pulcher*, ornate crevice dragon (*Ctenophorus ornatus*), *Hemiergis quadrilineata* and *Lerista christinae*. Some species occur only on a section of the mainland coast that lacks adjacent islands, e.g. the reptile species *Aprasia inaurita, Christinus alexanderi,* dwarf bicycle dragon (*Ctenophorus mackenziei*), painted dragon (*C. pictus*), *Ctenotus euclae*, *Lerista baynesi*, *Morethia adelaidensis*, Nullarbor bearded dragon (*Pogona nullarbor*), *Strophurus intermedius*, and Nullarbor earless dragon (*Tympanocryptis houstoni*). These are obviously precluded from occurring on islands.

**Pteridophyta** Twenty-three species of fern have been recorded on WA islands; 15 of these occur only on islands of the Kimberley region. One species is found on four Kimberley islands and Dolphin Island (Pilbara region), another species occurs on Boongaree Island (Kimberley region) and Dirk Hartog Island and Bernier Island (Shark Bay), and two other species occur on Dirk Hartog Island and Bernier Island. The remaining four species have been recorded only on islands off the southern coast of WA. The most interesting of these, *Asplenium obtusatum*, occurs in shaded crevices of boulders in the coastal salt spray zone of parts of NSW and Victoria and much of Tasmania (NG Walsh & Entwisle 1994; Brownsey 1998; S Harris et al. 2001). In WA it is extremely rare and has been recorded from only three coastal mainland sites between Mermaid Point and Cliffy Head (J Watson pers. comm.), and on two islands, Breaksea and Chatham (GG Smith 1978).

***Eucalyptus* and *Corymbia*** Twenty-three eucalypt species occur on WA islands, with 13 species on islands from Shark Bay to the South Australian border, and 10 species on islands north of Shark Bay to the Northern Territory border (Western Australian Herbarium 1998-). Three small (<10 ha) islands very close to the southern coast of WA have populations of *E. cornuta*. Otherwise the smallest offshore island with a eucalypt species is East Wallabi (*E. oraria*, 310 ha). In contrast, the genus *Corymbia* has 16 species present on WA islands, 14 of which occur in the Kimberley region (Western Australian Herbarium 1998-). The remaining two species occur on two islands off the Pilbara coast.

***Callitris*** Native pine in coastal mainland WA is represented by eight species. Only two species occur on islands: *C. columellaris* on four Kimberley islands and *C. preissii* on eight islands in south-west WA (Rottnest Island, Garden Island, Bald Island and five islands in the Archipelago of the Recherche). All species are sensitive to fire and plants are readily killed. On mainland Australia they are found in areas that are naturally protected from fire (rocky substrates) or which have experienced (historically) long intervals between higher intensity fires (deserts). Very extensive stands of *C. preissii* occur on Garden Island (McArthur 1957; Baird 1958; G Keighery et al. 1997).

***Xanthorrhoea*** Only one species (presumably *X. platyphylla*) has been recorded on WA islands. These are Sandy Hook and Mondrain islands, both in the Archipelago of the Recherche (JH Willis 1953).

***Allocasuarina*** Only three species of this conspicuous genus occur on WA islands: *A. helmsii* on Dirk Hartog Island; *A. huegeliana* on four islands along the south coast; and *A. trichodon* on two islands in the Archipelago of the Recherche.

***Leucopogon*** Eight species are known from WA islands. One species (*L. insularis*) occurs on three islands off the western coast of WA (West Wallabi, Rottnest and Garden islands). *L. parviflorus* is the only other species represented on west-coast islands (Rottnest, Garden, Hamelin), but it also occurs on two islands off the southern coast. Six species are restricted to islands off the southern coast. The smallest offshore island with a species of *Leucopogon* is 10 ha (Hamelin, 700 m offshore). Three *Leucopogon* species do, however, occur on small islands that lie very close to the coastal mainland (*L. parviflorus* on Hamelin Island, 700 m offshore; and *L. apiculatus* and *L. obovatus* on High Island, connected by sand to the adjacent shore of Duke of Orleans Bay).

***Hibbertia*** Eight species occur on WA islands, with five species recorded on islands in the Kimberley region, one species in the Archipelago of the Recherche, another present on four islands between Cape Naturaliste and Cape Arid, and *H. racemosa* on East and West Wallabi Islands (Houtman Abrolhos) and Middle Island in the Archipelago of the Recherche.

**Mangroves** Seventeen species occur in coastal WA, with all present in the Kimberley region. However, only eight species extend farther south, with only one of these occurring south of North West Cape. All 17 species occur on islands, with some extending to islands far offshore, namely Berthier, Macleay, Champagny, Trimouille, Hermite and Barrow islands, and 33 islands in Houtman Abrolhos (JM Harvey et al. 2001).

***Pisonia grandis*** Unlike cays in the Capricorn and Bunker Groups of the Great Barrier Reef, Queensland (Cribb & Cribb 1985; Batianoff et al. 2009a), this arborescent species (to 14 m in height) is absent from cays along the tropical coast of WA. Perhaps this is linked to insufficient rainfall. This species does occur, however, on Cocos (Keeling) Islands and Christmas Island (Telford 1993a; Du Puy 1993). The adhesive anthocarps of this species are dispersed by seabirds (Heatwole 1984, TA Walker 1991a).

**Mistletoe** The very striking arborescent *Nuytsia floribunda* does not occur on any island. Fourteen mistletoe species are known from WA islands, of which 10 occur only on islands in the Kimberley region. Mistletoe occurs sparingly on islands of south-west WA: *Amyema melaleucae* on Garden and Middle (Archipelago of the Recherche) islands, and *A. preissii* and *Lysiana* aff. *casuarinae* on Dirk Hartog Island.

***Paraserianthes lophantha*** This species (Mimosaceae) occurs widely (but not continuously) in coastal south-west WA, including 20 islands between Albany and Cape Arid (JH Willis 1953; Western Australian Herbarium 1998-). In contrast, it does not occur naturally elsewhere on mainland Australia but does occur (presumably as indigenous) on the remote Pearson and Dorothee islands (South Australia, T Robinson et al. 1996) and Craggy and Rodondo islands in Bass Strait (Bechervaise 1947; Kirkpatrick et al. 1974; S Harris et al. 2001).

**Restionaceae** Insular representation of this large family is limited to two species (*Desmocladus asper, Lepidobolus densus*) on only one island, Dirk Hartog Island.

***Nitraria billardierei*** Although this species is represented on many islands adjacent to its mainland range (south of North West Cape to Cape Naturaliste, east of Albany to the South Australian border), it has a surprisingly limited occurrence within the Archipelago of the Recherche, being recorded on only eight islands: Figure of Eight (on beach), North Twin Peak (one plant), Wickham (Stanley), Goose (one plant), Daw (on beach), New Year, Anvil and Bellinger islands (G Keighery 1995; JH Willis 1953). Although beach sand is present on Sandy Hook and Middle islands, the species has not been recorded there.

**Ticks on reptiles** Two species (*Amblyomma*) are widespread on both mainland and islands of WA (Sharrad and King 1981) and have been collected from a variety of taxa (snakes, varanids and skinks). New species (unnamed) in the genus *Aponomma* have been collected on five islands in the Kimberley region.

***Dromaius novaehollandiae*** The emu is absent from all but one WA island (Faure, 5100 ha). Surprisingly, it is absent from the largest WA island (Dirk Hartog, 59,000 ha) which is about half the area of the smallest island known to have supported a population (King Island, Bass Strait, 1100 km$^2$), suggestive of an area threshold between 580 and 1100 km$^2$. A simpler explanation, however, is that the lack of permanent standing fresh water on Dirk Hartog Island would have resulted in any emus that were isolated on the island not surviving droughts. Emus are able to swim (AJ Campbell 1900) and have been seen swimming to Faure Island (Shark Bay), 6 km from the mainland. Breeding has been recorded there. The island has bores and emus have been seen to drink from these (Dell & Cherriman 2008). It is not known if emus were present before a pastoral station was developed there.

**Rails** Although only three species of rail occur on WA islands, they are widely distributed (Johnstone & Storr 1998). Spotless crake (*Porzana tabuensis*) occurs on 12 islands in Houtman Abrolhos and six others in south-west WA; buff-banded rail (*Gallirallus philippensis*) occurs on nine islands; and chestnut rail (*Eulabeornis castaneoventris*) occurs on five islands with mangroves in the Kimberley region. None of these island populations show evidence of flightlessness, which is unsurprising given that the islands were only formed c. 7 ka BP. The lack of records of Lewin's rail (*Lewinia pectoralis*) from WA islands contrasts with its presence on some small (18–51 ha) satellite islands of Tasmania (Brothers et al. 2001).

**Pigeons and doves** Seven indigenous species are well represented on islands of the Kimberley region: emerald dove *Chalcophaps indica* (5 islands), common bronzewing (*Phaps chalcoptera*; 5 islands), white-quilled rock pigeon (*Petrophassa albipennis*; 4 islands), zebra dove (*Geopelia striata*; 19 islands), bar-shouldered dove *G. humeralis* (19 islands), rose-crowned fruit-dove *Ptilinopus regina* (8 islands) and pied imperial-pigeon *Ducula bicolor* (11 islands). Only one species, the brush bronzewing, occurs on islands of south-west WA (23 islands). *G. humeralis* is the only species present on islands of the Pilbara region, having been recorded from at least 20 islands (Johnstone & Storr 1998).

**Parrots and cockatoos** This group is poorly represented on islands of south-west WA (Johnstone & Storr 1998). This is probably because eucalypts occur on few islands and seldom as large trees. A scarcity of nesting hollows would thus limit breeding opportunities. Only one species, the ground-nesting rock parrot (see below) occurs on many islands of south-west WA. The claim that the western ground parrot *Pezoporus flaviventris* 'is likely to occur' on Bald and North Twin Peak islands (Ecosure 2009) is unfounded. In contrast to south-west WA, three cockatoo species and two parrot species occur on many islands off the Pilbara or Kimberley coasts: red-tailed black cockatoo (*Calyptorhynchus banksii*; 11 Kimberley islands); little corella (*Cacatua sanguinea*;12 Pilbara islands and seven Kimberley islands); Sulphur-crested cockatoo (*C. galerita*; seven Kimberley islands), red-winged parrot (*Aprosmictus erythropterus*; 16 Kimberley islands) and northern rosella (*Platycercus venustus*; six Kimberley islands). Eucalypt woodland is well represented on the Kimberley islands. The little corella does not depend on hollows in trees for breeding, and will instead use holes in rock crevices.

***Neophema petrophila*** The rock parrot has a geographic range in WA from Shark Bay to the Archipelago of the Recherche. It is more abundant on islands and is seldom seen on the mainland in large numbers (I Abbott pers. obs.). The species is absent from Houtman Abrolhos and from Termination and Salisbury islands in the Archipelago of the Recherche (Abbott & Black 1978, AA Burbidge et al. 1982, Johnstone & Storr 1998, V Serventy 1952), perhaps evidence of a distance effect.

***Climacteris*** WA has two species of treecreeper with a coastal component to their geographical ranges. Neither occurs on any WA island (Johnstone & Storr 2004). Elsewhere in Australia, *Climacteris* species occur only on four large islands (Fraser, North Stradbroke, Bribie, Peel) that lie close to mainland Queensland (Storr 1977, 1984). The smallest of these islands is Peel Island (650 ha), but the record there represents a vagrant (Agnew 1921).

***Daphoenositta*** The varied sittella (*D. chrysoptera*) has not been recorded on any WA island (Johnstone & Storr 2004). Elsewhere in Australia it is known from only four inshore islands of Queensland (Bribie, Peel, Coochiemudlo, South Stradbroke; Storr 1977, 1984). The smallest of these (Coochiemudlo) is 160 ha in area and close to the mainland. The record from nearby Peel Island is of a vagrant flock (Agnew 1921).

***Stipiturus*** Of the two species of emu-wren present in WA, there is only one insular occurrence offshore (*S. malachurus*), on the large (59,000 ha) Dirk Hartog Island (Johnstone & Storr 2004). Elsewhere in Australia this species is known only from very large offshore islands (Tasmania, Kangaroo Island) or large islands (Robbins, Hindmarsh, Quail) very close to source areas (Hyett & Gottsch 1963, Higgins et al. 2001), but is unaccountably absent from other large islands of southern Australia, such as King, Flinders and Cape Barren islands. The occurrence on Dirk Hartog Island is c. 450 km north-west from the nearest mainland population (Johnstone & Storr 2004).

***Malurus*** Six species of fairy-wren occur in coastal WA, but only three occur on offshore islands: variegated fairy-wren (*M. lamberti*) on 13 islands (Johnstone & Storr 2004; Pearson et al. 2013); white-winged fairy-wren (*M. leucopterus*) on two islands (Johnstone & Storr 2004); and red-backed fairy-wren (*M. melanocephalus*) on one island (Johnstone & Storr 2004). Only one 'island' has more than one species present (DEC 2006b): Both *M. lamberti* and *M. leucopterus* occur on Dampier 'Island' (now known as Burrup Peninsula), probably because the 'island' was originally connected to the mainland by mudflats which dried in places at low tide. The smallest offshore WA island with *M. lamberti* is c. 5000 ha in area and >25 km from the mainland. However, this species does occur on smaller, inshore islands (450 ha, <300 m from mainland). In south-eastern Australia, a related species, the superb fairy-wren, occurs on seven large offshore islands, three large inshore islands, and six small nearshore islands. The latter occur close (20 m – 1 km) to the mainland and range in area from 0.8–16 ha (T Robinson et al. 1996; Brothers et al. 2001). There is also one record of a vagrant on Rabbit Island, Victoria, a distance traversed of 1.6 km (Norman & Harris 1981; Norman et al. 2010), and on 'Boondabah' Island, NSW (Hull 1911). These data imply that the ability of *Malurus* species to fly across water is limited.

***Sericornis*** White-browed scrubwren (*Sericornis frontalis*), like *Malurus* species, occurs on few (11) WA islands (Johnstone & Storr 2004). Its occurrence on islands seems to be controlled by both area and degree of isolation (Abbott 1981b). The smallest remote island supporting the white-browed scrubwren is East Wallabi Island (310 ha, Houtman Abrolhos), only 1.5 km from the larger (590 ha) West Wallabi Island. These two islands are 60 km from the nearest mainland. The population on Mistaken Island (10 ha) lies only 200 m from the mainland coast. Ram Island (140 ha) is c. 2 km from the mainland and 'High' Island in Duke of Orleans Bay is joined to the mainland by a wide sandbar (JR Ford pers. comm.). In South Australia, this species occurs on a very small island (Yangie Bay, 5 ha) that lies very close to the mainland (T Robinson et al. 1996). In Victoria, the white-browed scrubwren is present mainly on large inshore islands, except for an occurrence on Wattle Island (22 ha, 500 m offshore from Wilsons Promontory). It is absent from all nearby islands, which vary in area from 9–138 ha, and isolation from the mainland of 4.5–8 km (SG Lane & Battam 1981; Norman & Brown 1979; Norman et al. 1980a; Wainer & Dann 1979; SG Lane pers. comm.). In NSW this species occurs (and breeds) occasionally on Dangar Island (26 ha, which is c. 900 m from the mainland (H Recher pers. comm.). It has not been recorded from any island situated offshore (Cabbage Tree Island, A D'Ombrain pers. comm. 1971; SG Lane pers. comm. 1980; D Portelli pers. comm.; Boondelbah Island, N Carlile pers. comm.; Broughton Island, Hindwood & D'Ombrain 1960; Lion Island, McGill 1954; SG Lane pers. comm. 1969 & 1972; Five Islands, Keast 1943; Brush Island, Hull 1916; Humphries & Lane 1954; Montagu Island, Hull 1912; Hindwood 1969; Fullagar 1989).

A related species, the Tasmanian scrubwren (*S. humilis*), is restricted to Tasmanian islands. It occurs only on large (>68 ha) offshore islands but has been recorded (as vagrant?) on small, nearshore islands (1.5–11.4 ha, 20–200 m offshore) (Brothers et al. 2001). These data imply that both *Sericornis* species have low vagility.

***Pardalotus*** Of the three species occurring in coastal parts of mainland WA, only one (striated pardalote) is recorded on islands (except as a vagrant). All eight of these islands occur in the Kimberley region, and have eucalypt woodland present, apparently sufficient to supply the necessary feeding substrates (leaves) and small nesting hollows. Elsewhere in Australia pardalote species occur only on large islands.

**Honeyeaters** Of the 16 species recorded on WA islands, only three honeyeater species (brown honeyeater, singing honeyeater and silver-crowned friarbird) occur on many islands (Johnstone & Storr 2004). This is surprising, as most species are nomadic. For example,the brown honeyeater *L. distincta* was seen flying in small parties between Eclipse and Sir Graham Moore islands and the Kimberley mainland (GF Hill 1911). However, this level of mobility does not apply to the singing honeyeater, which rarely occurs well offshore: Although present on Barrow Island (>40 km from mainland), it is absent from Houtman Abrolhos (60 km offshore), the Montebello Islands, Varanus Island and Salisbury Island. The New Holland honeyeater is known from 10 islands (Johnstone & Storr 2004). Almost entirely nectar-dependent, it is absent from large islands such as Rottnest, Garden, Eclipse, Breaksea, Remark, North Twin Peak and Daw islands. This may be because these islands do not support large enough populations of plant species that collectively supply sufficient nectar all year. Notable is the occurrence of all 13 honeyeater species present in the Kimberley region mainland on adjacent islands, no doubt reflecting the availability of suitable nectar sources. This is in marked contrast to the paucity of honeyeater species on islands of south-west WA (three species: brown honeyeater, singing honeyeater, New Holland honeyeater).

***Petroica goodenovii*** The red-capped robin occurs in low-rainfall regions and has limited occurrence on islands adjacent to low rainfall (<450 mm per annum) mainland coasts (three islands in South Australia, the smallest being 213 ha, T Robinson et al. 1996; Dirk Hartog Island, perhaps only a visitor, Johnstone & Storr 2004). However, it also occurs on Rottnest Island (median annual rainfall of 709 mm) and is absent as a breeding species from the adjacent mainland coast. This surprising insular occurrence seems to indicate that the region experienced a more arid climate at the time (c. 7ka BP) that Rottnest Island separated from the mainland.

***Megalurus gramineus*** The little grassbird is known from only three WA islands, in marked contrast to South Australia, Victoria and Tasmania where it has been recorded on more than 70 islands, from very small to very large, and from far offshore to nearshore (Hyett & Gottsch 1963; T Robinson et al. 1996; Brothers et al. 2001). On mainland Australia this species generally lives in vegetation in wetlands and is able to disperse between wetlands. Therefore its absence from WA islands cannot be attributed to a distance effect. As in WA, this species has limited occurrence of islands of Queensland (one; Storr 1984) and NSW (eight; N Carlile pers. comm., Fullagar 1989; Hindwood & D'Ombrain 1960; Hull 1916; Humphries & Lane 1954; Keast 1943; SG Lane 1965; AD Stuart 2002; van Gessel & Kendall 1972).

**Seabirds** The 25 species of seabird that breed on WA islands do not occur on every part of the coast. Some breed only on islands in the tropics, others breed only on islands of the south coast, and a few occur widely. The presence of the warm, south-flowing Leeuwin Current leads to an intermixture of warm-water and cold-water species, as on Houtman Abrolhos (16 species breeding). Seabirds are one of the most dynamic groups of species, as several species have spread south from Houtman Abrolhos and Fremantle since the 1840s (Table 17).

**Frogs** Most insular occurrences of frogs on WA islands are in the Kimberley region, with 20 species represented (WAM 2015). One species (little red tree frog *Litoria rubella*) is present on two islands in Kimberley region, as well as on Barrow Island (Pilbara region). The sandhill frog (*Arenophryne rotunda*) is known only on two islands in Shark Bay. The occurrence of frogs on south-west WA islands is idiosyncratic: Three species occur on Rottnest Island, one of which (moaning frog *Heleioporus eyrei*) is present also on Bald Island. Mondrain and Middle islands (Archipelago of the Recherche) both have the spotted-thigh frog (*Litoria cyclorhyncha*).

**Reptiles absent from cold, wet islands** Because these species occur along the mainland coast of south-west WA, their absence from suitable islands between Cape Leeuwin and Mermaid Point cannot be attributed directly to climatic factors. Examples include the southern barking gecko (*Underwoodisaurus milii*), also absent from Rottnest and Garden islands near Perth, the gecko *Strophurus spinigerus*, the pygopods *Aprasia repens* and *Delma australis*, the skinks *Menetia greyii* and *Tiliqua rugosa*, the typhlopod *Anilios australis*, the boid snake *Morelia spilota*, and the elapid snakes crowned snake (*Elapognathus coronatus*) and *Pseudonaja affinis*.

**Varanids** Goannas are well represented on WA islands (Table 4). Three species occur on many islands (Western Australian Museum 2013): *Varanus acanthurus* (26 islands), *V. glauerti* (26) and *V. glebopalma* (15). The largest species, *V. giganteus*, is found only on Barrow Island and Dampier 'Island'. (This 'island' is joined to the mainland by mudflats and has seven varanid species recorded; Kendrew 2007). In south-west WA only three islands have a varanid present: Bernier and Faure (*V. gouldii*) and Middle (Archipelago of the Recherche) Island (*V. rosenbergi*).

Several of the species show interesting distribution patterns on adjacent islands. In the Pilbara region, the Montebello Group has *V. gouldii* and *V. acanthurus*; the Lowendal Group has *V. acanthurus* only; Barrow Island has *V. giganteus* and *V. acanthurus*; Potter Island has *V. brevicauda*; and Thevenard and South Muiron islands have only *V. acanthurus.* In the Dampier Archipelago, *V. panoptes* occurs on Dolphin, Legendre and Hauy islands; *V. tristis, V. pilbarensis* and *V. gouldii* occur only on Conzinc, West Intercourse and Eaglehawk islands respectively; and *V. acanthurus* is present on Legendre and West Lewis islands.

Six species are present on islands of the Kimberley region (Western Australian Museum 2013). *Varanus acanthurus, V. glauerti* and *V. glebopalma* occur alone on nine, 10 and one island(s), respectively. *Varanus acanthurus* and *V. glauerti* occur on four islands; *V. acanthurus* and *V. glebopalma* occur on two islands; and all three species occur on three islands. *Varanus acanthurus, V. glebopalma* and *V. mertensi* are present on Evelyn Island, and *V. glebopalma* and *V. gouldii* occur on Boongaree Island. In the Dampier Archipelago, four species (*V. acanthurus, V. gouldii, V. panoptes, V. tristis*) occur, with most recorded alone on six of the islands studied (DCLM 1990). There are also three occurrences of two species on the same island: *V. gouldii* and *V. tristis* on Cohen Island (11 ha); *V. panoptes* and *V. tristis* on Dolphin Island (3200 ha); and *V. acanthurus* and *V. panoptes* on Hauy (105 ha). These combinations would seem to offer opportunities for detailed study to detect any evidence of character displacement and elucidate the ecological mechanisms that have caused these patterns of distribution.

***Egernia kingii*** This large skink occurs on more than 40 islands of south-west WA (Western Australian Museum 2013). Its occurrence on Three Bays Island in Shark Bay is >250 km north of the nearest mainland occurrence (Storr et al. 1999). The smallest islands between Fremantle and Becher Point on which King's skink occurs are Penguin Island (12 ha) and Carnac Island (16 ha) (Serventy & White 1943; Abbott pers. obs.), in marked contrast to islands between Dongara and Lancelin (0.7–3.2 ha; J Ford 1963).

***Tiliqua rugosa*** The bobtail is present on 10 islands. The population on Rottnest Island is smaller and darker than on the mainland (Storr et al. 1999).

***Ctenotus saxatilis*** The rock ctenotus occurs along the coast and hinterland of Pilbara region, and is widespread on islands in Dampier Archipelago and the Montebello Group. It occurs in the Dampier Archipelago on islands as small as 0.8–6 ha (Connell 1983; DCLM 1990; Dunlop et al. 1994a). The rock ctenotus is a generalist species and not a supertramp species (*sensu* JM Diamond 1975). *Ctenotus inornatus*, widespread in the Kimberley region, is similar in that it occurs on islands as small as 4–6 ha (How et al. 2006).

**Snakes** Snakes are surprisingly well represented on islands of south-west WA (Storr et al. 2002; Western Australian Museum 2013), with 12 species: *Anilios australis* (recorded on six islands); *Antaresia stimsoni* (three islands in Shark Bay); *Morelia spilota* (seven, including Seagull Island; O'Loughlin 1966); *Acanthophis antarcticus* (four islands in the Archipelago of the Recherche); *Demansia calodera* (two islands in Shark Bay); *D. psammophis* (one island); *Elapognathus coronatus* (nine islands, all in Archipelago of the Recherche); *Notechis scutatus* (two islands); *Pseudechis australis* (three islands, Shark Bay); *Pseudonaja affinis* (Rottnest and two islands in the Archipelago of the Recherche); *P. mengdeni* (one island); and *Simoselaps littoralis* (six islands). Most of these populations occur on large islands. The smallest south-west WA islands to support a snake species are Carnac (16 ha, possibly introduced, but disputed by B Bush et al. 2010 on the basis of its placid behaviour on this island), Boxer (166 ha) and North (Abrolhos) Islands (176 ha, extinct). As expected, snakes are well represented on islands in the tropics, with 15 and nine species recorded on islands of the Kimberley and Pilbara regions respectively. Some occurrences of snakes are on islands situated well offshore: Hermite Island, with *Anilios ammodytes*, *Antaresia stimsoni and Furina ornata*; Daw (Christmas) Island, with *Acanthophis antarcticus*; Salisbury Island, with *Elapognathus coronatus*; and Wallabi Islands, with *Morelia spilota* and *Simoselaps littoralis*.

***Tachyglossus aculeatus*** The short-beaked echidna is known from eight islands in the Kimberley region (LA Gibson & McKenzie 2012b) and one 'island' in the Pilbara region (Dampier 'Island', 11,800 ha; Kendrew 2007). The smallest islands (Naturalists, 170 ha; Jar, 210 ha) are close to the mainland. The unique record on Legendre Island, Pilbara region, (J Richardson et al. 2007) requires confirmation. This species has been recorded on at least 18 other Australian islands, the smallest with areas of c. 650 ha (Abbott & Burbidge 1995). Echidnas have the ability to swim but probably only for a short distance (Augee et al. 2006).

**Macropodoids** Numerous WA islands have wallabies present, but there is usually only one species per island (AR Main 1961a; AR Main & Yadav 1971; Abbott & Burbidge 1995). On the two large islands near Fremantle, the quokka is present only on Rottnest Island and the tammar occurs only on Garden Island. In the Archipelago of the Recherche, the tammar is present on five islands, and another species, black-footed rock-wallaby, occurs on four different islands. Island distributions do not overlap. Such 'chequerboard' patterns of distribution are suggestive of interspecific competition. However, an alternative explanation posits differences in floristic composition (and thus preferred food plants) that may have existed prior to the separation of islands from the mainland (Serventy 1953).

In the Kimberley region, the nabarlek (*P. concinna*) occurs on four islands and the monjon (*P. burbidgei*) is present on three different islands. These non-overlapping distributions are suggestive of interspecific competition. Other species also have limited occurrence on WA islands: Boodie *Bettongia lesueur* (five islands), spectacled hare-wallaby *Lagorchestes conspicillatus* (two islands, smallest area = 836 ha), mala/rufous hare-wallaby *L. hirsutus* (two islands) and banded hare-wallaby *Lagostrophus fasciatus* (two islands). It is very interesting that Bernier and Dorre islands (collectively c. 100 km$^2$ and very close together) both support three species (*B. lesueur, L. hirsutus* and *L. fasciatus)*.

The absence of the woylie (*Bettongia penicillata*) from all but one WA island (Faure, 5100 ha) is puzzling. This species occurred naturally on two South Australian islands (St Francis, 800 ha and St Peter, 3400 ha; T Robinson et al. 1996). The only other WA islands with an area >7 km$^2$ and within the mainland geographical range of this species are Rottnest, Garden, Bald, Mondrain and Middle islands, each of which has another macropodoid species present (Abbott & Burbidge 1995). Because St Francis Island had two species present, it seems unlikely that interspecific competition is responsible for the absence of the woylie on the five WA islands listed above.

Animals of large body mass, such as kangaroos (50–80 kg), should occur only on the largest islands. The red kangaroo (*Macropus rufus*) does not occur on any island *sensu stricto*, as Dampier 'Island' was originally joined to the mainland by mudflats. The western grey kangaroo (*M. fuliginosus*) occurs only on Kangaroo Island (South Australia, 4500 km$^2$), the eastern grey kangaroo (*M. giganteus*) occurs only on Tasmania and a south-east Queensland island (North Stradbroke, 26,000 ha), and the euro (*M. robustus*) is known as a permanent population only from Barrow Island (22,000 ha) and Dampier 'Island'. The total population size of this species on Barrow Island has been estimated at 1800 (J Short & Turner 1991). The western grey kangaroo has been introduced in recent times to several smaller islands, including Taylor Island (South Australia, 243 ha) and Woody Island (WA, 188 ha), and has persisted.

**Small carnivorous mammals** Dasyurid species are poorly represented on WA islands, except for the northern quoll (*Dasyurus hallucatus*; 13 islands in the Kimberley region, smallest = 39 ha; LA Gibson & McKenzie 2012b). Ningbing pseudantechinus *Pseudantechinus ningbing* also occurs in the Kimberley region, on Augustus and South Heywood islands. Nine other species occur outside the Kimberley region (Abbott & Burbidge 1995). In south-west WA these are: chuditch *Dasyurus geoffroii* (Dirk Hartog Island, now extinct); mardo *Antechinus flavipes* (Michaelmas and Middle Doubtful islands); dibbler *Parantechinus apicalis* (Boullanger and Whitlock islands); little long-tailed dunnart *Sminthopsis dolichura* (Dirk Hartog Island); and grey-bellied dunnart *S. griseoventer* (Boullanger Island). Five species occur on islands (or quasi-islands) in the Pilbara region: northern quoll (Dolphin Island); little red kaluta *Dasykaluta rosamondae* and Pilbara ningaui *Ningaui timealeyi* (Dampier 'Island', now known as Burrup Peninsula); and common planigale *Planigale maculata* and fat-tailed pseudantechinus *Pseudantechinus macdonnellensis* (Barrow Island).

**Bandicoots** This group shows very limited occurrence on WA islands (Abbott & Burbidge 1995; LA Gibson & McKenzie 2012b):Golden bandicoot *Isoodon auratus* on Augustus, Uwins, Storr and Lachlan islands in the Kimberley region, and Barrow, Hermite and Middle (near Barrow) islands in the Pilbara region, with the smallest island occupied = 350 ha); northern brown bandicoot *I. macrourus* on Saint Andrew Island; quenda *I. obesulus* on Daw (Christmas) Island, 210 ha; and marl *Perameles bougainville* on Bernier and Dorre islands, each c. 5000 ha in area. The bilby (*Macrotis lagotis*) does not occur on any WA (or other) island, but has been introduced to an island in South Australia (Woinarski et al. 2014b).

**Possums** The brushtail possum occurs in WA on only one island (Barrow) and the ngwayir (western ringtail possum; *Pseudocheirus occidentalis*) is absent from all WA islands. This contrasts with elsewhere in Australia, where there are c. 21 occurrences of brushtail possums on islands, with the smallest island occupied being 255 ha. The common ringtail possum (*P. peregrinus*) occurs on five eastern Australian islands, with the smallest island occupied being 75 km$^2$ (Abbott & Burbidge 1995).

**Honey possum** *Tarsipes rostratus*, endemic to south-west WA, has no insular representation. This species feeds on nectar and pollen of species in Proteaceae and Myrtaceae, which provide a supply of nectar in all months (V Smith 1991). On islands there is likely to be discontinuity in food supply during the year, as a result of the limited occurrence of species of *Banksia*, *Dryandra*, *Adenanthos*, *Beaufortia*, *Eucalyptus* and *Corymbia*.

**Rodents** Seven species of native rodents occur on only a few WA islands (Abbott & Burbidge 1995; LA Gibson & McKenzie 2012b; AA Burbidge pers. comm.): Golden-backed tree-rat *Mesembriomys macrurus* (nine Kimberley islands), sandy inland mouse *Pseudomys hermmansbergensis* (five islands), western chestnut mouse *P. nanus* (four islands), ash-grey mouse *P. albocinereus* (at least three islands), desert mouse *P. desertor* (Bernier Island), djoongari/Shark Bay mouse *P. fieldi* (Bernier Island) and short-tailed mouse *Leggadina lakedownensis* (Thevenard Island). Six species occur on more than 10 islands in WA: Grassland melomys *Melomys burtoni* (18 Kimberley islands), Kimberley rock-rat *Zyzomys woodwardi* (18 Kimberley islands), western bush rat (*Rattus fuscipes;* 17 islands), pale field-rat *R. tunneyi* (15 islands), common rock-rat *Z. argurus* (14 islands) and rakali/water-rat *Hydromys chrysogaster* (12 islands). The absence of the western bush rat from the largest island in the Archipelago of the Recherche (Middle) is both remarkable and inexplicable (Comer & Adams 2012).

In conclusion, although the distribution patterns described above are well documented, explanations of why there is such pronounced variation in the occurrence of individual species are lacking. Insufficient is known of the ecology of each species (including abundance), and it is seldom possible to attribute the absences of species to habitat preferences, scarcity of suitable habitat, dispersal difficulties, competitive interactions or other factors. Detailed studies of carabid beetles on islands in the Baltic Sea (Niemelä 1988; Niemelä et al. 1985, 1988) should provide a useful guide for future studies of distribution patterns of species on WA islands.

## ENIGMATIC ISLANDS

There are several groups of well-studied islands that provide intriguing—and so far unsolved—puzzles about their human history, ecology and remarkable dissimilarities in species composition.

### Dirk Hartog, Bernier and Dorre islands

Dirk Hartog Island was first visited by Europeans in 1616. Its northern end was visited seven times by Europeans during the period 1616–1822 (Playford 2007). None of these visitors reported sightings of Aborigines, signs of their presence (smoke, burned ground, faeces, dingoes), or Aborigines in watercraft on Shark Bay. Nor had the pewter plate left by Dirk Hartog in 1616 and re-inscribed in situ by de Vlaming in 1697 been removed by 1801 (Cornell 2006). Yet, this large (59,000 ha) island has species missing (and not represented by subfossils) that occur on nearby, smaller islands. Only one wallaby species, the boodie, occurred in modern times. Its population size was probably c. 10,000, based on estimates for other Shark Bay islands (J Short & Turner 1993). This species is now extinct on Dirk Hartog Island.

Nearby Bernier and Dorre islands (collectively c. 10,000 ha) have the boodie, as well as the mala and banded hare-wallaby present. Dirk Hartog Island could have supported populations of c. 460,000 banded hare-wallabies and c. 260,000 mala, based on estimates for Bernier and Dorre islands (J Short & Turner 1992). Dirk Hartog Island also lacks the short-beaked echidna, as well as the euro and brushtail possum, both of which occur on the smaller (20,000 ha) Barrow Island. Indeed, estimates of population density of the euro and brushtail possum extrapolated from Barrow Island (J Short & Turner 1991, 1994) suggest potential populations of c. 5,000 and c. 23,000 respectively on Dirk Hartog Island. A possible incentive for regular visits by Aborigines would be consumption of marine turtles when they come ashore at the northern end of the island to breed and the robbing of their buried eggs (Abbott 2012a).

These anomalous absences from Dirk Hartog Island are suggestive of either a lengthy residence of a population of Aborigines that disappeared before 1616 or of casual occupation during the past 7 ka resulting from Aborigines swimming across from the mainland at the closest point (c. 1 km). In contrast, AR Main and Yadav (1971) speculated that the absence of the black-footed rock-wallaby and euro from Dirk Hartog Island (relative to Barrow Island) may have resulted from the chance absence of rock piles and cliffs.

Although the floras of Bernier and Dorre islands are similar (112 native species, 12 introduced species versus 106 native species, nine introduced species respectively), 33 species recorded on Bernier have not been recorded on Dorre, and 25 of the species recorded on Dorre have not been found on Bernier (Claymore & Markey 1999). Bernier Island lacks the rufous fieldwren, which occurs on Dorre and Dirk Hartog islands. There is no obvious explanation for this in terms of island area or vegetation type.

### Rottnest and Garden islands

These islands are easily accessed from the metropolitan Perth region and thus have been thoroughly studied, although until recently the scientific focus on the two islands has been divergent (Hercock 2003). Both are large (Rottnest Island is 1700 ha excluding salt lakes;

Garden Island is 1200 ha), had similar dominant vegetation types when settled in 1829 (apart from extensive samphire vegetation on Rottnest), but differ in their proximity to the mainland coast (Rottnest Island is 18 km from the mainlaind while Garden Island is 2 km). These islands show remarkable disparity in their composition of native flora and fauna. Despite the numbers of native plant species being similar (Rottnest 105; Garden 102), Rottnest has 31 species not found on Garden, and Garden has 28 species absent from Rottnest (NG Marchant & Abbott 1981).

Although the number of original breeding landbird species is similar (Rottnest 13; Garden 14), five of the species present on Rottnest are not on Garden and five of the species on Garden do not breed on Rottnest (Abbott 1980f). The only clear explanation found is that the absence of the fan-tailed cuckoo from Garden is attributable to the absence of its host, the white-browed scrubwren (MG Brooker et al. 1995b).

Rottnest has three frog species, whereas Garden has none (MG Brooker et al. 1995b), and at least one of these absences (*Heleioporus eyrei*) cannot be attributed to lack of wetlands on Garden Island. Of terrestrial reptiles (Rottnest 16; Garden 14), five of the species found on Garden are not found on Rottnest, and seven species on Rottnest are absent from Garden (MG Brooker et al. 1995b; Wykes et al. 1999). The most striking difference is the occurrence of the dugite on Rottnest and the carpet python and tiger snake on Garden Island. Also noteworthy is that the skink *Lerista lineata* is more common on Garden Island than Rottnest Island and may now be extinct on the latter (Maryan et al. 2015).

Both islands have only one native species of mammal present—the quokka on Rottnest and the tammar on Garden (MG Brooker et al. 1995a). On the mainland both species require dense vegetation, with the shelter requirements of the quokka linked to moist areas such as wetlands and riparian zones.

Plausible hypotheses to account for most of these disparities include the biota present on the mainland coast already differed at the time of isolation of these islands because of a change in climate (Rottnest, c. 7 ka; Garden, c. 6 ka); the need by quokkas, but not tammars, for fresh water (Tyndale-Biscoe 2005); and chance extinctions of species occurred on one island but not on the other.

Invertebrates have not been well studied, except for butterflies (Powell 1998; AAE Williams 1997). Rottnest and Garden have 15 and 13 native butterfly species respectively, but five species on Garden are not recorded on Rottnest, and seven species on Rottnest are absent from Garden.

### Barrow Island, Montebello Group and Lowendal Group

The Montebello Group, an archipelago of some 265 islands, islets and rocks, includes three large islands (Hermite, 1022 ha; Trimouille, 522 ha; North West, 106 ha). It is situated c. 20 km north of Barrow Island (DEC 2006a), WA's second largest island. The Lowendal Group consists of some 40 islands, of which Varanus (83 ha) is the largest (Apache Energy Pty Ltd 1997). The vegetation of Barrow Island (23,000 ha) and the Montebello Group is similar, although it does not appear that many plant species are shared (AA Burbidge 1971; Serventy & Marshall 1964). Despite similarities in their landbird faunas (Butler 1970; AA Burbidge et al. 2000; DCLM 2000a), the larger Barrow Island lacks brown quail (possibly as a result of predation by naturally occurring golden bandicoots) and the swamp harrier (*Circus approximans*). The singing honeyeater is a common species on Barrow, but is absent from the Montebello and Lowendal Groups as a breeding species (AA Burbidge et al. 2000; Dinara Pty Ltd 1988–1993). Mangroves are uncommon on Barrow and Varanus island (Buckley 1983; V & C Semeniuk Research Group 1989), and so these islands lack the brown honeyeater (Butler 1970; AA Burbidge 1971; Dinara Pty Ltd 1988–1993).

Despite their different areas, Hermite and Trimouille islands (in the Montebello Group) have similar numbers of plant species (32, 26) but share only 15 (AA Burbidge 1971). However, these data are not based on an exhaustive list because radiation zones were not visited and the rest of the islands were visited only briefly (AA Burbidge pers. comm.).

In the Montebello Group, two species of goanna are present, with *Varanus gouldii* occurring commonly on several islands. On Hermite Island *V. acanthurus* occurs, where it is common, whereas *V. gouldii* is uncommon (AA Burbidge et al. 2000). Because *V. gouldii* is capable of swimming between islands, its rarity on Hermite Island may indicate interspecific competition. *Varanus gouldii* is absent from Barrow Island, which is also occupied by *V. acanthurus* and *V. giganteus* (Butler 1970; LA Smith 1976). Only *V. acanthurus* occurs on Varanus Island.

## REMEDIATION AND MITIGATION MEASURES APPLIED TO WESTERN AUSTRALIAN ISLANDS: RE-INTRODUCTION OF NATIVE SPECIES THAT HAVE BECOME EXTINCT ON ISLANDS AND ERADICATION OF INTRODUCED SPECIES

As well as the autonomous establishment of several native bird species on WA islands (Table 17), there have been government-sanctioned releases of three native bird species on two WA islands and 12 native mammal species on 21 WA islands (Table 12). The intent of most of these has been to return native species to islands where they once occurred naturally but had become locally extinct as a result of predation by introduced animals. In a small number of cases, some critically endangered mammal species have been established on islands as insurance populations. Conservation translocations to islands have been more successful than to mainland sites (K Morris et al. 2015).

Not listed in Table 12 are re-introductions planned for Dirk Hartog Island, on which pastoral activities ceased in 2009. This island has been a national park since 2009. Once feral cats are eradicated (Algar et al. 2011a, 2011b), it is planned to translocate 12 mammal species: boodie, woylie, banded hare-wallaby, mala, marl (western barred bandicoot; *Perameles bougainville*), chuditch (*Dasyurus geoffroii*), crest-tailed mulgara (*Dasycercus cristicauda*), dibbler, greater stick-nest rat (*Leporillus conditor*), desert mouse (*Pseudomys desertor*), Shark Bay mouse (*P. fieldi*), and heath mouse (*P. shortridgei*; K Morris & Sims 2006).

Claims that some introduced species on islands, such as the common pheasant (*Phasianus colchicus*) and common peafowl (*Pavo cristatus*) on Rottnest Island, should be valued as 'cultural heritage' elements and thus retained (Rottnest Island Authority 2003) ought to be rejected. The occurrence of other introduced species, such as rats, rabbits and cats, may be serendipitous for them but is invariably detrimental to the native species present. Species that had previously been introduced (or self-introduced) have been targeted by the Department of Parks and Wildlife and its predecessors, through mustering and removal (sheep), shooting (goats), or baiting (rabbits, cats, foxes, rats; Table 12).

Island ecosystems recover relatively quickly, in a few years to several decades, after the adverse in situ event ceases. Examples include the recolonisation by seabirds of an island severely damaged by a volcanic eruption (Brattstrom 1963), and the recolonisation by seabirds of an island degraded by guano mining once the cats and rats were removed (Dunlop 2013; Dunlop et al. 2015). These reverses would not be predicted by the alternative states hypothesis (HP Jones 2010). This hypothesis presumes that islands are irreversibly locked and thus should fail to recover following removal of the disturbing factor. Indeed, recoveries should in time reinstate ecological processes such as nutrient cycling to their previous nature.

The plant species *Lycium ferocissimum*, probably introduced by birds, can form dense stands that are inimical to seabirds (although bushes provide potential nesting sites for small landbird species). Plants are being progressively removed from some WA islands (Table 13).

## DISCUSSION

Darwin (1839) made two important deductions about island biotas. First, the affinity of species on remote islands lies with the adjacent mainland. Second, factors other than geology, climate and soil are important in shaping island biotas within the same archipelago. He later identified this key factor as interspecific competition, particularly mediated by the presence (or absence) of congeneric species or functionally similar species (Darwin 1859). This idea was further developed and analysed by Lack (1969, 1971). Criticism by Andrewartha and Birch (1954) was dismissed by Brown and Wilson (1956) and Lack (1966), but was not explicitly addressed by MacArthur and Wilson (1963) and JM Diamond (1975). However, a detailed ecological study of the food and beak morphology of ground finches in the Galápagos demonstrated that both interspecific competition and floristic differences between islands were influential (Abbott et al. 1977). Abbott (1980b) took a more pluralist perspective of the factors relevant to explaining bird species richness, species composition, micro-evolutionary change, and extinction of species on islands.

A recurrent tendency in some literature about island ecology and island biogeography is to exaggerate the general applicability or relevance of parochial studies. There is also a danger in extrapolating results obtained from a study of one taxonomic group in one situation to others in other situations (Thornton 1967). Papers based on the investigation of a few islands and published as books or in prominent scientific journals gain a significance that is not warranted. Readers of highly cited papers and authors of textbooks then generalise conclusions limited to local or subregional studies as if to imply universality. The essential intermediate step of reviewing all relevant studies, analysing their results, and then synthesising the conclusions is omitted. An example is the claim that islands are 'less insular than is generally perceived' (Rose & Polis 2000). This was based on a 10-year study of 21 islands in the Gulf of California. This paper exaggerated the ecological contribution of bird species accidental to these islands, was based on an inadequate review of global literature about islands, and did not evaluate evidence contrary to the view espoused.

Another weakness of studies of island ecology, as part of the broader literature, is geographical bias (LJ Martin et al. 2012). It is suspected that the Hawaiian, Galápagos and New Zealand archipelagoes and other remote islands are over-represented and that continental islands (other than those of north-western Europe) are under-represented in the literature. It seems that, for island ecologists, 'le beau idéal' of an island is one situated in the tropics, lushly vegetated, and little affected by Europeans. Undue prominence has also been accorded to spectacular disturbances, such as the volcanic explosion on Krakatau in 1883 (Thornton 1996).

As previously mentioned, there is widespread reluctance in the island biogeographic literature to explicitly consider factors other than island area and isolation in explaining reduced species richness. This does not seem to result from authors being unaware of these factors. For example, Lawlor (1986) acknowledged that species–area curves for islands in different parts of the world differ because of variation in source pool size, taxonomic and ecological composition of the source pool, ages of islands, island locations relative to the mainland, and differences in environmental diversity among islands.

## Extinct species

The disproportionate extinction of bird and mammal species on islands is well documented (Curnutt & Pimm 2001; Grayson 2001; Greenway 1967; MacPhee & Flemming 1999; HD Pratt 1994; Steadman 2006). Early accounts of the extinction of species on islands, including the moa species in New Zealand (R Owen 1844) and the dodo on Mauritius (Strickland & Melville 1848), created great scientific interest. It is now known that 11 moa species became extinct (Holdaway et al. 2001). These instances (possibly because of their unfamiliarity) attracted much more attention than the loss (remote in time) of the wolf (*Canis lupus*), moose (*Alces alces*) and Eurasian beaver (*Castor fiber*) from the British Islands.

During the late 1830s to early 1840s, William Colenso described the rapid decline of bird and mammal species native to New Zealand. He attributed this to human intervention by means of hunting, introduction of mammal species, and extensive firing of vegetation by Māori (Abbott 2012b). Bennett (1860: 243), in referring to the extinction of the Norfolk Island kaka (*Nestor productus*; a species of parrot) on Norfolk and Phillip islands, attributed this to a 'wanton disregard for their perpetuity', implicating their large body size (thus 'rendering them conspicuous objects') and small population size. Both factors increased the vulnerability of this species to the arrival of Europeans. Extinction was thus seen as an ongoing process, not necessarily an occurrence only in the past.

During the period 1850-1898, >70 articles (too numerous to cite here) were published about the decline of bird species in New Zealand. Depending on the locality, this is only 10-50 years following European settlement. There are no other large islands in the world on which rapid contractions in distribution, reductions in abundance, and in some cases extinction were observed and reported. Potts (1872: 5) in particular drew attention to 'the peril of extermination that hangs over many interesting indigenous species'. Changes in distribution and abundance were variously attributed to habitat destruction, the spread of feral dogs, feral cats, and accidentally-introduced rats, shooting (for food and skins), bushfires, and deliberately introduced ferrets (*Mustela putorius*), weasels (*M. nivalis*), and stoats (*M. erminea*). Both Kirk (1895) and WL Buller (1895) elaborated the causes of these extinctions.

Wallace (1881: 60) considered that extinctions of species on islands resulted from 'pressure of other species, whether as enemies or merely as competitors'. Newton (1893–6: 215) noted that the 'inhabitants of islands are especially subject to this fate [of extinction]'. He attributed losses to 'civilized' man, and criticised the introduction of the ferret, stoat, and weasel to New Zealand. Rothschild (1907a, 1907b) also emphasised the direct and indirect impact of humans in causing extinctions of birds, and implicated cats, rats, dogs, and pigs. The only extinctions of bird species listed by him for Australian islands related to the emu on Kangaroo and King islands (continental islands), a species of rail on Lord Howe Island, and a parrot species on Norfolk Island (both oceanic islands).

The most modern analysis records 10 definite extinctions of landbird species endemic to Australian islands, with three on continental islands and seven on oceanic islands. The exact number depends, however, on the taxonomy followed: King Island emu (*Dromaius ater*), Kangaroo Island emu (*D. baudinianus*), Tasmanian emu (*D. diemenensis*), Norfolk Island rail (*Gallirallus* sp.), white gallinule (*Porphyrio albus*, Lord Howe Island), Norfolk Island kaka, Norfolk Island pigeon (*Hemipaga spadicea*) and Norfolk Island ground-dove (*Callicolumba norfolciensis*), Lord Howe Island gerygone (*Gerygone insularis*) and robust white-eye (*Zosterops strenuus*) on Lord Howe Island (Garnett et al. 2011; Holdaway & Anderson 2001; Hume & Walters 2012). In contrast, only one landbird species has become extinct on the Australian mainland since European settlement.

A further eight subspecies of landbird endemic to islands have become extinct. All instances involve the oceanic islands of Lord Howe, Norfolk, and Macquarie (Garnett et al. 2011).

Western Australia does not have any landbird species endemic to an island and has few landbird subspecies endemic to one or more islands (Table 8). None of these has become extinct. No endemic subspecies of landbird on an Australian continental island has become extinct, although the Tiwi Islands hooded robin (*Melanodryas cucullata melvillensis*) is regarded as critically endangered (possibly extinct) by Garnett et al. (2011). Complacency needs to be avoided, however, because each visit to an island escalates the risk of introducing a plant species, the house mouse or black rat and ultimately causing a local extinction of a native species or subspecies (Chown et al. 2005).

## Extinction of insular populations

In the New Zealand archipelago, 76 (31%) bird species present in the Holocene are either extinct or have no natural populations remaining in the archipelago; 29% of the original species are extinct globally. Of the 174 endemic species, 41% are extinct (Holdaway et al. 2001).

The probability of extinction on islands varies inversely with population size, well exemplified by the breeding birds of Bardsey Island, Britain (JM Diamond 1984b) and plant species on islands of British Columbia (Burns & Neufeld 2009). It is generally assumed that species on large islands occur in greater numbers than on small islands. This decreases the risk of extinction as a result of chance events (MacArthur & Wilson 1967; IN Nilsson & Nilsson 1982; JM Diamond 1984c). The time to local extinction of a lizard species introduced to 30 islets (the largest 0.806 ha) in the Bahamas increased with island area (TW Schoener & Schoener 1983b). Larger islands are also likely to retain species that are rare, either through stenotopy (Medway & Wells 1976) or occurrence in restricted habitat (Udvardy 1969). Based on a long-term data set of landbird species on islands near Britain, extinction rate tends to vary with the number of species breeding in the previous year and does not decline with increasing island area (Manne et al. 1998). The risk of extinction per year for landbird species on these islands varies inversely with population size (Pimm et al. 1988). Rarity on the mainland is not a good predictor of the probability of extinction for bird species on Barro Colorado Island, Panama (Karr 1982b). Instead, population variability predisposed species to local extinction. In contrast, population variability did not correlate with extinction rate of spider species on islands in the Bahamas (TW Schoener & Spiller 1992).

Nearly 20 factors that influenced the extinction of vertebrates on oceanic islands after the arrival of humans on Pacific Ocean islands have been identified (Steadman & Martin 2003). These comprise seven abiotic factors (area, topography, bedrock, soil, isolation, climate, sea-level), five biotic factors (plant diversity, faunal diversity, terrestrial mammals, marine resources, species-specific traits), and six cultural factors (occupation, settlement pattern, population growth and density, subsistence, introduced plants, introduced animals). Note that island area is only one of these many factors.

Some of the identified factors are also relevant to understanding the process of extinction of populations of species on WA continental islands that were occupied by Aborigines. For example, Aboriginal visitors to islands of the Pilbara and Kimberley regions probably depended more on marine resources than terrestrial resources, particularly on smaller islands which lack mammals. Aboriginal impact on these islands is likely to have been transient, except on nesting seabirds. Larger islands were often used for cultural purposes such as rock art, and this probably increased occupancy time and thus exacerbated impacts of foraging and hunting activities on palatable species.

Plant species are known to have become extinct on Tasmania (23 species; ML Baker & de Salas 2012), King Island (one species; DPIPWE 2012), and Fraser Island (one species, Stephens 2011). Many island populations of marsupials have disappeared following European colonisation of Australia. As noted previously, 9% of wallaby and bettong populations are no longer present on WA islands, fewer than the corresponding figures for South Australian islands (78%) and islands in the Furneaux Group, Tasmania (58%, including *Thylogale* and *Potorous*) (T Robinson et al. 1996; Hope 1973).

Local extinction of a species is generally inferred from the comparison of the biota of the same island at different periods (e.g. Amchitka Island; Kenyon 1961). It is most unusual for the process of extinction to be observed on islands, but such was the case in 1912 when PD Montague found on Hermite Island dried corpses of the golden bandicoot, the 'defenceless' spectacled hare-wallaby, and large feral cats which 'appear to be breeding rapidly…They will, no doubt, in a few years time have accounted for the wallabies, as they have for the bandicoots' (Montague 1914: 632). Montague generalised his observations made on the Montebello Islands thus: 'it is of great importance that the fauna of the small islands should be studied and recorded as soon as possible, for the indigenous animals are disappearing so rapidly before introduced species that in a very few years' time little or nothing will remain' (Montague 1913: 35).

In 1897 hundreds of terns were found dead on Rat Island (Houtman Abrolhos), many with only the head bitten off (Helms 1898). Helms (1898: 428) correctly deduced that the cats introduced by guano miners 'bid fair to exterminate the birds or drive them off the island'. Alexander (1922: 472) showed similar prescience in noting the 'absurd tameness' of the common noddy on Rat Island in 1913. He correctly predicted that 'it would doubtless not be long before the Noddies were exterminated' by cats.

Nevertheless, caution needs to be exercised in declaring an island population extinct. For example, the monitor lizard *V. rosenbergi* was first recorded in 1889 on Middle Island in the Archipelago of the Recherche as 'common enough', where it created a nuisance by preying on poultry (Andrews 1959). It was next reported in 1904 (Aborigines Department 1904) and tentatively recorded in 1950 (Serventy 1954). None was reported by subsequent visitors until 1976 and 1984, when the first specimens were collected and lodged in the WA Musem. Tracks and one individual were seen in 1988 (Anon. 1989). Monitors were often seen in 2003 (AAE Williams & Powell 2006). The reason for the rarity of this species on Middle Island after 1904 until recent times is not known.

In some instances, expected local extinctions have failed to eventuate. Feral cats were recorded on Rottnest Island as early as 1884 but the quokka, a small marsupial, still persisted when the cats were removed nearly 120 years later (Barker 1885; Algar et al. 2011c). In contrast, the rock parrot on the same island occurred in 1884 in 'numberless flocks' and were fearless and friendly and visited the vice-regal residence where they were fed canary seed (Barker 1885). By the 1950s few occurred and this decline was attributed to nest robbing by aviculturists and not to feral cats (Saunders & de Rebeira 1993). At present the population seems to have recovered (Saunders & de Rebeira 2009), although concerns remain about the small size of the population in relation to the great abundance of seeds of exotic plant species that are eaten (Wykes & Blythman 2013). In addition, none were seen on 7–8 February 2015, despite many searches (WABN 1943–2016 No. 154: 34).

In elucidating the mechanisms of local extinction on WA islands, care needs to be taken in applying explanations based on studies elsewhere. For example, extinctions of rodent species on islands near western Mexico caused by predation by cats were minimised if alternative prey species were present (Donlan & Wilcox 2008). This factor did not prevent the extinction of the water rat on three islands in the Montebello Group (Table 16).

The previous paragraphs of this section make grim reading about the historical consequences of human occupation of islands. Nevertheless it has long been recognised that islands also offer opportunities to conserve declining species. d'Urville and Resolution islands (New Zealand) were proposed as suitable refuges from dogs and shooters (Potts 1872) and subsequently from ferrets, stoats, and weasels (H Martin 1885). Relevant to this point is the generalisation made by WL Buller (1877: 211) that 'expiring races of animals and plants linger longest and find their last refuge on sea-girt islands of limited extent'. Translocation of animal species to islands has in recent decades become widely practised in New Zealand and Australia.

## Introduced species

Introduced or exotic plant species are sometimes termed neophytes, distinguishing them from native species (archaeophytes). Britain provides an instructive benchmark, with introduced species comprising c. 32% of its flora (Kent 1992). Another long-settled archipelago, Azores, shows an even higher proportion of introduced plant species (52–69% across nine islands), with a strong positive correlation with human population density (Silva & Smith 2004).

The extent of occurrence of European and other non-indigenous species on islands remote from Europe is well documented. Darwin (1859: 380) drew attention to the fact that species indigenous to islands 'have everywhere yielded to continental forms [species] naturalised by man's agency'. Ten years later, he recognised that this was an ongoing process, and updated this sentence to: 'as the inhabitants of real islands have everywhere yielded and are still yielding to continental forms naturalised through man's agency' (Darwin 1869: 458). Hooker (1864) referred to English weeds and European animals spreading rapidly in New Zealand. For example, the proportion of introduced plant species on islands in the Southern Hemisphere is 28 % (New Zealand), 16% (Falkland Islands) and 15% (Tierra del Fuego; DM Moore 1979). Only two remote islands in the Southern Hemisphere are known to lack introduced plant species (Chown et al. 2008). Islands have continued to accrue naturalised plant species since European discovery (Sax & Gaines 2008). Many British, European, and African plant species were introduced to mainland southern Australia soon after settlement in the period 1788–1836 (Kloot 1985). These, and later arrivals, have had many decades to colonise those islands close to mainland ports.

Australian oceanic islands that were settled and farmed or mined have a higher proportion of naturalised plant species than those that were not (usually because of remoteness, unsuitable climate, and small size): Norfolk Island (62%; PS Green 1994), Lord Howe Island (48%; PS Green 1994), Cocos–Keeling (47%; Telford 1993a) and Christmas Island (42%; Du Puy 1993) versus Coral Sea islands (19%; Telford 1993b), Ashmore Reef (15%; Kenneally 1993), Macquarie Island (11%; Hnatiuk 1993), and Heard and McDonald islands (8%; Hnatiuk 1993). Comparative data for the flora of some of the larger Australian continental islands outside WA are: Stradbroke Island, Queensland 30% (Stephens 2011); Tasmania c. 24% (ML Baker & de Salas 2012); King Island, Tasmania 24% (DPIPWE 2012); Kangaroo Island, South Australia 21% (A Kinnear et al. 1999); Moreton Island, Queensland 21% (Stephens 2011); and Flinders, Cape Barren and Clarke islands in Bass Strait 11–13% (S Harris et al. 2001).

The 10 cays situated in the southern portion of the Great Barrier Reef, Queensland, have been colonised by many introduced plant species, which now comprise 14–51% of the total flora. This variation has been attributed to either the number of visitors to the islands each year (Chaloupka & Domm 1986) or the nature of human activities on each island (Heatwole & Walker 1989). Furthermore, there has been a gradual increase in the proportion of introduced plant species through time, well exemplified by the well-studied Heron and North West islands (Heatwole 1984; Chaloupka & Domm 1986) and the less-studied Lady Elliot and Wilson islands (Batianoff 1998; Batianoff & Hacker 2000). The proportion of exotic species in the floras of the cays in the Capricorn–Bunker group is strongly correlated with the level of disturbance experienced on these islands (Batianoff et al. 2009a).

Introduced plant species on islands of Victoria constitute 0–45% of the total flora (Norman 1971a; Norman & Brown 1979; Norman et al. 1980ab). The gradual increase over time of introduced plant species has also been noted for several of these islands (Mud Island, Gillham & Thomson 1961; Rabbit Island, Norman & Harris 1981; Norman et al. 2010; Citadel Island, Norman & Brown 1979; Dannevig Island, Norman et al. 1980a).

Islands in Bass Strait have a long history of grazing by sheep, cattle, goats, and pigs and of vegetable growing (S Harris et al. 2001) and have a high proportion of introduced plant species. For example Big Green and Preservation islands have 50% and 38% of their flora represented respectively by introduced species. On Bathurst and Melville islands, Northern Territory, the length of human settlement is strongly linked with the number of naturalised plant species present (Fensham & Cowie 1998). On the 12 Northern Territory islands examined, the number of naturalised plant species present increased with the size of the human population present (Fensham & Cowie 1998). Similarly, introduced plant species on WA islands (Table 13) tend to be weeds of cultivated ground on the mainland, ruderals (occupying disturbed sites on the mainland), or escapes from gardens (G Keighery 1993). Nearly 380 introduced plant species have so far been recorded on WA islands (I Abbott unpubl. data).

The causes of the high proportion of exotic plant species on islands have been much debated, but the emphasis by Lonsdale (1999) on island area and the number of native plant species seems too indirect. Some of the data presented in this paper about visitor numbers suggest that alternative factors are more relevant (Heatwole & Walker 1989). For example, an important source of introduced plant species on islands is seagulls, which often feed in landfill sites and other disturbed areas on the mainland and nest on small islands where they regurgitate and defaecate seeds (EH Hogg et al. 1989). The proportion of alien annual species is four times higher on islands in Lake Huron (Canada) used for nesting (8.2%) than on islands not nested on by gulls (2.0%).

Many exotic plant species have also established on WA islands, particularly small islands (Abbott 1980a; Abbott & Black 1980). The inverse relationship between the proportion of exotic plant species and the number of native plant species for islands and mainland peninsulas near Albany WA may indicate that assemblages with many interacting species are better able to utilise any spare resources and prevent new species becoming established (Fox & Fox 1986). Introduction of plant species under scientific supervision can be revealing. In the Bahamas, two species were planted on 5–10 non-vegetated islands and most persisted for 15 years (Morrison 2011). This experiment did not, however, identify the mechanism involved.

The occurrence of non-indigenous invertebrate species on islands is poorly documented. Of the 25 remote islands well-studied in the Southern Hemisphere, only four remain free of introduced insect species (Chown et al. 2008).The African big-headed ant (*Pheidole megacephala*) is thought to have been introduced to cays in the southern Great Barrier Reef in the mid-1900s but has not been able to occupy forests of *Pisonia grandis* (Hoffman et al. 2009). The best-studied WA island, Barrow Island, has 32 introduced invertebrate species recorded, all from sites disturbed by human occupation (Majer et al. 2013). Each of the five spider species collected on this island is known to be associated with buildings on mainland WA.

Introduced species that establish on islands undisturbed by humans provide the best demonstration of the natural availability of vacant niches, i.e. undersaturation of the native biota (Mayr 1965a). The only example for bird species on WA islands is of the rock dove breeding on several of the Shoalwater Bay islands. This is in contrast to four British bird species (Eurasian skylark *Alauda arvensis*, common blackbird *Turdus merula*, common starling *Sturnus vulgaris*, house sparrow *Passer domesticus*) that were released on mainland Victoria and Tasmania in the 1860s and which then self-introduced to many islands seldom visited by humans around Tasmania (Abbott 1974d; Abbott 1974e; Brothers et al. 2001), South Australia (T Robinson et al. 1996) and Victoria (Wainer & Dann 1979; Norman et al. 1980; Dann et al. 2004; Warneke & Dann 2013). Similar examples apply to the islands around New Zealand (Abbott & Grant 1976).

In contrast to birds, there are numerous examples of undersaturation of the mammalian fauna. Rats, house mice, rabbits etc. have been recorded on many pristine (i.e. unfarmed or unsettled) WA islands (Abbott & Burbidge 1995). The imprudence (maleficence or thoughtlessness) exhibited by humans in deliberately releasing animals on islands is well known. The most unusual example known from WA concerns a sighting in the 1960s of a fox on remote Adele Island (Coate 1997).

## Endemic species

The extent of endemism among the species present on an island is largely determined by remoteness (Darwin 1859; Thornton 1967), area (Mayr 1965b; Price 2008), barriers to dispersal within an island (e.g. large islands with complex topographic diversity), and vagility of the taxon being considered. The smallest island with obvious in situ speciation of bird species is Madagascar, with an area of 590,000 km$^2$ (Coyne & Price 2000). The late Holocene breeding avifauna of the New Zealand archipelago is instructive, with a higher proportion of endemic species on remote islands (Chatham islands, 43%; Norfolk Island, 35%) compared with the larger source islands (South Island, 16%; North Island, 8%; Holdaway et al. 2001).

Oceanic islands tend to have higher levels of endemism than continental islands. For example, no endemic non-volant mammals occur on islands in south-east Asia smaller than Java (126,000 km$^2$) that are within the 120 m bathymetric line, whereas endemic species occur on oceanic islands as small as 4700–34,500 ha (Heaney 1986). In the Philippines, bird species endemic to a single island are unrecorded for islands smaller than c. 9000 km$^2$ (Peterson et al. 2000).

Exceptions do occur (e.g. butterflies; Gillespie & Roderick 2002). Interestingly, the floras of only two of the oceanic islands of Australia confirm this point: Lord Howe Island (44%; Green 1994) and Norfolk Island (28%; PS Green 1994). In contrast, the others have low levels of endemism: Christmas Island (7%; Du Puy 1993), Macquarie Island (5%; Hnatiuk 1993), Heard Island (0%; Hnatiuk 1993), Cocos–Keeling (0%; Telford 1993a), Ashmore Reef (0%; Kenneally 1993) and Coral Sea islands (0%; Telford 1993b).

The floras of Australian continental islands also show a range of levels of endemism: Tasmania 27% (RS Hill & Orchard 1999; ML Baker & de Salas 2012); Kangaroo Island (South Australia) 4% (A Kinnear et al. 1999); Stradbroke Island (Queensland) 0.4% and Fraser Island (Queensland) 0.2% (Stephens 2011); Flinders, Cape Barren, Clarke and King islands in Bass Strait 0% (S Harris et al. 2001; DPIPWE 2012); and Barrow Island (WA) 0% (Buckley 1983).

The proportion of landbird species endemic to continental islands of Australia is either zero or close to zero for most islands (Abbott 1973). The figure of c. 15% for the avifauna of Tasmania (Mayr 1965b) is incorrect *sensu stricto*, as it includes species shared with the larger islands in Bass Strait (Abbott 1973). Fifteen landbird species are considered to be endemic to the continental islands of Australia (HANZAB 1990–2006). In the Tasmanian region, most endemic species also occur on the three largest satellite islands of Tasmania that have been sufficiently studied (King, Flinders and Bruny islands). We have assigned a score of 1, 0.5, 0.33 or 0.25 to species endemic to one, two, three or four of these islands. Using this method of scoring, endemic species of landbird are known from only four Australian continental islands: Tasmania *sensu stricto* (4.4 species), Bruny Island (4.4), King Island (3.9) and Flinders Island (2). No endemic species of landbird is present on any of the other islands listed in Table 3, although the inadequately studied Cape Barren Island is likely to have a score identical to that of nearby Flinders Island.

As expected, more continental islands of Australia possess endemic subspecies of landbird (HANZAB 1990–2006). In order of decreasing island area (Table 3), the well-studied islands have the following score: Tasmania *sensu stricto* 20.0, Tiwi Islands (Melville and Bathurst islands) 7, Kangaroo Island 17, Groote Eylandt 1, Fraser Island 0, Flinders Island 6.8, King Island 12.3, Dirk Hartog Island 3, Bruny Island 12.7, Barrow Island 1, Dorre Island 1.5, Bernier Island 0.5, Wallabi Islands (Houtman Abrolhos) 1, Coral Sea and Great Barrier Reef islands 1, and cays of the southern Great Barrier Reef 1. These data are puzzling. We suggest that many of the Tasmanian *sensu lato* and Kangaroo Island subspecies recognised by HANZAB (1990–2006) are tenuous and confound phenotypic differentiation (in terms of plumage, body size and bill dimensions) as a result of rainfall and temperature gradients (Gloger's and Bergmann's rules) with genetic divergence due to insularisation per se.

We question why the subspecies *Gavicalis virescens insularis* on Rottnest Island, with its large size and dark plumage, is no longer accepted, whereas many of the subspecies described on a similar basis for Tasmania and Kangaroo Island continue to be recognised by HANZAB (1990–2006). A study, particularly one applying modern molecular techniques, of all subspecies of landbird described for Australian continental islands is needed. We note that a recent DNA study did not support the continued recognition of the Kangaroo Island subspecies of white-eared honeyeater (*Nesoptilotis leucotis*; Dolman & Joseph 2015).

Only six mammalian species are considered to be endemic to the continental islands of Australia (Woinarski et al. 2014; S Jackson & Groves 2015). In the Tasmanian region, none of the four endemic species (Tasmanian devil *Sarcophilus harrisii*, Thylacine *Thylacinus cyanocephalus*, long-tailed mouse *Pseudomys higginsi* and Tasmanian long-eared bat *Nyctophilus sherrini*) occurs on the three largest satellite islands of Tasmania that have been sufficiently studied (King, Flinders and Bruny islands). Outside the Tasmanian region, the only islands with endemic mammal species are Percy Island, Queensland (with the Percy Island fruit-bat *Pteropus brunneus*, now extinct) and Bramble Cay (with the Bramble Cay melomys *Melomys rubicola*). Bramble Cay is small (3.6 ha) and close to New Guinea (Ellison 1998). Although this species is unknown from New Guinea, Limpus et al. (1983) questioned its status as an endemic species. It has recently become extinct.

Seventeen continental islands of Australia possess endemic subspecies of mammals (Woinarski et al. 2014; S Jackson & Groves 2015). We have assigned a score of 1, 0.5, 0.33 or 0.25 to subspecies endemic to one, two, three or four islands. In order of decreasing island area (Table 3), the well-studied islands have the following score: Tasmania *sensu stricto* 6.8, Tiwi Islands (Melville and Bathurst islands) 2, Kangaroo Island 2, Groote Eylandt 1, Fraser Island 0, Flinders Island 2.8, King Island 2.8, Dirk Hartog Island 1, Bruny Island 3.5, Barrow Island 2.5, Dorre Island 0.5, Bernier Island 0.5, Mondrain Island 1, Franklin Island 1, Fitzroy Island 1, Boodie Island 0.5, and North Pearson Island 1.

## Evolutionary change

Differences in morphology between island and mainland populations are usually attributed to different ecological interactions that directly favour an increase or decrease in body size on islands, particularly reduced predation, less interspecific competition, increased intraspecific competition and fewer available resources (Lomolino 1985). However, if this is indeed so, why then do so few species respond? As reported in section 'Morphological changes' above, differences in morphology between island and mainland populations of WA species are not extensive.

A more recent explanation of the mechanism of changes in body size in island populations argues that reduced predation decreases mortality, resulting in shifts in age and size at maturity, thereby increasing body size (Palkovacs 2003). Similarly, decreased availability of resources on islands should reduce growth rate, resulting in smaller body size.

Birds on islands often have smaller clutches than on the nearest mainland (Crowell & Rothstein 1981; Blondel 2000). This is usually attributed to limitation of resources, caused either by ecological impoverishment on islands or by climatic stability (which limits the food supply). Breeding birds are assumed to be unable to feed more young. Another hypothesis is that less reproductive effort allows energy to be directed to foraging more efficiently, avoiding predators, or countering intraspecific and interspecific competition (Cody 1966).

## Species turnover

The ancient Greek (pre-Socratic) philosophers proposed distinctive and extreme views about the world, with Parmenides advocating complete stasis (no change, enduring continuity) and Heraclitus arguing for complete instability (continuous change). Subsequent observations of the real world by natural historians recognised that a position between these two opposites is more usual. For example, San Nicolas Island (California) has five bird species that bred in each of the eight years of survey (complete stasis), three species that bred less frequently, and four species that bred occasionally (complete instability). This island lacks, however, any record of 170 bird species present on the adjacent mainland (Lee & Diamond 1976).

Change with time is characteristic of all ecosystems and involves decrease of some components and increase of others. The continental islands of WA illustrate this in exemplary fashion, with most of the species presumably present at the time of separation from the mainland (c. 6–14 ka BP) having become extinct by the time scientific studies commenced 200 years ago. As noted by Lack (1942), the liability of small populations to accidental extinction and the delay in recolonisation due to isolation are theoretically sufficient to account for much species turnover.

The degree of change is of course expected to vary inversely with isolation. Abbott (1980) demonstrated that the landbird faunas of remote Christmas and Cocos–Keeling Islands in the Indian Ocean and Raine Island (Queensland) changed little or not at all during a period of 90–120 years. Subsequent study confirms this (James & McAllan 2014; Johnstone & Storr 2004; Batianoff & Cornelius 2005). Lack (1976) documented little change in 150 years on Jamaica, and suggested that its avifauna was stable. The landbird fauna of the Canary Islands (Atlantic Ocean) has not changed in 100 years, and that of the Faroe Islands was 'exactly as it was about 500 years ago' (Salomonsen 1976). Nor had the landbird fauna of Cocos Island (Pacific Ocean) changed during the period 1891–1963 (Slud 1976). In contrast, a small cay distant only 1 km from Puerto Rico (West Indies) exhibited considerable dynamism of plant, reptile and invertebrate species during three years of study (Heatwole & Levins 1973), as did the ant faunas of two other islands near Puerto Rico (Torres & Snelling 1997). Passerine bird species also showed much turnover on five Greek islands (Foufopoulos & Mayer 2007). On cays in the Coral Sea, two plant species became extinct and five species were recorded for the first time (Batianoff et al. 2009b).

However, for the period from c. 1840 to the present, determining that a record of a few individuals on a WA island constitutes establishment is not straightforward, nor is determining that no record of a species previously established on an island constitutes absence and thus local extinction. Recall Kingsley (1863: 67): 'no one has a right to say that no water-babies exist, till they have seen no water-babies existing, which is quite a different thing…from not seeing water-babies'. Decisions based on arbitrary criteria are sometimes necessary in well conducted studies. For example, based on a high frequency of resampling (27 times), Rey (1981) defined an 'extinction' event as the failure for two consecutive weeks to collect a species (of arthropod) that previously occurred on the island.

Even a nine-day visit to a large island (Cockatoo Island, 508 ha, Warham 1957) is insufficient to adequately determine the status of all but widely distributed or abundant bird species. In contrast, a 10-year residence on Koolan Island (2712 ha, NL McKenzie et al. 1995) is more than sufficient to determine status, except for habitat (in this case, mangal) that is difficult to visit.

We found little evidence of gradual or incremental change in the faunas of WA islands and no evidence that immigrant species are superior competitors that replace or substitute the ecological function of the species that have become extinct on islands. We suspect that most changes are the result of ecological destabilisation caused by humans and introduced species. In contrast, changes in the floras of WA islands are much more frequent, but knowledge of the competitiveness of plant species on WA islands and the relevant adjacent mainland coast is too meagre to invoke this factor. A few of the well-studied islands of WA show evidence of change in vegetation structure and/or dominant plant species (Abbott et al. 2000). Of particular interest is change in the areal extent of dominant plant species on several islands of South Australia (T Robinson et al. 1996; AC Robinson et al. 2008a), apparently unrelated to human activity. Matched photographs taken up to 10 times during the period 1923–2006 on Pearson Island show remarkable changes in vegetation cover (Symon 1971; T Robinson et al. 1996; AC Robinson et al. 2008a). We know of no comparable documentation available for any WA island.

Insularity is a relative characteristic, dependent on the type of organism involved (Peake 1971; Heatwole et al. 1981). As pointed out by Williamson (1981), species absent from islands but present on the mainland adjacent should be thought of as perceiving these islands as either continental or oceanic. That is, species with high dispersal rates can easily reach such islands, which are not effectively isolated (KW Dammerman 1948 in Thornton 1996; Haila et al. 1979; Haila & Järvinen 1980). Species with low dispersal rates cannot. Thus, the same island may be 'continental' to raptors and bats but 'oceanic' to land snails and wallabies. On One Tree Island (Queensland), species turnover of epigeal arthropods is frequent, whereas soil microarthropods showed little species turnover (Heatwole et al. 1981). In addition, some species on small islands may in fact be part of a metapopulation that includes the source area, thereby reducing the probability of extinction on small islands (Mayer & Chipley 1992).

Much research remains to be conducted for determining which species fit the core–satellite model (mainland or large islands with stable biotas versus smaller islands with unstable biotas) or the source–sink model (mainland or large islands producing large numbers of emigrants versus smaller islands receiving only emigrating species; Ås et al. 1997).

The extent of ocean separating an island from the mainland (or nearest source area) obviously presents a fatal barrier to most non-volant native vertebrate and plant species occurring on the mainland coast. Other relevant factors include the areal extent, the source area, its direction from the island, and the size of the species population on the source area (Udvardy 1969). Many bird species seem unwilling or reluctant to cross small distances over water (Mayr & Diamond 2002; WD Robinson 1999). Although some species of kangaroos are capable swimmers (GR Wilson 1974), and some species of kangaroos and wallabies have been recorded swimming (Anon. 1861; Gould 1863; DH Johnson 1964), we are not aware of any observations of macropodoids reaching WA islands (other than deltaic ones) by this means.

Abbott (1973, 1974a) showed that most bird species absent from Tasmania or Kangaroo Island (South Australia) had either never been recorded on these islands or had arrived there in small numbers at irregular intervals. Subsequent studies on One Tree Island (Queensland), Rottnest Island (WA), Montagu Island (NSW) and Seal Rocks (Victoria) confirm this conclusion (Fullagar 1989; Heatwole et al. 1981; Saunders & de Rebeira 1983, 2009; Warneke & Dann 2013). Other frequently studied islands of Victoria also illustrate this point (Gabo Island, Fullagar et al. 2006; Rabbit Island, Norman & Harris 1981; Norman et al. 2010; Great Glennie Island, Wainer & Dann 1979; Lady Julia Percy Island, Dann et al. 2004; Norman et al. 1980b). Most of the 20 landbird species recorded as vagrant to Kangaroo Island since the synthesis of Abbott (1974a) were present as singletons (Baxter 2015). Birds that form flocks are more likely to colonise islands successfully (Abbott 1974d; Estoup & Clegg 2003; Mayr 1965a; Salomonsen 1976).

A potentially significant confounding factor with landbirds is the false positive—when a species is recorded as present but is not actually established (i.e. breeding). Such transient species can inflate the number of immigrations. Montagu Island (NSW) provides an outstanding example (Fullagar 1989). It was visited 22 times each for about one week during the period 1965–1988. Only six of the 42 landbird species recorded bred. The other 36 species were seasonal visitors, passage migrants or vagrants. Another well-studied island (Seal Rocks, Victoria, 1.5 km from its source area and only 2.8 ha in area) shows a similar pattern. It was visited frequently during a period of 40 years (Warneke & Dann 2013). Only two of the 36 landbird species that were recorded bred on the island. Apart from these and four migratory species, most of the rest were recorded as single birds on one to 11 occasions. Finally, One Tree Island (Queensland, 80 km from the mainland and 4.9 ha in area) was visited numerous (c. 17) times (Heatwole et al. 1981). Four of the 16 landbird species are resident, and the others were recorded as one or two individual(s). An earlier study had recorded 17 vagrant species, usually as a single individual (Domm & Recher 1973).

Similar comment applies to plants and invertebrates. Few of the seeds that wash up on beaches germinate. Most epigeal arthropods, transported by winds blowing from the mainland, fail to establish populations (Heatwole et al. 1981).

How much confidence can be placed in data used to demonstrate species turnover on islands? There is an underlying ambiguity in most studies, and valid criticism of the methodology can be directed at several relevant characteristics of the data collected:

- Completeness of the study, including sampling errors (IN Nilsson & Nilsson 1982, 1983; Stoddart & Fosberg 1982). Some species may be present and established but were overlooked or not noticed when the island was searched (false absence, N Davies & Smith 1997; Heatwole 1984; HL Jones & Diamond 1976). For example, the Ningaloo worm lizard (*Aprasia rostrata*) was first collected on Hermite Island WA in 1952, not collected in 1970–1971, 1994, or 2000 (J Richardson et al. 2006), but collected again in 2006 (Maryan & Bush 2007). Subjective decisions as to how 'missing' species should be treated are often required (IN Nilsson & Nilsson 1982, 1983, 1985; Rey 1981). Strictly speaking, only the careful monitoring of small populations can demonstrate extinction (N Davies & Smith 1997).
- The time period of the study (Solem 1990). Some species may have repeatedly colonised, established and then become extinct but infrequent censuses underestimate such change (Heatwole 1984; Lack 1942; Rogers & Morrison 1994). Such undetected turnover is termed cryptoturnover by Lynch and Johnson (1974).
- 'One swallow does not a summer make': Transient, intrapopulational movement should not be confused with local extinction or immigration (Simberloff 1983a). The occasional presence of one or two individuals of mobile species (termed 'Crusoe species' by Solem 1983), as is the case with many landbird species (Remsen 1994), does not necessarily imply that these individuals constitute an established (breeding) population. This is obviously so if the individual is male or a 'non-pregnant strandee', to use the designation of Solem (1990). Such misclassification (pseudoturnover) inflates species turnover (Lynch & Johnson 1974). Records of casual occurrence of landbird species on WA islands are summarised in Table 14. These records support the conclusion of Lynch and Johnson (1974: 373) that 'the presence of nonbreeding land birds on continental islands is the rule [for many, but not all, species] rather than the exception'. The criterion used by Simberloff and Wilson (1969) for defining a propagule of an arthropod admitted three possibilities: An adult female, an adult of indeterminate sex, or an immature animal. However, none of these necessarily implies breeding on an island and all invite scepticism. Rey (1981) has provided a checklist comprising six criteria applicable to invertebrates, including testing the ability of species to persist in temporary cages placed on islands. For plant species, a single seed of an obligate allogamous species can be regarded as a propagule and as an immigrant should the seed germinate and establish an individual plant which might persist 'for some time' (Whitehead & Jones 1969). However, establishment is not guaranteed:

Of the 46 sowing experiments conducted on islets near Karpathos, only 10 succeeded (Höner & Greuter 1988). Nor should extinction be accorded to seeds incapable of reproduction.

- Sessile species (plants) may still be present but in a dormant state (as seeds, bulbs, corms, tubers, rhizomes). The absence of above ground parts (foliage, flowers) does not necessarily represent extinction (Rogers & Morrison 1994).
- Some species commute between islands or between islands and mainland in large numbers without necessarily breeding on islands. Examples include the pied imperial-pigeon and red-tailed black cockatoo on various islands in the Kimberley region (Coate 2008b; NL McKenzie et al. 1995; LA Smith et al. 1978).
- Some species may have been misidentified and in the absence of a voucher specimen no further checking is possible (Heatwole 1984). For example, the exotic grass species *Avena fatua* was recorded on Penguin Island WA in 1959, 1984 and 1997–98, but *A. barbata* was recorded in 1975 (Rippey et al. 1998). In the absence of a voucher specimen, is it prudent to regard *A. barbata* as a misidentification of *A. fatua*? Another example of doubtful records concerns the white-winged fairy-wren on Hermite and Sholl islands, WA (Sheard 1950). Finally, the rat species on Woody Island WA was misidentified as the black rat instead of the native species *Rattus fuscipes* (AA Burbidge et al. 2012).
- The baseline may not be an adequate point of comparison (Lynch & Johnson 1974), particularly if it lists all species ever recorded on the island up to the baseline.
- Some species may not be truly isolated from the source area. Their occurrence on islands may be embedded in a metapopulation with the mainland, in which frequent immigration compensates for frequent local extinction, the so-called rescue effect (Brown & Kodric-Brown 1977). BY Main (1984: 254) suggested that some populations of spiders on WA islands are 'undoubtedly reinforced with windblown spiderlings'.
- Successional changes induced by grazing, fire or volcanic ash may result in changes in the floristic and structural composition of vegetation (Panitsa et al. 2008), as well as species richness (Hannus & von Numers 2010; Thornton 1996). On small islands such complications may mask baseline extinctions and introductions that occur solely in relation to island area, isolation and other natural factors. Forest closure and loss of open habitat contributes to the local extinction of species (Thornton 1996).

Most of these criticisms can be avoided by ensuring that the maximum area of islands searched is commensurate with the body size, conspicuousness, or mobility of the taxa studied (Abbott & Black 1978; Goldstein 1975). For example, it would be a very difficult task to prove the colonisation or extinction of a species of native ant on a very large island. Heatwole (1971) successfully documented species turnover of invertebrates on a sand cay with an area of 0.49 ha and 464 km distant from the mainland. Caution also needs to be exercised in declaring inconspicuous, small or cryptic vertebrate species to have colonised islands. Examples include the recent discovery of the skink *Menetia greyii*, the western whipbird (*Psophodes nigrogularis*), the heath mouse, Kangaroo Island dunnart (*Sminthopsis aitkeni*), and little pygmy possum (*Cercatetus lepidus*) on Kangaroo Island, South Australia (MN Hutchinson and Tyler 2002; Inns 2002; Kemper et al. 2010), the swamp antechinus on Rabbit and Kanowna islands, Victoria (Norman et al. 2010; Sale et al. 2006), and the moss froglet (*Bryobatrachus nimbus*; Rounsevell et al. 1994) and the New Holland mouse (*Pseudomys novaehollandiae*) on Tasmania (Hocking 1980). The southern death adder (*Acanthophis antarcticus*) was first reported on Daw Island (Archipelago of the Recherche) in 1986, despite many previous visits (LA Smith et al. 2005). None of these discoveries represent new colonisations. They are instead an indication of the failure of previous observers to record.

Conspicuous landbird species are, however, less easily overlooked. For example, three species (galah *Cacatua roseicapilla*, willie wagtail and magpie-lark) have established in recent decades on Kangaroo Island (South Australia). This is probably linked to the increasing conversion of native vegetation to pasture (Abbott 1974a; Paton et al. 2002). Another nine species have either increased in occurrence or established since settlement (Carpenter & Horton 1999).

Brief visits to large (>100 ha) islands generally do not permit reliable determination of the status of conspicuous species such as birds. In contrast, the sustained effort of Lee Fontanini, who recorded birds present on Koolan Island (2600 ha) during a period of residence from 1983 to 1993, allowed resident species to be distinguished from regular visitors and vagrants (NL McKenzie et al. 1995).

Inherent in some of the biogeographic literature is the assumption that all or most natural species turnover is the result of competitive exclusion. Indeed, from the 1940s to the 1980s this was the accepted paradigm (e.g. Lack 1966, 1976; Serventy 1951). It was held that species too similar in their preferred habitat or diet (e.g. congeners) could not coexist (GE Hutchinson 1959; MacArthur & Levins 1967; TW Schoener 1965). When this paradigm began to be questioned, the vague concept of diffuse competition was formulated (MacArthur et al. 1972), making it very difficult to test this hypothesis (Abbott & Grant 1976; Simberloff 1983a). Over-emphasis of interspecific competition by Lack (1976) was criticised by Vuilleumier (1977). In addition, evidence of one-for-one replacement of obvious competitors is either weak or non-existent (Abbott & Grant 1976; Simberloff 1983a).

One potential limitation of focus on species turnover is that it diverts attention from individual species. For example, Diamond and May (1977) used a long-term (29 year) data set comprising annual counts from 1946 to 1974 of the number of breeding pairs of landbird species on the Farne Islands. The more interesting question arising from these data is why six of the species were occasionally recorded only as one pair. Did this result from dispersal difficulties, lack of suitable habitat, interspecific competition, predation or extreme weather events? Indeed, these authors hint at several of these factors in explaining extinctions on these islands. One gains the impression that examining numbers within a conceptual framework is more important than understanding the ecology of the species involved.

## Small-island effect

Attention in the literature to this phenomenon seems to have resulted from excessive focus on species–area relationships, for some small islands provide awkward exceptions to the expected monotonic increase in number of species with area (Lomolino & Weiser 2001). The small-island effect should instead lead the attention of island biogeographers to examine the role of factors such as island exposure, elevation and distance to the source area (Heatwole & Levins 1973). In fact, Whitehead & Jones (1969) had attempted this by separating out plant species of the strand and the interior of atoll islands. They suggested that strand species are salt tolerant in contrast to the interior species, but this is unconvincing given the likely widespread influence of salt spray on these islands (Niering 1963). It seems more likely that the colonisation by non-strand species is linked to the better-developed soils in the interior of the larger islands.

The existence of an ecological basis for the unpredictability of species richness on small islands (MacArthur & Wilson 1967) appears tenuous, based on the demonstration that variation in species richness independent of area on small islands is sometimes merely a statistical artefact (Burns et al. 2009). Great Barrier Reef (Queensland) islands show no small-island effect: Plant species richness increases gradually from the smallest to the largest islands (Heatwole 1991). WA islands do, however, provide evidence of the effect. Analyses presented in this paper (particularly Fig. 5, Fig. 6) indicate that the presence of vegetation (i.e. at least one plant species) is jointly determined by island area and maximum elevation. In fact, small-island effects are likely to have different explanations for different taxa: Landbird species depend on the availability of a sufficient area that provides both suitable habitat and appropriate levels of food/nutrients, and this area will be larger than for plant species.

Scavenger and detritus-feeding invertebrate species are likely to precede omnivorous species in the colonisation of small, newly formed cays (Heatwole & Levins 1973). The lack of habitats related to inland waters on small islands accounts for the absence of some isopod species on islands in the Aegean Sea (Sfenthourakis & Triantis 2009).

Despite controversy about the existence of the small-island effect, small islands do have great intrinsic interest. This is because they have an almost purely oceanic biota (MacArthur 1972). In addition, in archipelagoes, small islands considered together may possess more species than an equal area on the largest island (or on several of the largest islands; Quinn & Harrison 1988). This of course depends on a low degree of species overlap among the smaller islands.

We suggest that small-island effects may arise because the locus where populations are viable is not necessarily related to island area. The area defined by this locus may be related to the number and area of different habitats (Triantis et al. 2006) and the area of suitable habitat where conditions for persistence exist. Three key conditions need to be met for successful establishment and persistence of species on islands. For species with propagules arriving in sufficient numbers to reproduce, there needs to be available: A, safe sites; B, suitable habitat; and C, sufficient supply of food and water, nutrients or hosts (Fig. 24). These conditions can be imagined as three overlapping domains creating a locus where all three conditions are present and viable populations are possible, and loci where only two, one, or none of the conditions are present and where viable populations are not possible and populations decline and become extinct. For simplicity, these domains are represented in Fig. 24 by equal sized circles and populations move between loci as conditions change. In actuality, island populations are confined to the island and the domains can change in size and overlap, or disappear, as conditions become more or less favourable. Thus, small-island effects may arise because the locus where populations are viable is not related to island area, but the domain defined by this locus maybe related to the number and areas of different habitats (Triantis et al.2006). Competing species or predators may be absent from small islands, or separated within archipelagoes, leading to larger domains where viable populations are possible.

The maximum size of the locus where populations are viable may be determined by island area if the whole island satisfies the key conditions. Notionally, the minimum areas of the domains where populations are viable are related to the species' requirements for persistence and will be different for different taxa: Square centimetres for crevice-dwelling herbs; square metres for terrestrial invertebrates; tens of square metres of sufficient soil depth for shrubs and small trees; hundreds of square metres for birds; and hectares for grazing mammals. Turner and Tjørve (2005) and Tjørve and Tjørve (2011) outlined how the interaction of island area and minimum area requirements for species could lead to apparent small-island effects. We are suggesting a model that includes how minimum area requirements arise in species, accounting for situations where competing species or predators may be absent on small islands, or separated on different islands within archipelagoes, leading to larger domains where viable populations are possible.

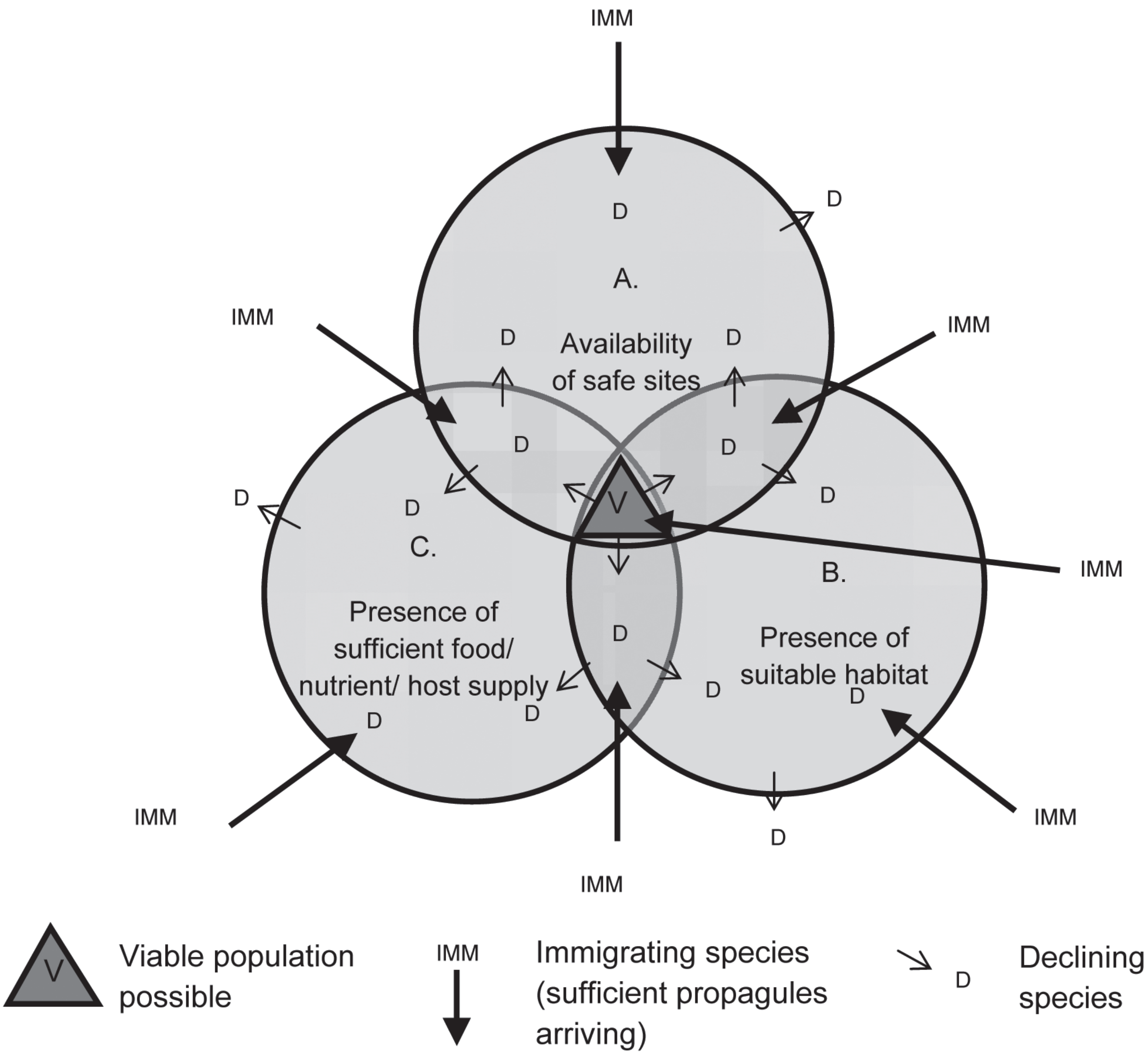



*Figure 24. Diagram of key conditions that have to be satisfied in order for species to either establish or persist on islands. Immigrant species (bold arrows) arriving in sufficient numbers to reproduce need conditions A, B, and C to be satisfied (locus V) before populations can establish and persist. These conditions can be considered to exist in overlapping domains or areas defined by the circles. A domain or area defined by the locus where all three conditions overlap needs to be present on an island to sustain a viable population. Where conditions change unfavourably (fine arrows), and where only two, one, or none of the conditions are satisfied, populations decline leading to local extinction. For species established on islands (within locus V), transition to only two, one or none of the conditions being satisfied (loci marked D) leads to population decline and local extinction.*

## The dynamic equilibrium theory of island biogeography (DETIB)

A major aspiration of scientific inquiry is to subsume a mass of empirical data into a coherent theoretical framework. The prize of all useful theory is a generalised abstraction of elements common to all situations, balancing realism with generality. If the theory is too realistic, generality may be reduced (Simberloff 1983a). Thus, theory should ideally be simple, comprising a minimum set of factors both necessary and sufficient to explain the phenomenon under investigation. An explicit mechanism that links the operation of these factors must also be embodied in the theory. Best practice (rarely attainable) is that the data available have been derived from experimental investigations in which samples have been obtained at random.

The disciplines of island ecology and biogeography have, however, developed in a more piecemeal way, relying instead on correlations between variables in soundly collected data sets, as well as ad hoc comparisons and case studies based on accumulated data and other evidence. Until the 1960s, island biogeography was 'almost entirely empirical – the making of observations and the accumulation of data' (Fosberg 1987: 418). An outstanding contribution to the theoretical foundation of this discipline is the luminous and coherent equilibrium theory of MacArthur and Wilson (1963), which proposed that the number of species on an island resulted from a dynamic equilibrium between rates of immigration and local extinction of species. Islands that differ in area and isolation from the mainland are expected to differ in their equilibrial number of species. This theory has proved attractive to researchers because of its effective blend of realism and imagination.

Before DETIB, comparison of the results of repeated censuses was ad hoc and unfocused. For example, bird species present in 1922 and 1930 on Lundy Island near south-western Britain were compared, with more attention given to explaining changes in population size of species rather than the considerable turnover of landbird species documented (Wynne-Edwards & Harrison 1932). Indeed, it was incorrectly assumed that isolation is 'probably complete'. In a comparison of the vegetation of cays near Jamaica in 1939 and 1952, changes in island size, extent of vegetation and dominant plant species were mapped but no attention was given to species turnover (Asprey & Robbins 1953). Lists of plant species present on 32 islands (mostly <5 ha in area) in the Gulf of Bothnia, Finland were compiled in 1947–49 and 1959 (Vartiainen 1967). Although many instances of immigration and extinction were recorded, the focus of this study was on ecological succession and not on species turnover.

Two predictions that follow from DETIB are (1) species richness on islands should be predictable and constant, despite (2) changes in species composition. It remains unclear how stringent is the definition of 'constant' (Abbott & Grant 1976). Assumptions, strengths, ambiguities and limitations of the theory are summarised in Table 19. We do not share the need for nebulous concepts such as 'dynamic disequilibrium, in which geological and climatic processes are always a step ahead of the biotic systems, and [mammal] faunas, in effect, chase their changing equilibrium point through time, always a step or two out of phase' (Heaney 1986: 159–160). It should also be unnecessary to over-interpret the result of species turnover as, for example, 'possibly approaching some long-term equilibrium level' (Morrison 2010: 669).

The biogeographer JD Sauer was highly critical of DETIB, disagreeing with the abandonment of the particulars of natural history for universal generalisation (JD Sauer 1969). He queried the testability of the theory and suggested that most of the terms used in the mathematical formulations are 'probably unobtainable for anything larger than an islet' (JD Sauer 1969: 591) and potentially the collection of the relevant data might destroy the biota. Indeed, MacArthur and Wilson (1963, 1967) over-reached when they changed their interpretive framework from 'an' equilibrium theory of insular zoogeography to 'the' theory of island biogeography. Yet, further inappropriate exaggeration occurred when HS Walter (2004: 177) considered that DETIB had been 'largely invalidated and superseded by new field data and more realistic concepts'.

The essence of DETIB (as described above) has not always been properly grasped. Many papers have been published that have focused on curve-fitting (Haila 1986), demonstrating a linear relationship between species richness and island area (Williamson 1988), and over-interpreting the value of the slope of the double logarithmic species–area equation (Abbott 1983). Neither characteristic has relevance to detecting equilibrium. It is instead necessary to study species turnover in order to assess whether an equilibrium number of species does indeed exist. There should be equal numbers of immigrations and extinctions in a specified period (Crowell 1986). On islands in the tropical Pacific Ocean, extinctions of landbird species much exceed immigrations (Steadman 2006). Equally surprising is the failure to discuss the implications of research in terms of the validity of DETIB. For example, introduced plant species greatly exceed extinctions of plant species on oceanic islands (Sax et al. 2002; Sax & Gaines 2008). This is not what DETIB predicts. Even the use of long-term counts of landbird species on 13 islands around Britain failed to support DETIB for half of these islands (GJ Russell et al. 1995).

The distinguished island biologist Raymond Fosberg (1908–1993) thought that some of the ideas and possibilities expressed in DETIB were ingenious and perceptive. 'However, their varied nature, mutual discrepancies, and sheer complexity make it extremely unlikely that the equilibrium theory is applicable to cases in real life or can be used as any sort of guide or framework on which to arrange observational data and to interpret or explain their significance' (Fosberg 1987: 418). Appraisals published in a special issue of *Global Ecology and Biogeography* in 2000 agreed that this seminal theory had stimulated considerable research, which had rendered it either obsolete or largely superseded (Brown & Lomolino 2000; Heaney 2000; Lomolino 2000a; Lomolino b; Ward & Thornton 2000; Whittaker 2000). Lomolino (2000a; 2000b) emphasised the need for a new paradigm and suggested a tripartite model of what he envisaged as the key processes of immigration, local extinction and speciation. This proposal is not particularly useful for continental islands, where the evolution of new species seldom occurs for most taxa.

In addition, some well-executed studies of species turnover have not confirmed the predicted inverse relationship between extinction rate and island area and between immigration rate and distance to the mainland (Burns & Neufeld 2009; Manne et al. 1998; SJ Wright 1985). One study has, however, confirmed that the extinction rate is greatest on small islands (Roden 1998).

The geographer David Stoddart, an experienced researcher of island ecology, has questioned the counting of extinction of different species as equivalent events, citing the sparrow and osprey as an example. This is because these species occupy different trophic levels and thus should have different levels of impact

**Table 19**

Identified assumptions, strengths, ambiguities and deficiencies of the dynamic equilibrium theory of island biogeography (DETIB), as the theory was proposed by MacArthur and Wilson (1967).

| Issue | Comment/example |
|---|---|
| DETIB is original and highly significant, stimulating much research (Lack 1976; TW Schoener 2010). | 'the theory may revitalize ecology' (Hamilton 1968: 71); 'As a document for discussion, [MacArthur & Wilson 1967] can be highly recommended' (Goodall 1968: 904); 'a book which is very different from previous treatments of island biogeography…This book will permanently influence the nature of island studies' (Stoddart 1969: 781-782); aims to 'lead [island] biogeography out of the natural-history stage and to reformulate it in terms of first principles of population ecology and genetics' (Sauer 1969: 586); 'The authors visualize a meshing of new experimental data with quantitative theory that will galvanize [island] biogeography' (Sauer 1969: 588); 'a revolutionary influence' (Lynch & Johnson 1974: 383); 'established a clear framework for studies of island ecosystems' (Armstrong 1980: 494); 'a turning point in modern insular biogeography' (Heatwole et al. 1981: 20); 'an important conceptual advance' (Thornton 1996: 209); 'a turning point in the advance of ecological science' (May 2010: ix) |
| Concinnity. | Sophistication tempered by simplicity has facilitated comprehension of the theory. 'an elegant conceptual framework' (Armstrong 1979: 100); 'elegantly simple and intuitively appealing' (Brown 1986: 232); 'The attraction of the theory is undoubtedly its simplicity and its universality' (Williamson 1989: 3). |
| High heuristic value. Predictive nature of DETIB is that it provides a set of ideas offering new insights and viewpoints (Haila & Järvinen 1980). | 'The great value [of these models] is that, in being predictive, they compel reassessment of familiar data…by stimulating the reinterpretation of old data and suggesting the need for new' (Stoddart 1969: 782);; DETIB 'provided renewed interest in [island biogeography], stimulated research along new lines, and fostered an experimental approach to the subject' (Heatwole et al. 1981: 343; 'one of the most successful heuristic models in ecology' (SJ Wright 1985: 332). |
| Defects of DETIB are readily drawn attention to by its founders (MacArthur & Wilson 1967: 5, 64–65). The authors 'disarm criticism by frequently pointing out limitations and objections to their formulations' (Williamson 1969: 38) and 'admit to certain weaknesses and crudities in their models' (Sauer 1969: 589). | '…remote islands with their lower immigration rates also take longer to reach equilibrium. There is no need to assume that all islands have reached equilibrium.' (MacArthur 1972: 100); 'many islands on the continental shelf may have more than the equilibrium number' (MacArthur 1972: 101); 'The larger island may have a slightly higher immigration rate because it forms a larger target for immigrants to hit' (MacArthur 1972: 101); 'History even leaves its mark on equilibria, although how long its influence will be felt is unknown.' (MacArthur 1972: 247). |
| Extreme oversimplification. | The non-mathematical biologist is 'likely to miss many of the hidden assumptions, restrictions, and approximations which may be necessary to the validity of the argument, and which are not always incontestable' (Goodall 1968: 904); 'it is not clear that the real complexity has yet lent itself to a mathematical treatment that approximates physical reality' (Preston 1968: 592); islands are treated as 'functional units with no attention to internal habitat diversity' (JD Sauer 1969: 590); 'The immigration and extinction curves shown in the basic model are not derived from mathematical formulas but are artistic compromises between extremely wide possibilities (Sauer 1969: 589); 'too far removed from the diversity and complexity of island life itself' (Stoddart 1969: 782); 'The authors are in such a hurry to abandon the particulars of natural history for universal generalization that they lose the grand theme of natural history' (Sauer 1969: 590); '[DETIB] is essentially very simple, its intuitive simplicity being one of its more beguiling aspects' (Reed 1985: 23); 'the theory proposed seems a mixture of the self-evident with the unlikely, at the very least a vast oversimplification (Fosberg 1987: 418); 'the troublesome feature of the equilibrium theory is its oversimplification of the factors influencing the distribution of species among islands' (Wiens 1991: 169). |
| Lack of realism (too many simplifying assumptions made in the pursuit of broad generality) (JD Sauer 1969; Stoddart 1969; Lack 1970; Reed 1985). The neologism 'taurosod' was introduced by Lazell (2005: 138) to describe such a postulate. | The traditional view was ultra-realistic, i.e. to regard each island as a 'unique locus of species assembled for idiosyncratic reasons that can tell us little about other islands' (Simberloff 1974: 163). However, all models necessarily offer a compromise between realism, precision, and generality (Levins 1966). Explicit, patently unrealistic (i.e. idealising) assumptions facilitate study of the problem. 'A perfectly realistic model is just a dull imitation of nature' (Haila & Järvinen 1980). 'a theory is a lie which makes you see the truth' (Crowell 1986: 233, quoting a paraphrase by Robert MacArthur of a remark by Pablo Picasso). |

| Issue | Comment/example |
|---|---|
| Risk of reification and of ideas becoming a straightjacket (Swinebroad 1969; Slobodkin 2001). | Applicable to all worthwhile models. |
| Definition of what constitutes an immigration or extinction (Lynch & Johnson 1974; Järvinen 1985; Stoddart 1986: 277, Solem 1990). | The presence of a species as a vagrant does not constitute immigration. One propagule is not a colonist as soon as it arrives (Sauer 1969), as posited by MacArthur & Wilson (1967: 41, 64). Risk that databases 'in large part' consist of Crusoe species rather than established breeding populations (Solem 1983: 310). '[F]requent extinction is a signal that the system under study is not large enough to include the processes being studied' (FE Smith 1975: 5). |
| Extent to which interspecific competition shapes island biotas (Preston 1968: 594); Wiens 1977b; Järvinen 1985; Dueser & Porter 1986; Case & Cody 1987). | The 'number of other species is totally irrelevant for species unconditionally barred from the island by the absence of suitable habitats and also for those uniquely adapted to available niches' (JD Sauer 1969: 589). |
| Omission of consideration of the identity of species and thus of their ecology—species are treated as fungible when in reality not all species are equal (JD Sauer 1969; Reed 1985; Stoddart 1986: 277; Slobodkin 1996; Brown & Lomolino 2000). | Islands experience colonisation, extinction, and recolonisation 'at a great rate', yet islands are 'often' refugia populated by relict biotas that have become extinct on continents (Preston 1968: 592). Some dominant species, such as the ants *Pheidole megalacephala* and *Solenopsis geminata*, are aggressive to other ant species (Torres & Snelling 1997). Note, however, that measurement of species turnover does require species identification. |
| Role of historical legacies and geological and climatic changes overlooked (Case & Cody 1987; WR Turner & Tjørve 2005; Steadman 2006). | DETIB should be regarded as one of several competing theories that explain insular phenomena, e.g. species richness increases with area only for islands under the same climate (MacArthur & Wilson 1967: 8). |
| Role of environmental heterogeneity in determining species richness on islands inadequately considered (Williamson 1989). | Over-emphasis of island area as it is easily measured. MacArthur & Wilson (1967: 8) conceded that area 'seldom exerts a direct effect on a species' presence. More often area allows a large enough sample of habitats, which in turn control species occurrences'. 'Pure area effects are hard to sort out from effects of increasing environmental diversity as the sampled area is expanded' (JD Sauer 1969: 584). Effects of island area are 'usually completely masked' by elevation, wind direction, substratum, moisture and accidents of early colonisation (Fosberg1987: 418). |
| Interpretations of species richness are not based on the demography of each species considered separately (Goodall 1968; Dueser & Porter 1986). | Better to direct research to the factors that affect rates of immigration and extinction of species in different situations (Haila & Järvinen 1980). It is particularly useful to study the biological mechanisms thought to underlie the equilibrium interpretation. |
| Significance of the size of $z$ (the slope of the species–area curve) is predicted to increase more rapidly on distant islands than near islands. | Other factors can influence the occurrence of species on islands (Abbott 1983). |
| If islands are saturated with species (because of intense interspecific competition), why can species introduced to the adjacent mainland successfully establish on islands? | Continual increase of introduced plant species on Great Barrier Reef (Queensland) islands without displacement of native flora. Many introduced plant species occupy natural habitats and do not depend on habitats articially produced by human activities (Heatwole 1991). |
| If islands (because of limited resources) are saturated with species, why can species of native mammals be successfully introduced to islands? | Examples (Woinarski et al. 2014b): *Bettongia penicillata* (Wedge, Venus Bay SA); *Macropus eugenii* (Greenly, Wardang, Granite, Boston SA); *Petrogale lateralis* (S Pearson, Thistle, Wedge SA); *Potorous gilbertii* (Bald WA). |
| Purported rebalancing of biota as species become extinct on an island and new species establish: Gains and losses do not always involve close competitors (Abbott & Grant 1976). | Reconceptualisation is required: Instead of new entrants waiting to invade ecological communities and being repelled until a competitor becomes extinct, chance arrival and then establishment if ecological requirements are satisfied. |
| Amalgamation or premature comparison of incomplete data sets (Sauer 1969); Stoddart 1969; Lynch & Johnson 1974; Stoddart & Fosberg 1981; Hopkins & Harvey 1989; Steadman 2006). | Armchair biogeographers often too willing to presume that data available are reliable. |
| Validation of immigration and extinction of species impeded because of non-disclosure of identity of the species involved (Lynch & Johnson 1974). | Focus on numerical calculations of rates should not overshadow consideration of the biological attributes of the species involved. |
| Necessity of adducing biological facts about, and relevant observations of, species. | The sacred kingfisher bred on Rottnest Island in the 1980s (unlike in the 1950s) but this was associated with the presence of palm trees, which are not native to the island (Saunders & de Rebeira 2009). The house sparrow is limited to inhabited areas and has become extinct on formerly inhabited islands of Scotland (Reed et al. 1983). |

| Issue | Comment/example |
|---|---|
| Distance from source area and island area equally determine species richness. | Distance from source area is only of minor importance for Great Barrier Reef islands (Heatwole 1991). |
| Difficulties (subjectivity, arbitrariness) in determining if and when a balance exists between species becoming extinct and species establishing ('equilibrium') (Preston 1968; Abbott & Grant 1976; Pielou 1979; Simberloff 1983b). For example, either the number of species is a constant towards which the observed number of species is tending (but the biota is in non-equilibrium because of recent disturbance) or the biota is at equilibrium but the number of species varies with time because of variation in climate. | Numerous empirical studies show evidence of non-equilibrium (e.g. Batianoff 1998, 1999; Batianoff & Hacker 2000, JMB Smith & Heatwole 1985, TA Walker & Ogilvie 1988). |
| Predicted continual increase in species richness with increasing island area. | Cays in southern Great Barrier Reef level off in plant species richness once an area of c. 60 ha is attained, implying that further increase in island area does not add additional habitat, just more habitat of the same type (Heatwole 1984). |
| Confusion in distinguishing between colonisation of existing habitat and colonisation dependent on primary or secondary succession (Lynch & Johnson 1974). | 'of course the change in habitat as the island [Krakatau] became forested is responsible for some of this turnover, at least in the early decades' (MacArthur & Wilson 1967: 47). |
| r selection (species with high natality and mortality rates) cannot be important if species equilibrium is general (Haila & Järvinen 1980). | Implication is that k selected species (low natality and mortality rates) are most relevant to testing DETIB. |
| Species turnover is predicted by DETIB to apply uniformly to all species (Roughgarden 1995). | Some species ('core species') are always present, and others ('non-core species') may immigrate but not persist, or may become extinct and not re-immigrate. |
| Small islands are predicted by DETIB to have species randomly selected from the source pool (Roughgarden 1995). | Nested subsets of species are suggestive of deterministic effects and not of turnover. |
| Species turnover should not be associated directly with human activities on islands or applied to islands highly modified by human activity (Thornton 1996; Steadman 2006). | 'turnover should reflect the stochastic nature of an equilibrium condition (i.e., the turnover should not be attributable to some systematic bias, such as ecological succession, human disturbance of habitats, introduction of exotic species, etc.)' (Lynch & Johnson 1974: 371). |
| Use of heterogeneous groups of species may be inappropriate (Thornton 1996). | For example, plant species with different modes of dispersal. |
| Immigration and extinction are independent opposing forces (Brown & Lomolino 2000). | Extinction is not affected only by island area, but also by proximity to the source (an early anticipation by Sauer 1969 of the rescue hypothesis); immigration is not affected only by isolation, but also by the pool of species that can reach an island and the area of the target island (Sauer 1969). |
| Rates of immigration & extinction are sufficiently high that contemporary patterns of species richness and composition result from a dynamic equilibrium between these opposing rates (Brown & Lomolino 2000). | DETIB overlooks the role of human disturbance on source area and island, as well as the fact that arrivals often are too few to establish a population. |
| Unnecessarily mathematical. | 'Some will object that the mathematical analysis is unnecessarily complex when compared with the conclusions reached' (Stoddart 1969: 781); The 'ideas were not presented simply or clearly, but were elaborated and expressed in intricate mathematical…terms. Little was gained in either clarity or understanding by this lengthy exercise' (Fosberg 1987: 418). Mathematics sometimes 'used to baffle and dazzle, rather than illuminate' (Lazell 2005: 2). |

on ecosystem function and structure. Moreover, the processes of immigration and extinction are seldom amenable to direct study (Stoddart 1986).

We disagree with the conclusion that island biogeography, as a result of DETIB, has changed 'from an idiographic discipline with few organizing principles to a nomothetic science with predictive general laws' (Simberloff 1974: 178). However, we suggest that it is premature to dismiss DETIB as a useful theory, as claimed by HS Walter (2004), or accept that it has been largely superseded (as claimed by Lomolino 2000) or should be regarded as a failed paradigm (Table 19). Simberloff (1976b) and TW Schoener (2010) provide evidence consistent with our opinion. Nor do we accept that DETIB fits the definition of a fad as discussed by Abrahamson et al. (1989). Disappointingly, even the most prized of ecological studies—those conducted for long periods—have failed to clarify the existence of species equilibrium. It remains unclear whether the species richness of plants on cays in the Bahamas represents a non-equilibrium system or part of a natural oscillation around a long-term equilibrium (Morrison 2010, 2013).

Although we admire the transformative vision of the originators of DETIB and acknowledge its substantial imprint on the discipline of island biogeography, this theory is not as universal as claimed by MacArthur and Wilson (1967). It also has many shortcomings (Table 19). We thus propose an alternative perspective, not particularly novel, but a modernised revival of the approach to island biogeography prevalent until the 1960s (JD Sauer 1969; Van Balgooy 1969). We do not think that this approach fits the rather glib characterisation 'increasingly elaborate narrative description' of Simberloff (1983b: 78).

To contribute to the development of theory, this approach requires:

(1). A database of islands that contains comprehensive, accurate and relevant geographical and biological information.

(2). Astute comparisons and contrasts between sets of islands of the information synthesised from this database and other sources.

(3). Recognition of a broader set of key factors influencing changes in biodiversity on islands.

(4). Acknowledgement that biotas are the result of a blend of dynamic and stabilising processes (historical and current), so that there is a continuum with some islands having non-equilibrial biotas (e.g. isolated continental islands) and others having equilibrial biotas (e.g. small, close islands; Crowell 1986).

(5). Realisation that some species show continuous occurrence and others may at times be either present or absent (Morrison 2013).

A good start has been made with (1) the compilation of databases (e.g. Lawlor 1986), but analyses have faltered on (3), with island area and measures of isolation only being considered. Crowell (1986) has addressed (4) adroitly. Point (5) requires improved knowledge of the ecology both of island and mainland species.

The narrative and equilibrium approaches of course have their strengths and weaknesses. In recent decades, several authors (Solem 1990; Mayer & Chipley 1992; Torres & Snelling 1997; Lazell 2005; Steadman 2006) have challenged the value of the equilibrium theory, with some offering more of a return to the narrative viewpoint. Dynamic equilibrium has not proved to be the unifying theme of island biogeography that it promised to be in the 1960s.

DETIB has been much debated during the past 50 years, and the study of many additional islands has augmented data that were not available to MacArthur and Wilson (1963, 1967). Disregarding DETIB at this stage seems inappropriate and premature, for several reasons. By our reckoning (extrapolated from Fig. 1b), there are almost one million islands currently present in the world, with perhaps <1% of these studied to the extent that an accurate listing of species of at least one higher taxon (plants, birds, ants, mammals) has been completed. Even fewer islands have been studied adequately enough to examine changes in biodiversity (species turnover). Furthermore, the islands studied have tended to be close to major cities (convenient for study), remote and thus enticing to biologists (not typical of the world's islands), or relatively little impacted by humans. In our view, a more cautious approach is warranted before DETIB is rejected, as unrepresentative sampling may have led to bias.

This prudent approach has been adopted by Frey et al. (2007), who have proposed four island biogeographic models, named as: Equilibrium (DETIB); non-equilibrium vicariant; non-equilibrium relaxation; and non-equilibrium island age. The attributes of island area, isolation and age influence species richness in different ways in these models.

Another source of bias is that biologists tend to avoid studying the most numerous type of island, those that are small (<1 km$^2$) (Fig. 1) and those close to a larger land mass. Indeed, it has been suggested that very small islands may be 'bad examples of biogeographical laws due to the stochastic problems associated with small population sizes' (FS Gilbert 1980: 224). With very small sandy islets, this may include physical instability (Flood & Heatwole 1986; MacArthur & Wilson 1967). An additional source of bias is that most studies of insular biodiversity focus on vascular flora, landbirds or land mammals; these taxa comprise only c. 1–5% of biodiversity. Given these several sources of bias, can we be confident that DETIB has been fairly tested?

Like all theories, DETIB presented an idealised set of circumstances. A useful analogy for MacArthur and Wilson's bold, simple and elegant theory is the important advance made in understanding change and motion by each of the pre-Socratic philosophers (Popper 1963: 136-165). The first of these, Thales of Miletus, attempted to provide a cosmology based on water as the ultimate foundation of the universe. Later philosophers disagreed, and offered alternative conjectures based on air, fire and earth. It took c. 2000 years for a more developed understanding of the issue to eventuate. Ideas held by the ancient Greeks about islands are similarly crude (Heatwole et al. 1981). MacArthur and Wilson's theory is likely to remain a key benchmark which subsequent island biogeographers should not dismiss lightly. We also think that some biologists have an unrealistic expectation that theories necessarily are universally applicable, leading to a false expectation of the existence of the biological equivalent of the laws of physics (cf. Bartholomew 1982).

Just as the pioneering and rather heroic efforts of the pre-Socratics played a useful role in developing theory in cosmology, the modernity of MacArthur and Wilson's key simplifying concept of dynamic equilibrium between immigration and extinction rates provides the essential and ongoing context for assessing the nature and evolution of biodiversity on islands.

DETIB is most likely, however, to become a special case in a more general theory of insular biogeography (Haila 1990; Whittaker 1998). Two major criticisms of the MacArthur–Wilson model are that it unnecessarily over-emphasises, and fails to substantiate, the role of interspecific competition in explaining failure of some species to establish (e.g. MacArthur & Wilson 1967; Wiens 1991) and under-estimates local habitat as a major factor (Abbott 1980b). Interspecific competition is not an essential part of the dynamic equilibrium concept but simply reflects the strong emphasis given to this factor in the conventional ecological wisdom of the 1960s, as well as the narrow focus of ecology during this period (Rohde 2013). An example of this legacy is the perspective of islands as 'experiments in competition' (Gorman 1979). It is noteworthy that Thornton (1996) took a cautious approach to invoking interspecific competition to explain the absence of various species from Krakatau. Other limitations or questionable assumptions of DETIB (summarised in Table 19) have been discussed by Connor and Simberloff (1979), FS Gilbert (1980), Goodall (1968), Jehl and Parkes (1983), Preston (1968), JD Sauer (1969) and Williamson (1981).

On occasion, criticism of DETIB has been unnecessarily captious (Sismondo 2000). For example, the avifauna of three vegetated islands comprising the Islas Revillagigedo was used to question the theory (HS Walter 1998). The 16 landbird species present, at least since the 1860s when livestock was introduced, persisted until the 1930s. However, the remoteness of the islands (>400 km from Mexico), the large area of the islands (14,000, 2800 and 630 ha), and their elevated nature (330–1040 m) had served to minimise natural extinction and immigration before human settlement altered the natural vegetation. The stability of these island avifaunas is, however, not inconsistent with DETIB.

Rosenzweig (1995) has provided a useful appraisal of some of the studies stimulated by DETIB. However, a pressing need is for a comprehensive, rigorous, and objective review of the many papers published since 1967 that purport to test DETIB. This should, based on our extensive knowledge of this literature, reinforce several of the points raised above.

## An alternative approach: Comprehensive synthesis of existing empirical information

In the past, researchers have selected islands for study, usually with reference to the adjacent mainland and evaluation of the role of island area, elevation and isolation. We offer a simpler alternative to the approach called for by Heaney (1986) and Lomolino (2000). While it appears that the key concepts of island biogeography are well established, insufficient use has been made of the vast (mostly unco-ordinated) amount of empirical information available about islands, their environments and their biotas (e.g. Fosberg 1983; Van Balgooy 1969). A holistic perspective embraces the Humboldtean approach. This does not overemphasise reductionist analysis; rather, it adopts a broad, comprehensive theoretical viewpoint that acknowledges extreme complexity (Mayr 1961) and focuses on chains of connections between human, biotic, and abiotic factors, particularly those that are mutually dependent upon one another (Hercock 1998a). The ultimate aim is coherent synthesis of the parts to form a whole. In addition, the framework outlined here has implications for a global perspective, and may also contribute to the development of new or improved paradigms.

The key components of this framework may be outlined as follows:

- Location and cultural history of an island are paramount.
- Primary factors influencing biotas on islands differ among species and higher taxa.
- Productivity and disturbance are key factors influencing island biodiversity.
- Special local factors can impact on biodiversity.
- Ongoing change in insular biotas is best explained by a punctuated equilibrium perspective.

### *Location and cultural history*

If a previously undiscovered island were to be found next year, our first question would not be how large or how isolated it is, but where is it? The more general concept of geographic location (latitude, longitude) embodies the key concepts of climate, productivity, island type, and exposure to wind and the toxic nutrient chloride. All of these factors convey more useful information than area or isolation. Knowing in which zoogeographical realm the island is located, particularly whether an island is situated near the poles or in the tropics, is oceanic or a detached piece of a larger landmass (island or continent), is of great antiquity, and has a human history will immediately help characterise the expected nature of biodiversity and the size of the biota (Sauer 1969). Furthermore, the size of the source pool decreases with increasing isolation and latitude, and both of these factors will influence immigration rates (TE Martin 1981).

If the island is continental or land bridge, local extinctions will have predominated and in situ speciation will be negligible, except for non-flying invertebrates. If the island is oceanic (i.e. empty of species when physically created), founder and priority effects may be pronounced.

MacArthur and Wilson (1967: 8) used island area because 'good information on diversity of habitats' was lacking. They recognised that area itself seldom exerted a direct effect on a species' presence, but noted that large islands often had more habitats present than small islands. They also emphasised the primacy of island area by presuming that the orderly relationship between area and number of species applied within a region that is 'more or less uniform in climate and topography' (pp. 8, 13, 17), thus selectively excluding climate and topography when geographically-broader studies are performed. MacArthur and Wilson (1967) viewed ecological differences among islands as a source of distortion of the species–area relationship. Similarly, JM Diamond (1984c) regarded island differences in factors other than area as of minor importance, utilising these as one of several 'simplifying assumptions'.

Rosenzweig (1995: 377, 381) identified area as the 'primary regulator' of species richness on islands and advocated that its role be taken into account first 'before we can assess the role of another variable'. We, for the reasons outlined previously in this review, find this overly prescriptive. However, we do concur with his suggestion of the appropriateness of what he termed 'guided multiple linear regression', i.e. forcing 'the variables you already know must be accounted for' (Rosenzweig 1995: 378).

Because most islands are small, the risk of inundation and the degree of exposure to wind and seaspray are of the utmost importance (Fig. 3). A small island exposed to direct wave action has fewer species than a nearby island that is sheltered (examples in Abbott 1980e; Abbott & Black 1980). Small islands protected by reefs are more likely to support biota than if they rise sheer from the ocean floor (cf. Abbott 1977a; Abbott & Black 1980). In the Archipelago of the Recherche WA, Salisbury Island (316 ha) has its long axis aligned along the predominant wind direction. Lacking a sheltered side, none of its vegetation is taller than heath. Woody Island (188 ha) lies across the prevailing wind direction and has retained patches of forest (Abbott & Black 1978).

By cultural history, we are referring to the extent to which the island has been or is being affected by humans, both Aboriginal and European. So if our newly discovered island were unoccupied by humans, it would have a richer biodiversity than if it were settled. If the latter, some or all of the original vegetation will have been cleared (e.g. St Helena), natural resources will have been exploited (e.g. trees felled for fuel, seals and sea birds reduced in population size), vegetation will have been burned, much of the vegetation will be in secondary succession, and weeds, herbivores and predators will have been introduced. Familiar examples include the British Isles, Polynesia, and Australia. Probably the world's least disturbed islands are those of south-west WA and South Australia, where Aborigines lacked the technology of watercraft (Abbott 1980c). These islands remained unvisited by humans for c. 7 ka until 1616 CE, when Europeans briefly landed on Dirk Hartog Island.

MacArthur and Wilson (1967: 64) were dismissive of island history when they referred to 'the individual vagaries of island history' and relegated history to being necessary only to understanding the taxonomic composition of island biotas. Subsequent studies have demonstrated otherwise (e.g. Lawlor 1986; Fattorini 2007b). In his final publication, Robert MacArthur did acknowledge the importance of history, conceding that it 'even leaves its mark on equilibria' (MacArthur 1972: 247).

## Primary factors differ among species and higher taxa

This concept was not incorporated into DETIB. It is a fact that the likelihood of extinction or immigration differs among species. For example, species differ inherently in their capacity to cross water. Animals with wings have an advantage, although many winged species may be psychologically unwilling to cross water. Thus, some bird species present in southern Victoria or coastal South Australia have never been recorded on Tasmania or Kangaroo Island respectively (Abbott 1973, 1974a). For plant species, the size of the diaspore is important, with small spores and seeds more likely to be aerially dispersed than would large or heavy seeds. Terrestrial animal species differ in their swimming ability; the agile wallaby (*Macropus agilis*) is an excellent swimmer whereas most other marsupials are not. Species that flock are more likely to establish viable populations e.g. species in the bird genus *Zosterops* (Abbott 1974d). In summary, species biology is important in explaining the presence or absence of species.

## Productivity and disturbance

Disturbance can bring either temporary instability or permanent change to island biotas, according to the type of disturbance and its magnitude, areal extent and transience. Islands damaged by volcanic eruptions or newly formed as a result of volcanic activity have constituted a popular focus of research (Thornton 2007). Such studies, however, essentially document the process of primary succession, without the necessary parallel studies of the source area. They are thus of little interest to the island ecologist. In contrast, islands that are formed from deposition of sand on reefs (cays) lack an equivalent on the mainland, but are more relevant to understanding the processes of island colonisation (Flood & Heatwole 1986; Heatwole 1991; JMB Smith et al. 1990).

According to our reckoning, only 74 islands of the world exceed 10,000 km$^2$ (one million hectares) in area. A species–area plot would not, however, yield the expected strong linear relationship because 26 of these islands have the low productivity associated with cold or ice-bound landscapes (the tundra islands of northern Canada and the barren islands of northern Russia). As noted by Williamson (1981: 16), the 'obvious and general point that the biota of an island will reflect its climatic type is often overlooked in theoretical discussions'.

Islands that have experienced environmental extremes (in terms of duration, intensity or regularity) such as glaciation (e.g. northern Canadian islands), cyclones or hurricanes (cays washed over by waves) and vulcanism (lava flows as on Isabela [Galápagos], Krakatau, Surtsey, White Island/Whakaari [New Zealand]) also have impoverished biotas.

Even in tropical environments, climatic differences among islands can be significant (Mueller-Dombois & Fosberg 1998). For example, in the Marshall Islands, the native vascular flora is least in the driest, northern islands and greatest in the wet, southern atolls (Fosberg 1990).

With small islands, disturbance in the form of total or partial inundation by waves, resulting in removal of soil, together with pulses of deposited chloride ions, are crucial in inhibiting the establishment of vegetation. The interplay between island area, elevation, topography and protection from the predominant wind direction facilitates successful colonisation and persistence of plant species (Fig. 3). It is surprising that investigators of food-web organisation have not followed the lead set by Heatwole (1971) in studying the naturally simple ecosystems of small islands. As stated by Fosberg (1987: 418-419), 'Only a far more complete collection and recording of numbers of species on islands, their ecology, habitats, and geographical relationships, and the nature and direction of change in their numbers, will give a proper assessment of the validity of the MacArthur and Wilson equilibrium theory of island biogeography'. One intriguing study, of land snails on islands in the Aegean Sea, implicated disturbance by humans in creating new habitats on small islands, thereby increasing species richness. Larger islands have fewer species as a result of habitat destruction (Mylonas 1984). Stoddart and Walsh (1992) have provided a useful overview of disturbances and related factors relevant to islands.

The dynamic equilibrium model of Huston (1994, 2014), which links biodiversity to levels of productivity and disturbance, merits application to the biogeographical study of islands. This is probably best done first at the regional level, then global level, if the equivalent of the various disturbing factors (e.g. intense low depressions, droughts, fires, floods) can be calculated objectively. The model predicts that species richness is greatest on islands with low productivity (low population growth) when disturbance is low (causing low mortality), and also greatest on islands with high productivity (high population growth) when disturbance is high (causing high mortality and suppressing competitive dominance). Clearly, however, islands will need to be matched for area, isolation and other factors as identified in Figure 3. We would expect the location of islands along the maximum diversity diagonal (Huston 1994) to group according to island area and distance to the source area.

Another method of applying this model to islands would be to record biodiversity at quadrat-level within islands. Quadrats would be located in seabird colonies (seabirds nesting in burrows increase soil nutrients but do not trample vegetation; surface-nesting seabirds trample vegetation as well as enriching soil nutrients), distant from seabird colonies, in exposed sites (high chloride input), and sheltered sites.

It is an attractive idea that a combination of productivity and disturbance factors may help explain why the biodiversity of continental islands has become depleted during a period of c. 70–100 centuries. However, human activities are not essential for changes in biodiversity to take place. This is well illustrated by the mammal fauna of the 24,000 ha Barrow Island near the north-western coast of WA (Baynes & Jones 1993). On continental islands the sequential local extinction of large species of carnivores and herbivores (with large home ranges and hence smaller population sizes) should have had far reaching consequences on the ecology of prey species and plant species. However, we must avoid the presumption that all species currently present on the adjacent mainland were present there at the time of isolation (e.g. Richman et al. 1988). It is just as likely that many species found currently on the mainland arrived there after the sea level rose, the so-called post-glacial intrusives (Littlejohn & Martin 1965).

## *Special local factors*

Sometimes knowledge of unusual local factors on islands is necessary to explain unexpected biodiversity patterns. For example, species richness of plants on small islands may be modified by large colonies of nesting sea birds and pinnipeds, which induce soil toxicity and trample vegetation (Gillham 1961a; Vidal et al. 1998). Islands with diverse soil types may support a larger flora than if only one soil type were present (e.g. South Australian and WA granite islands with and without an aeolianite mantle have soils with different pH). Presence of hills introduces topographical gradients that may increase habitat heterogeneity and biodiversity. Plantations of woodlands on otherwise treeless islands may also enrich the avifauna (Cunningham 1979; Reed 1982; Reed et al. 1983).

## *Change in biodiversity in terms of a punctuated equilibrium model*

Changes in biodiversity (species turnover and abundance) can be an elusive concept unless related thoughtfully to space and time scales. MacArthur and

Wilson (1967: 41) defined a propagule to be a colonist 'as soon as it lands on an island'. One of the most telling criticisms of DETIB concerns the trivial nature of much species turnover. For example, most sexually reproducing species arriving on islands as single individuals have no chance of establishing a population. Although MacArthur and Wilson (1967) recognised that the occurrence of rare, transient species inflated the size of the biota present on mainland area, 'sink' species are actually an irrelevant part of island biotas (Rosenzweig 1995).

It is reasonable to suppose that most, if not all, ongoing change in biodiversity on islands is caused by natural disturbances, including extreme weather events, volcanic eruptions, climatic changes and those related to human occupation, both on the island and on the adjacent mainland. Most of these changes are small, of the sort to which allusion was made above. Occasionally, large changes occur, with the most dramatic being the biotic relaxation of continental islands following the close of the last glacial period, the waves of immigration and extinction coinciding with major changes in habitat resulting from volcanic disturbance (Thornton 1996), and the colonisation of islands by humans (Polynesians, Vikings, Portuguese, Spanish, Dutch, French and English) in the past 150–1000 years. We concur with the conclusion of Mueller-Dombois (1981) that if humans had not entered the island environment as a new dispersal agent, island ecosystems could be considered biologically very stable. Large changes will still occur occasionally. In addition, future alteration in the geographical configuration of islands will necessarily result in island biotas. For example, many of the world's continental islands will in the next glacial period join to the mainland. In the more distant future, Australia and its islands, through continental drift, will in c. 50 Ma lie close to China. It is important to note that not even large islands are exempt from extinctions (Steadman et al. 1999).

These examples suggest that when a long-term scale is taken, for most of this period few changes in biodiversity will take place. Island life is uneventful. Change is discontinuous. Occasionally there will be dramatic increases or reductions in biodiversity with a new equilibrium being established. This pattern of stasis ('semper idem') and occasional abrupt episodes of change seems to accord best with the well-known model of punctuated equilibrium proposed by Eldredge and Gould (1972).

Finally, we concur with the emphasis that WR Turner and Tjørve (2005) place on avoiding searches for single causal factors in explaining variation in species diversity on islands. It is more appropriate to adopt a pluralist perspective and view species diversity as the outcome of numerous potentially interacting processes, as outlined in Figure 4. A 'bottom-up' approach, of determining the factors that best predict the occurrence on islands of each species, should be more informative than predicting species richness (Adler & Wilson 1985).

## A proposed new global 'research program' for island ecology and biogeography

The Hungaro-British philosopher and historian of science Imre Lakatos (1922–1974) developed the concept of the 'research program' to represent a particular set of ideas, hypotheses and methodologies found useful by one or more groups of scientists (Chalmers 1999; Oldroyd 1986). The research program collectively embodies the interesting problems worth solving, the non-problems (i.e. those considered irrelevant or insoluble), and the standard of evidence required; in doing so, it sharpens the contrast with research programs of competing scientific groups. Hypotheses considered fundamental (unalterable) to the research program are termed 'hard core', whereas those more peripheral and readily modifiable are termed the 'protective belt'. These latter hypotheses serve to protect the 'hardcore' from falsification, thereby allowing the research program to realise its full potential. Research programs that require ad hoc changes to the protective belt in order to retain coherence are termed 'degenerating'.

DETIB is now widely considered to be a degenerating research program, in Lakatos' terminology. Haila (1986) offered a similar viewpoint, and emphasised that a paradigm may suppress creative research for alternative approaches. The concept of interspecific competition being the prime factor influencing island ecology also appears to fit the description of a 'degenerating' research program (Lewin 1983). Lakatos' concepts have been overlooked in a recent review of the theories of island biogeography (Lomolino & Brown 2009), as has criticism of TS Kuhn's ideas of scientific revolutions by Stoddart (1986).

The key element of the research program proposed here is that considerably more systematic comparative studies at different scales are needed. See, for example, possible mangrove studies suggested by Bowden (1995) and many other useful topics suggested by Ewel and Högberg (1995). By assembling the available empirical data currently scattered in many hundreds of scientific papers and books, it should be possible to synthesise in a methodical way lists of species for various taxa and consider the implications of such lists in a context of integrated information on geography, history, productivity and disturbance. The major risk would be to fail to balance the environmental complexities of individual islands with valid generalisations applicable to all islands and avoid exaggerating either.

The first step is assembling a database of the world's islands (Table 20). Although the study by Kalmar and Currie (2006) of birds is based on an impressive global data set of 346 islands, it neglects many Australian islands for which pertinent information is readily available.

The second step is to search for all relevant papers about the vegetation of islands and then standardise the vegetation types to a common structural framework. Information collected about the vegetation and biota of

**Table 20**

Points requiring explicit consideration when collating, and before analysing, data sets.

| Issue | Recommendation | Rationale |
|---|---|---|
| Distinguish types of islands | Analyse separately oceanic islands (never connected to a continent) and continental islands (last connected to a continent in the late Pleistocene to early Holocene epoch) | All species on oceanic islands had to disperse overwater from somewhere else |
| Distinguish freshwater species from terrestrial species | Analyse separately | Aquatic habitat differs from habitat formed by terrestrial vegetation |
| Distinguish vagrant from breeding species | Records of species occurring casually or accidentally on islands should not be combined with those of breeding species (either resident or visiting) | The variable 'species richness' depends on accurate inclusion of species and comparison of island biotas on the same basis |
| Eliminate bias in the search for relevant publications | Global synthesis requires a concerted attempt to obtain all relevant information, and this entails recognition of the value of all journals irrespective of their international ranking | Regional journals should not be overlooked in the discovery of lists of island species |

subsets of the world's islands could then be compared and contrasted with considerable ease. Van Balgooy (1969) has made a worthwhile, although not completely satisfactory, start with his analysis of 68 islands. It is unacceptable to compile information from field guides. Lists of bird species for Australian islands (identity not disclosed) were derived from a 1980 edition of one field guide by Kalmar and Currie (2006), and no attempt was made to discover papers available in journals.

The two steps outlined above should allow better hypotheses to be formulated, which would then serve to re-invigorate field research on islands, as well as fill in gaps in information. As noted by MacArthur and Wilson (1967), the variation in area, degree of isolation, and other attributes provides the requisite replications by which hypotheses can be scrutinised. However, a return to the approach prevailing before DETIB of a 'mass of detail and air of travelogue' (Williamson 1989: 3) is not being advocated by us. The challenge is rather to seek universality by epitomising the general characteristics from many studies of specific islands from all parts of the world. Finally, the tendency to imply general applicability (or even universality) from local or regional studies must be resisted (Haila et al. 1982). The conclusions of such studies do no more than point to the need to test them on other islands. We await with great interest the broad synthesis of the thousands of papers that have been published to date.

For those islands that are most prevalent globally (i.e. those with areas between 1 ha and 1000 km$^2$ in area), it should be possible to compile databases that are geographically balanced (i.e. inclusive of islands from all regions of the world).

The following lists and itemises some possible foci of the proposed research program:

- The world's 74 largest islands (area >10,000 km$^2$).
- The world's remotest islands (Abbott 1974b; Chown et al. 1998).
- The world's newest islands.
- The world's oldest (oceanic) islands.
- Islands in archipelagoes, e.g. West Indies, Canary Islands, Scilly Isles, Shetland islands, Orkney islands, Hebrides islands, Adriatic Sea, Aegean Archipelago, Seychelles, Philippines, Sir Joseph Banks Group, New Zealand, Hawaiian Islands, Alexander Archipelago and Galápagos Islands. The comparison of the Hawaiian and Galápagos islands demonstrates what can be achieved (Loope et al. 1988).
- Islands close to the mainland, especially those connected intermittently to the mainland. In addition, along the eastern coast of Australia, many inshore islands have been captured in the last c. 5 ka by the mainland and now form capes, peninsulas, or promontories.
- Islands in arcs or chains, e.g. Kuril Islands, Aleutian Islands, Lesser Antilles (West Indies), Philippines and Florida keys).
- Islands actively, regularly or considerably disturbed by abiotic factors, e.g. ice, volcanic eruptions, inundation, salt-laden winds or tropical cyclones.

It is also desirable to compare islands similar in, for example, area. The area categories listed below are purely illustrative. Other area categories could equally validly be selected (e.g. 5000 km$^2$; 50,000 ha; 5000 ha). Other plausible categories are islands of similar area 1, 5, 50 or 100 km offshore.

- Islands ≤1 ha in area.
- Islands c. 10 ha in area.
- Islands c. 100 ha in area, e.g. Inishbarra, Skokholm, Kaunissaari, Ramsø, Aix, Riou, Ventotene, Todos Santos Sur, Michaelmas, Roxby, South Neptune, Trefoil, North West (Queensland) and Nui).

- Islands c. 1000 ha in area, e.g. Likiep (Marshall Islands), Middle (Archipelago of the Recherche), Badger (Tasmania), Femø, Canna, Youra, Pianosa, Capri, Le Levant, Megisti, Inishbofin and Hog (Virginia).
- Islands c. 10,000 ha in area, e.g. Unst, Rhum, St Agnes, Laesø, Sylt, Formentera, Kythnos, Kalimnos, Mljet, Santa Maria (Azores), Ascension, Badu, Espiritu Santo (Mexico) and Easter.
- Islands c. 1000 km$^2$ in area, e.g. Shetland (main island), Hiiumaa, Martinique, Njazidia (Grande Comore), Great Nicobar, Ternate, King (Tasmania), Normanby, Banks (British Columbia), Angel de la Guarda, Upolo, Tahiti and Santa Cruz (Galápagos).
- Islands c. 10,000 km$^2$ in area, e.g. Prince Charles, Bylot, Eilef Ringnes, Jamaica, Hawai'i, Viti Levu, Mindoro, Sumba and Bangka.

The theme 'islands disturbed by humans' has been adequately studied (Wace 1978, as well as many hundreds of papers). This theme actually requires the implementation of practical measures, particularly the assessment, management and mitigation of risk set in an adaptive management framework.

All of the well-known features of the 'classic island', including endemism, archaic species, disharmonic composition, degree of unsaturation of the biota, nanism, gigantism, density compensation by some species, and phenotypic and genetic change, should be included in the research program.

Studies of species turnover *sensu stricto* (i.e. uninfluenced by human activity on islands and source areas) should be directed to those remote or inaccessible islands that have offered, or continue to offer, few opportunities or enticements for humans to visit. In Australia, candidate islands include cays in the Coral Sea (remote and little disturbed since guano diggers were active during the period 1860–90; Telford 1993b; Bourne et al. 2005) and cliff-girt islands along the southern coast (landing on which requires a helicopter).

Although MacArthur and Wilson (1967) recommended that biotas of small islands be manipulated experimentally (local extinction by manual means or by poisoning), such research activities are ethically dubious. Few have been tried (EO Wilson & Simberloff 1969; Levins & Heatwole 1973; Rey 1981). Similarly, the introduction of species as a means of studying interspecific competition (Nevo et al. 1972) or persistence (Crowell 1983; TW Schoener & Schoener 1983b; Morrison 2011) ought to be regarded with circumspection. Non-scientists have already intentionally or accidentally 'experimented' on islands and there are now few islands that have escaped impact by humans, such as deforestation, reforestation, and introduction of predators or competitors. It is these modified islands to which biogeographers should direct their attention in gaining a better understanding of how changes in biodiversity caused by anthropogenic processes can be reversed.

After detailed consideration of the use of one factor (in this case, island area) to predict species richness, Boecklen and Gotelli (1984) suggested that models derived from this approach should be subordinate to autecological matters. Species identity, habitat heterogeneity, population size, habitat requirements, minimum area, disturbance regime, resource availability and human impact cannot be neglected.

## Nature conservation on Western Australian islands

In contrast to the pessimistic outlook on the future of oceanic islands of Heywood (2011), we are very optimistic about the future of biodiversity on WA islands if current policies, management and monitoring are maintained and strengthened as recommended below. Many WA islands possess important natural advantages that have minimised human activities inimical to nature conservation (Abbott 2006). First, all of the coastal Aboriginal people of south-west WA lacked watercraft, so that islands beyond wading distance remained undisturbed by human intrusion. Second, European visitors and colonists were unimpressed by the infertile soils (also shared with the mainland coast). The coastal climate was also unfavourable to the growing of wheat. Thus, there was little incentive to farm on islands. Third, most south-west WA islands are too small and waterless during summer to provide economies of scale necessary for profitable depasturing of cattle and sheep. Finally, the islands of the Pilbara and Kimberley regions were until the 1860s and 1880s respectively too remote from Perth to interest graziers. Most of these islands were also too small and unproductive to match the financial returns that could instead be secured from the very large holdings available in the hinterland.

Nonetheless, the presence of humans on islands is not necessarily inimical to the conservation of nature. WA provides two outstanding examples of the coexistence possible between biodiversity and naval and mining infrastructure. Garden Island (site of a naval base) and Barrow Island (an oil and natural gas extraction hub) are well managed from a nature conservation perspective. The industrial users of these islands have also been historically supportive of ecological research and monitoring, well before the strict conditions set in recent times by governments (Butler 1983, 1987; MG Brooker et al. 1995a, 1995b, 1996; Heatwole & Butler 1981; Lagdon & Moro 2013; Pearson et al. 2002a, 2002b; DH Perry 1972; Sedgwick 1978; LA Smith 1976; Smithers 1984a, 1984b, 1985, 1988; Smithers & Butler 1983; Wykes et al. 1999). The factor in common between both islands is that the navy and the mining company have complete control over all human access (Sedgwick 1978; Department of Defence 1993). Both islands have provided practical models of the successful operation of environmental management and monitoring programs, adopted subsequently by the oil and natural gas industry on Thevenard and Varanus islands (LeProvost et al. 1988; WAPET 1991).

As detailed by Abbott (2006), most human activities involving WA islands have been shaped by convenience (proximity to towns, presence of a lighthouse station on islands along well used shipping routes, absence of dingoes), presence of highly desired produce or products (seals, guano, whales, iron ore, oil), or strategic considerations (defence). These activities differ in intensity, frequency and duration, and thus their impact on insular nature varies from small, intermittent or short-term effects to large, continuous or permanent ones (Abbott 2006). Often the indirect factors such as the deliberate or inadvertent release of goats, cats, rats, and rabbits have had greater deleterious effect upon the indigenous island flora and fauna than has habitat destruction caused directly by humans.

All WA islands continue to face a period of acute uncertainty, with the ever present possibility of introduction of invasive ants, rats, cats, mice, mongoose, weeds, and disease. These factors constitute the primary threat to nature conservation on WA islands (AA Burbidge et al. 1997; G Keighery 1993; MT Lohr & Keighery 2014, 2016). The survival of island populations thus becomes precarious in proportion to the presence of these detrimental species. Frequent monitoring of islands should allow early detection of these species, rapid management responses, and avoidance of a tipping point being reached (Laurance et al. 2011).

The remainder of this section briefly outlines the history of nature conservation on WA islands (Whittell 1946 provides a succinct overview of the history of faunal legislation in WA). Proclamations by the Governor of WA, declaring islands as reserves for 'native game' under the Game Act and thereby prohibiting shooting, were issued at a slow pace after the first one, Houtman Abrolhos (all islands). This also included the taking of birds' eggs (*WA Government Gazette* 10 June 1898: 1644). Then followed Pelican Island (Shark Bay, *WA Government Gazette* 15 March 1900: 931).

It took the lengthy collecting expedition by the zoologist GC Shortridge to highlight the value of islands in conserving WA mammal species (*The West Australian* 25 December 1906: 2). His comments were reported as follows: 'if all of the small islands off the coast were made Government reserves…or at least if the native mammals on them were strictly preserved, it would ensure against the extermination of fourteen kinds of native mammals, ten of which do not occur or are getting very rare on the mainland. Many of the islands are of little or no value for any other purpose'. The islands noted by Shortridge as having wallabies present were Barrow, Dampier Archipelago, Bernier, Dorre, Houtman Abrolhos, Rottnest, Garden and Archipelago of the Recherche.

Shortridge reiterated the importance of islands in protecting wallabies almost extinct on mainland WA just before his departure from WA (*The West Australian* 18 June 1907: 7). The next day this newspaper editorialised on the matter, criticising the government for having done 'little in the past' and having decreased the number of scientists employed by it.

The issue was then taken up by the WA Natural History Society, which petitioned the government to reserve Barrow, Bernier, Dorre and Mondrain islands for the protection of native mammal species occurring there (*The West Australian* 28 September 1907: 5; Woodward 1907).

Further proclamations followed this agitation: Dorre Island (*WA Government Gazette* 2 August 1907: 2534; rescinded 5 November 1909: 3533; re-instated 27 June 1913: 2109); Barrow Island (*WA Government Gazette* 27 November 1908: 3239; declared Class A in 1910); Bernier Island (*WA Government Gazette* 3 October 1919: 1799); Rottnest Island (*WA Government Gazette* 2 March 1917: 359) and Dirk Hartog Island (*WA Government Gazette* 4 May 1917: 659, at the suggestion of the ornithologist Thomas Carter; Carter 1917). The Archipelago of the Recherche, although given Class C status in 1948, was not fully proclaimed Class A until 1969 (*WA Government Gazette* 26 June 1969: 2920). Up to 1961, Class A status for protection of flora and/or fauna was conferred on only the Doubtful Islands (1952), Bernier and Dorre islands (1957), Sandy Island (1958), and Seal and St Alouarn islands (1960). Lancelin and Edward islands (1958) and Bald Island (1961) merited only Class C status (Western Australian Sub-Committee of the Australian Academy of Science Committee on National Parks n.d.). Since the 1970s many other islands have been accorded Class A status for the 'conservation and protection' of flora and fauna. Following an appraisal of natural bushland in the Perth metropolitan region, Carnac, Garden and the Shoalwater Bay islands have been listed as 'Bush Forever' sites on the basis of their outstanding value for conserving nature (Government of Western Australia 2000).

We agree with Conservation Commission of Western Australia (2009: 30) that the 'foresight of people who successfully sought the reservation of many of the State's islands for [nature] conservation should be commended'. AA Burbidge and Fuller (1996) provided an extensive list showing the land tenure status of >300 WA islands on which seabirds breed. Most of these islands are nature reserves. However, only 635 islands (c. 25% of all WA islands) are vested in the Conservation Commission of Western Australia (Conservation Commission of Western Australia 2009).

## Recommendations for future research on, and management of, Western Australian islands

The following suggestions, built on the eight points outlined by Brockie et al. (1988), are not necessarily listed in priority order.

- Strengthen the biodiversity inventory and ecosystem monitoring of WA islands by applying FORESTCHECK sampling protocols (McCaw et al. 2011) to large (>1 km$^2$) islands in order to document plant, macrofungal and invertebrate diversity in relation to vegetation type and soil properties (macronutrients, salinity).

- Apply the detailed ecological approach of Heatwole et al. (1981) to at least one small (5-10 ha?) island that can be conveniently accessed and camped on. Their study, on the 4.93 ha One Tree Island (Queensland), studied conventional components of biodiversity (plants, vertebrates) as well as invertebrates (in soil and on plants). It also conducted studies of processes, including phenology of flowering and fruiting, leaf production, litter fall, leaf damage, plant biomass, and the interaction of marine and terrestrial communities.
- Undertake comparative genetic studies of selected taxa on islands and the adjacent coastal mainland in order to elucidate phylogeographic patterns and better understand the role of genetic processes in enabling some species to persist on islands and congeneric species to persist only on the mainland. Molecular phylogenetic study may help distinguish between species that have colonised islands after their separation from the mainland and those species that are relictual (cf. Ricklefs & Bermingham 2001; CE Smith & Filardi 2007). Genetic studies are also likely to identify population differentiation across islands (e.g. Australian sea lion; RA Campbell et al. 2008), and thereby offer a new perspective for the conservation management of such species. These studies may also identify previously unknown taxa.
- Undertake experimental germination and growth studies of plant species in relation to levels of phosphorus and nitrogen in soil (building on the phytometer experiments of Bancroft et al. 2005b) and chloride sprayed on foliage (Oosting 1945), so as to understand more fully why some species are absent from islands.
- Establish central databases that enable information collected on island visits to be consolidated in one place so as to increase the availability, accessibility and contextualisation of factual (rather than interpreted) data (cf. Callan et al. 2011; C Lohr 2013; Majer et al. 2013). This is necessary if superficial assessment and use of erroneous information (e.g. Ecosure 2009: 31) are to be avoided.
- Apply the method proposed by T Robinson et al. (1996) for South Australian islands to rating WA islands on the basis of their physical (area, isolation, tenure) and biological attributes (including vegetation variety, extent of natural vegetation, native species richness, introduced species, presence of rare species). We suggest that this method be modified by including the occurrence of endemic species, phylogenetically distinctive species, distinctive habitat types, and large nesting populations of seabirds. When combined with an assessment of risk of loss of biodiversity values (e.g. Conservation Commission of Western Australia 2009), monitor the foreseeable risks on the highest rated islands regularly and vigilantly from a biosecurity perspective (Whittle et al. 2013), as 'an ounce of prevention is better than a pound of cure' (e.g. see Greenslade et al. 2013a, 2013b).
- Eradicate all introduced vertebrate animals, remove dominant introduced plant species, control invasive ant species, and ensure that all actions are considered in an adaptive management framework and are properly documented in a central database. When eradication involves deployment of toxic baits, ensure that non-target species are not impacted (Bennison et al. 2016; Howald et al. 2009).
- Continue to translocate threatened species to appropriate islands, but only after rigorous and transparent assessment (e.g. based on the protocol suggested for mammals by Abbott 2000). Neglected professional advice (such as the release of wing-clipped young Cape Barren geese on Bald Island; T Spence, letter dated 5 January 1970, Department of Fisheries and Fauna file) should be reappraised. Many of the islands between Albany and Cape Leeuwin appear suited to this species (Abbott et al. 2006).
- Utilise more fully WA's natural advantage of numerous archipelagoes and compare the autecology of particular species on different islands.
- Monitor in 'real time' the process of local extinction on the many islands relative to the peninsulas formed in Lake Argyle in the Kimberley region in 1973, and further modified in 1996 when the dam wall was increased in height.
- Complete knowledge of the plant and vertebrate species present on WA islands by progressively visiting all islands for which such lists do not exist (mostly in the Kimberley region), and publish this information and records for other islands that are held in grey literature and field notebooks. Prioritise these visits by the area and regional location of islands.
- Finalise the mapping of vegetation types (classified by dominant plant species and structure) present on WA islands.
- Maintain nature conservation as the prime value of WA islands, provide consistent policy advice to government so as to minimise further islands being leased to private, industrial or commercial interests, particularly avoiding 'Queensland-style' island resorts (Hegerl 1984) and other undesirable side effects of tourism (Heywood 2011), and encourage the formation of committed friends groups so as to assist regional staff of the Department of Parks and Wildlife with monitoring and ecological restoration (e.g. Rippey et al. 1998).
- Appraise the value of particular islands as refuges from increasing temperatures, decreasing rainfall, and rising sea level resulting from anthropogenic

and natural climate change (Abbott et al. 2006; Bureau of Meteorology 2016, IOCI 2012).

- Continue performing regular censuses of breeding seabird populations on islands, particularly of those species that are expanding their breeding range, and use these data to investigate the role of increasing sea surface temperature (LE Chambers et al. 2011; A Pearce & Feng 2007).
- Compare the biodiversity of islands in estuaries (e.g. Peel Inlet, Harvey Estuary, Broke Inlet, Wilson Inlet), in deltas (Murray, Deep rivers), in rivers (Blackwood River), in coastal lakes (e.g. Lake Clifton, Lake Preston) and inshore (all protected in varying degrees from ocean waves and seaspray, and very close to the mainland).
- Prepare one management plan to apply to all WA islands, instead of the current regional or archipelago approach. Assume that all islands are in 'a state of precarious equilibrium' (Preston 1968: 592). Threats to island biotas (unmanaged tourism, including camping and use of open cooking fires; introduction of species) are shared by all islands, and the desirable management responses (biosecurity planning and education) are very similar, differ only in detail, and transcend regions.
- Establish 'friends' groups for islands that are close to mainland settlements (e.g. Shoalwater Bay islands, islands offshore from Fremantle), and thus are most at risk from high numbers of visitors.
- Consider the judicious and appropriate use of fire to regenerate senescing plant communities (cf. McArthur 1996a; Wykes & McArthur 1995). Lightning-ignited fires should only be suppressed in special circumstances, such as in the presence of translocated species or of valuable infrastructure.
- Take advantage of the rich diversity of reptile species to test theories (e.g. Meiri 2007) about insular biogeography and ecology.
- Conduct well-planned flotation experiments with reptiles and mammals in order to compare the capability of species to disperse to islands by floating and/or swimming (A Schoener & Schoener 1984). The period since this landmark study has seen the formation of ethics committees, which are unlikely to approve such informative studies of the swimming abilities of active-dispersing species and the persistence abilities of passive-dispersing species. Without this knowledge, however, it is difficult to distinguish the relative role of both processes in explaining genetic structure of island populations (Harradine et al. 2015).
- Replace 'benign neglect' (predicated on the absence of any industrial or other obviously harmful human activity) and 'naïve optimism' (predicated on the belief that a warning sign suffices to deter casual visitors) with an approach that assumes 'perpetual risk' and invokes 'preventive maintenance'. Monitor regularly and vigilantly those islands that are important breeding sites for seabirds and seals, and those islands with mammal species that have declined on the mainland (Nias et al. 2010). The consequences of inadequate biosecurity and inaction in promptly removing or abating detected threats are potentially catastrophic (local extinction). An outstanding recent example of vigilant monitoring is the eradication of black rats on Penguin Island in 2013, soon after they were first noticed in 2012 (Bettink 2015). A potential example of the consequence of inadequate monitoring of islands would be the accidental or deliberate presence of just one large (>3.5 kg) cat, as such cats disproportionately account for predation events on vertebrates (Moseby et al. 2015).
- Reinforce the value of the 'living museum' approach of Wingate (1985), now being applied in WA to Dirk Hartog and Rat islands following the removal of the threats that have caused declines and extinctions of species. The value of the restoration of ecosystems for education, research and tourism should also be emphasised (AW Diamond 1985).

## CONCLUSIONS

It is difficult to imagine a world containing just the five continents of Eurasia, Africa, America, Antarctica and Australia, collectively some 150 million km$^2$ of land. Although the nearly one million islands are estimated to increase the world's land area by only another c. 12 million km$^2$, islands have contributed much to the world's diversity of species, in the conventional sense of numbers of endemic species (e.g. Simberloff 1974; Stattersfield et al. 1998), but more significantly in novel combinations of species. Yet, it is difficult to resist the claim that 'islands are backwaters and dead ends' in an evolutionary sense (Preston 1968: 592).

The early literature on island biology emphasised a single factor, isolation, doubtless because this is what distinguishes an island or archipelago from the mainland. The emphasis in recent and current literature on two factors, island area and isolation, mischaracterises what is potentially a complex interaction of multiple variables. This caricature hides many subtleties. It has diverted attention from at least 13 other relevant factors that are neither minutiae nor inconsequential. Many of these factors do not act independently but instead combine synergistically. The study of small (<100 ha) islands reveals most clearly the joint operation of several of these 15 factors, particularly island shape, topography and orientation to the prevailing winds. These factors need to align, thereby facilitating the operation of processes conducive to the formation of habitable conditions that allow species to thrive.

Many of the concepts that have been devised from insular studies elsewhere cannot be usefully or validly applied to WA islands. We found no evidence of supertramp species (species found only on small species-poor islands, supposedly eliminated from larger islands by strong interspecific competition) or of taxon cycles (evolution of new species at high elevations or in interior habitats on large islands following immigration into coastal habitats), little evidence of species turnover for native species of birds and mammals unconnected to European civilisation, and only limited support for the existence of vacant niches (evidenced most convincingly by the presence of self-introduced plant species on islands seldom visited by humans). It appears to us that many of the principles of island biogeography espoused in the literature fit the islands studied but do not necessarily extend to other islands. Attempts to universalise the role of particular factors therefore need to be treated with caution. Theory needs to be as bold and simple as possible and as subtle and complex as necessary.

The revitalisation of island biogeography stimulated by MacArthur and Wilson's influential conceptual insights has waned. Island biogeography (i.e., biogeographical studies conducted on land surrounded by water) is no longer mainstream ecological research or a conspicuous and successful research program, as it was in the 1970s and 1980s (Brown 1986). MacArthur and Wilson's innovation was to apply a quantitative approach emphasising current factors of extinction (mediated by area) and immigration (mediated by isolation). MacArthur was a leader in the field of mathematical ecology, which had a powerful influence and promised much in the 1960s but eventually delivered little of enduring value (Simberloff 1982). DETIB incorporated what was fashionable thinking in the 1960s. Like all fads, previous approaches suddenly appeared to be unsophisticated and outmoded, and could be dismissed as historical, natural history or descriptive (MacArthur & Wilson 1967). Once again it seems desirable to reassert and rehabilitate the comparative/narrative approach, but apply it more systematically and rigorously from a global perspective, and combine it with appropriate quantitative methods. The ideas and concepts that derive from the comparative approach need to be balanced with potentially transformative ideas and concepts emerging from current research. The search for subtleties and the detection of new nuances within the familiar need to be pursued relentlessly. The set of unique circumstances provided by each island needs to be recognised, assessed, and not overlooked in the application of sophisticated numerical methods.

The continental islands of WA are 'so near' in a geographical sense to the mainland but 'so far' in biological similarity from the mainland. After labouring intermittently on this review and synthesis for 15 years, we conclude that a fuller understanding of the ecology of these islands remains elusive. If our suggestions for future research are taken up, the many lacunae in knowledge should reduce substantially.

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