Department of Environmental Biology

Diversity of butterflies and day-flying moths in urban habitat fragments, south-western Australia

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Statement of originality

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

Signed

Dated

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Abstract

This study adapted and developed methods of assessing and modelling biodiversity of butterflies and day-flying moths in habitat fragments, and determined those factors affecting their presence, abundance and species richness in a sample of 46 isolated urban remnants in south-west Western Australia. The specific objectives were to: (i) assess the effectiveness of transect–based sampling to quantify the species richness of habitat fragments; (ii) examine patterns of species richness in habitat fragments and quantify the detectability of each species recorded; (iii) review and rationalize the methods used to fit species–area–habitat models; and (iv) model species incidence, abundance and total richness of butterflies in urban habitat fragments and determine implications and priorities for their conservation.

These objectives were achieved and the principal findings of the research are:

(i) The transect method provides an accurate assessment of butterfly species richness in isolates provided that the level of sampling (proportion of area surveyed) is adequate, that sufficient surveys are conducted during the flight season to ensure high levels of detectability, and that surveys are conducted at appropriate times and during suitable weather conditions. Although randomly placed transects are preferable, logistic constraints often dictate the use of existing pathways, roadsides or management tracks – which requires the use of longer transects but is more practical in urban remnants.

(ii) Two main groups of taxa were identified in urban areas: species reliant on remnant native vegetation for breeding and entirely or predominantly restricted to remnant bushland (resident species or urban avoiders); and species that disperse readily through the urban matrix and have adapted to breed on introduced plants, but which also visit remnant bushland and sometimes breed there (non-resident species or urban adapters). The reliance of many resident species on specific host plants and the ability of others to adapt to introduced weeds are important factors in their presence in remnants. For both groups of species, detectability was strongly influenced by their abundance, with rare species the most likely to be overlooked.

(iii) Almost a century of fitting species–area curves has failed to produce agreement on which function is the best model of the relationship. Many of the proposed functions are identical, special cases of others or have arisen from

transcription errors. Empirical comparison of these functions requires methods suited to the distribution of species number such as the generalized linear model, method of maximum likelihood and the information-theoretic approach, and proper attention to covariates and their interactions.

(iv) Site area and vegetation condition were the dominant determinants of the presence, abundance and total species richness of resident butterflies and day-active moths in 46 urban habitat fragments in south-west Western Australia. Larger sites with more high quality (undisturbed) vegetation favoured 16 of 20 native species and only one benefited from disturbance. A further nine species not sufficiently widespread or abundant to enable individual analysis were collectively more prevalent in larger sites. Resource quality and quantity dominated the patterns of site occupancy, and increased site connectivity did not favour any species – results consistent with habitat resources, not metapopulation effects, determining current distribution patterns. As expected, the presence of non-resident species was unaffected by site area. The total number of resident species at each site reflected the collective responses of the individual species: increasing with area and declining with vegetation disturbance. The effects of area and vegetation quality were not simply additive: disturbance had a far greater impact on small remnants. This interaction is inconsistent with the area *per se* hypothesis: in the absence of disturbance there was no evidence of a species–area effect.

This study is the first comprehensive, quantitative assessment of the distribution and ecology of butterflies and day-flying moths in Australian urban habitat fragments and provides a baseline against which future changes in species distributions may be measured. The results have important implications for the conservation of butterflies and day-flying moths in the region. Maintenance of vegetation quality is of paramount importance and is vital in smaller remnants. Large remnants, being less susceptible to local extinctions, will be essential for the persistence of many species. Many functions have been proposed to model the species–area relationship but empirical comparisons have been hindered by methodological problems – this study conducted a re-examination of the relationship and presents an appropriate framework to compare functions. This study is also one of few to demonstrate and quantify the importance of interactions in explaining patterns of species richness and should stimulate future research into the importance of these effects.

Chapter 1 – General Introduction

1.1 Habitat fragmentation

In natural landscapes the uneven distribution of resources required for the persistence of plant and animal populations has created an environmental mosaic (Hutchinson 1959). Islands (Wallace 1892), mountaintops (Brown 1971) and soil types (Ehrlich *et al.* 1980) are all examples of natural habitat fragmentation that affects the distribution patterns of wild species. The Earth's biota has adapted to this natural resource mosaic and these adaptations, which characterize each species, enable them to persist. Alteration of natural landscapes by humans for the creation of cities, towns and farms or the harvesting of mineral and biotic resources has resulted in another form of environmental mosaic. This new landscape of natural and altered areas contains structurally and functionally dissimilar habitats and few species are adapted to both. As the population and impact of humans on the environment has increased, anthropogenic fragmentation of habitat has become a major threat to global biodiversity (Saunders *et al.* 1991, Hobbs and Yates 2003, Noss *et al.* 2006).

The isolated remnants of original habitat that result from fragmentation are in many ways analogous to landbridge islands and the study of their ecology has roots in island biogeographic theory (Cook *et al.* 2002, Whittaker and Fernández-Palacios 2007). This analogy assumes that the intervening areas between islands (the sea) and habitat fragments (the matrix) are comparable, with few resources for dispersing individuals. Understanding the ecological impacts of habitat fragmentation is important for the conservation of native taxa and the design and maintenance of reserves (Simberloff and Abele 1982, Steffan-Dewenter and Tscharntke 2000).

1.1.1 Ecological impacts of fragmentation

Habitat fragmentation has two direct impacts on wild species: (i) reduction in the area of the original landscape, which changes the amount of resources available to them; and (ii) habitat alteration, which changes the configuration of resources within the landscape and disrupts the connectivity of populations. These direct impacts also have secondary impacts on the biota: introduction of barriers between fragments, creation of edges between the dissimilar areas, degradation of habitat within remnants, and creation of new habitats (Whittaker and Fernández-Palacios 2007). Interactions between these effects also produce synergistic effects that may exacerbate their separate impacts (Brook *et al.* 2008). The interplay of these with the characteristics of each species determines the overall effect of habitat fragmentation on biodiversity.

1.1.1.1 Habitat reduction

Reducing the extent of original habitat removes a portion of the resources available to sustain each species. For most native species habitat fragmentation alters or destroys these resources within the matrix and they become reliant on remnant habitat (Noss *et al.* 2006). If the amount or quality of resources available to a species within a fragment falls below the levels needed to sustain a population (the minimum viable population) then local extinction results. If no populations are able to persist, global extinction results. Species that are unable to adapt to the altered landscape have reduced population sizes and an increased risk of extinction (Lawton and May 1995).

1.1.1.2 Habitat alteration

The intervening matrix varies widely in the extent to which it is altered from its original state. While some features such as roads, dams, buildings and paved areas are devoid of resources for most species, other forms of alteration are less pronounced and the distinction between habitat and non-habitat is not always clear-cut (Hobbs and Yates 2003). Examples include management practices that retain all or some of the original vegetation: ranching of herbivores; mowing, burning or regular clearing to maintain specific vegetation types; and maintenance of corridors and other linear features such as road verges or powerline easements (Swengel 1996, Yahner 1996, Swengel 1998b, Rudolph and Ely 2000, Clausen et al. 2001, Swengel 2001, Ross et al. 2002, Forrester et al. 2005, Saarinen et al. 2005, Newland 2006). The extent to which this new landscape contrasts with the original has important consequences for conservation of native species.

1.1.1.3 Edge effects

Habitat fragmentation introduces edges between remnants and the matrix. Edges have altered abiotic conditions (temperature regimes, light levels, humidity and exposure to wind) that affect the biota (Yahner 1999, Schultz and Crone 2001, Whittaker and Fernández-Palacios 2007). These changes make ecological processes more variable at edges (Ewers and Didham 2006) and may favour or disfavour particular species, although they often have higher diversity than either matrix or remnants because they sample species from both (Ramos 2000, Kitahara and Watanabe 2003, Samways 2007). From a conservation perspective, the presence of matrix species at habitat edges is of little importance and in this context edges can be thought of as zones of degraded habitat (Whittaker and Fernández-Palacios 2007).

1.1.1.4 Connectivity between fragments and barrier effects

The degree of connectivity between patches of remnant habitat depends on whether the intervening matrix facilitates or impedes the movement of individuals between fragments (Ewers and Didham 2006). Dispersal between patches is also a function of the distance between them and species' dispersal capabilities – for example, some species of birds and butterflies can cover considerable distances although others are sedentary (Wiens 1992, Holloway 1996).

For species persisting as metapopulations, increased impediments to dispersal may cause extinction of individual populations (Gotelli 1991). Although patches that are connected by corridors of original habitat are not strictly separate (but are merely unusually shaped patches), the concept of narrow corridors connecting patches is intuitive. These corridors of original or restored habitat provide physical continuity between fragments and have often been proposed as a means of ameliorating the impact of habitat fragmentation because they facilitate the dispersal of species between fragments (Hill 1995, Haddad *et al.* 2003, Brown and Freitas 2004, Ewers and Didham 2006).

1.1.1.5 Habitat degradation

Isolation of remnant habitat exposes it to degradation through the incursion of non-native plants and animals, altered fire regimes or other forms of disturbance that reduce the amount and quality of the resources needed to sustain native species. The ecological impacts of decline in habitat quality has been a neglected facet of landscape–scale fragmentation studies as most emphasis has been on the amount of resources (area effects) (Dennis *et al.* 2003, Shreeve *et al.* 2004, Maes *et al*. 2006, Whittaker and Fernández-Palacios 2007). For example, the concept of a 'minimum viable area' – the area needed to sustain a minimum viable population – ignores the impacts of habitat degradation on resource quantity and quality.

1.1.1.6 New habitats

The replacement of original habitat with human-created landscapes also creates new habitats for wild species. Many invasive and some native species adapt to this new landscape and thrive within it (Shapiro and Shapiro 1973, Shapiro 2002, Forrester *et al.* 2005, Saarinen and Jantunen 2005, Saarinen *et al.* 2005). Some forms of anthropogenic alteration such as power line rights-of-way or specific agricultural regimes not only favour some species but are now essential to maintain them (Gall 1984, Arnold 1993, Bramble et al. 1997, Saarinen 2002b, a, Saarinen and Jantunen 2002, Wahlberg et al. 2002, Forrester et al. 2005, Saarinen and Jantunen 2005, Saarinen et al. 2005, Strevens et al. 2008). Landscapes containing a mixture of original and disturbed areas may support more species than either landscape in isolation (Ramos 2000, Garden *et al.* 2006, McKinney 2008).

1.1.1.7 Interactions

While many of the ecological impacts of habitat fragmentation are known, the interaction between them has received relatively less attention. Although it has been stated that "the basic geographical factors (e.g. isolation, area, landscape heterogeneity) and the way they interact to influence island faunas are well known …" (Dapporto and Dennis 2008b), this understanding of interactions has often been intuitive or qualitative, not quantitative. A review of the interaction between area and isolation concluded that such an effect exists (Rosenzweig 1995), but quantitative studies that demonstrate it are lacking. Similarly, reviews of habitat fragmentation discuss synergies between effects, but quantitative analyses to demonstrate them are also lacking (Ewers and Didham 2006, McKinney 2006). Understanding how effects interact is important for conservation, but studies to determine their nature are few (Garden *et al.* 2006).

Typically, analyses of species presence and richness on islands and isolates have followed the island biogeographic approach of comparing the separate and combined impacts of such factors as remnant area, spatial arrangement or connectivity, vegetation condition or diversity, level of disturbance or the presence of particular resources (Welter-Schultes and Williams 1999, Cowley et al. 2000, Steffan-Dewenter and Tscharntke 2000, MacNally et al. 2003, Brown and Freitas 2004, Koh and Sodhi 2004, Jimenez-Valverde et al. 2006, Cassel-Lundhagen et al. 2007, Clark et al. 2007, Dapporto and Dennis 2008b, a, Dennis et al. 2008). Studies that incorporate interactive effects into island or habitat fragmentation models (Lomolino 1986, Burbidge and Manly 2002, Triantis *et al.* 2003, Russell *et al.* 2004, Kallimanis *et al.* 2008) have been the exception rather than the rule (Whittaker and Fernández-Palacios 2007).

1.1.1.8 Species responses

Habitat fragmentation typically reduces the diversity and population sizes of native species but not all species are affected equally (Steffan-Dewenter and Tscharntke 2000, Thomas 2000, McKinney 2008). With few exceptions the total number of native species declines within the matrix as most do not adapt to this new landscape (McKinney 2008). Those with specialized resource requirements and limited dispersal abilities are restricted to remnant habitat and are the most endangered by fragmentation (Gaston *et al.* 2000). Such species often have low or highly fluctuating population densities, or restricted geographical ranges – characteristics that also make them intrinsically more prone to extinction (Lawton 1995, Thomas and Morris 1995, Davies *et al.* 2004). However, generalist species may benefit from fragmentation (Shapiro 1975, 2002). Thus studies comparing the relative importance of the effects of habitat reduction and other impacts often report inconsistent or conflicting results because different species or guilds respond differently to the same factors (Hobbs and Yates 2003).

1.1.2 Urban fragments

Urban areas have high levels of habitat heterogeneity resulting from the diverse land uses and plant cultivation choices at small spatial scales. Although urbanization is a major cause of the decline of native species the complex nature of urban land use has complicated effects on local biodiversity (Garden *et al.* 2006, McKinney 2006). On one hand, some aspects of urbanization promote the loss of species diversity. One of these is a species–area effect: the large expanse of impervious surfaces in urban areas reduces the area of original habitat available for biota, effectively reducing the resources available to sustain them. Similarly, structural simplification of vegetation (landscaping and maintenance of residential, commercial and recreational areas) reduces shrubs and dead wood and increases grasses and herbs, altering resource availability for native species (Koh and Sodhi 2004). This has a negative impact on the diversity of many animals, which tends to increase with vegetative complexity and plant species richness (Hutchinson 1959). On the other hand, some aspects of urbanization promote increasing levels of biodiversity by the addition of non-native species (Shapiro 2002, Koh and Sodhi 2004). This spatial heterogeneity can produce high levels of β diversity and greater species richness than surrounding rural areas, especially in groups such as insects which require relatively small areas to support a viable population.

Key questions in urban ecology are whether this addition exceeds the loss of native species to produce a nett gain in species richness, and whether this increase is sustained over time (McKinney 2008). However, long-term studies in urban areas are rare in the literature because accurate inventories are unavailable for early periods and many losses occurred prior to initial surveys (New 1997, Kadlec *et al.* 2008, McKinney 2008). Studies of the effects of urbanization on species richness that examine changes along an intensity gradient are more common and these usually support the intermediate disturbance effect, with species-richness increasing at intermediate levels of urbanization (Ruszczyk and De Araujo 1992, Kitahara and Fujii 1994, Hogsden and Hutchinson 2004). However, this effect is not necessarily simple: species richness may peak at moderately disturbed sites if spatial scale is large, but the impact of disturbance may be uniformly negative at smaller scales (Hogsden and Hutchinson 2004).

Roads are one of the most common features of urbanized areas and are increasingly recognized as one of the most insidious impacts on native animals (Munguira and Thomas 1992, McKenna *et al.* 2001, Trombulak and Frissell 2001, Saarinen *et al.* 2005, Severns 2008). Roads cause direct mortality by vehicle impact and the toll on some taxa such as invertebrates can be enormous (estimated at > 20 M butterflies / week for the state of Illinois, USA; (McKenna *et al.* 2001)). Indirectly, roads also create barriers to dispersal and disrupt metapopulation dynamics (Munguira and Thomas 1992, Trombulak and Frissell 2001, Severns 2008).

1.2 Butterflies

Butterflies are one of the most commonly used groups for conservation studies (Pullin 1995, Ulrich 2003). In Europe and North America there is widespread public interest in butterflies, comparable to that in birds, and as a result the distribution and status of the fauna is well known and unrivalled by any other invertebrate group (Konvicka *et al.* 2006, Dennis *et al.* 2008). They have also been a model organism for the study of metapopulations (Hanski 2004).

More than four hundred species of butterflies are recorded from Australia and the taxonomic inventory is more than 90% complete, making them the best-known insect group (Kitching *et al.* 1999, Braby 2000, Edwards *et al.* 2001).

1.2.1 Decline of butterflies

Butterflies have shown marked declines in distribution that often exceed declines in other taxa (Warren *et al.* 2001). The threats to butterflies are generally the same as for other fauna: habitat destruction or alteration; changes to management practices; isolation of remnant habitat; pollution and use of chemical insecticides and herbicides; climate change; and in some cases overcollecting or trade in specimens (New 1991, Pollard and Yates 1993, Beaumont and Hughes 2002, Brown and Freitas 2004, Eastwood et al. 2008). Disease and predation by introduced species seems unimportant.

1.2.1.1 World-wide

Declines and extinctions of butterflies have been documented since the mid 19th century, notably in Britain (large copper, 1840s and large blue, 1880s), North America (Xerces blue, 1870s) and Australia (Banks' brown, 1890s) (New 1991). In the best studied region, Britain, half of the resident butterfly species are threatened or extinct and most have reduced geographic ranges (Warren *et al.* 2001, Ewers and Didham 2006). Changes in land use, particularly the cessation of traditional agricultural practices, have been the greatest cause of butterfly declines (Thomas and Morris 1995). Most of Europe's threatened butterflies (van Swaay and Warren 1999) have declined because of altered agricultural practices (63 of 69 species), habitat fragmentation (62 species) or urbanization (58 species). Early industrialization, increased human population density and urbanization are correlated with the greatest number of extinctions (Konvicka *et al.* 2006).

1.2.1.2 Australia

In Australia, several studies have documented the conservation status of individual species and genera (New 1993, Kitching *et al.* 1999, Braby 2000) and a major review of the fauna has been conducted (Sands and New 2002). Although substantial distributional data are available for Australian butterflies, unbiased estimates of changes in abundance or range to enable objective assessment of population declines are lacking. Identification of priority taxa for conservation relies upon such objective data and estimates of changes in the abundance of butterflies, and potential causes, remain unresolved until these data are obtained (New 1997). In the absence of this information threatened taxa have been identified by censusing expert opinion (Sands and New 2002). The lack of systematic surveys in conservation reserves and a national database were seen as the major impediments to establishing the conservation status of many species and such surveys are needed to advance understanding of butterfly conservation in Australia.

1.2.1.3 Western Australia

Four Western Australian taxa, all endemic, have been identified as threatened by urban development (New and Sands 2002). Only one, *Hypochrysops halyaetus*, has been closely studied. Restricted to coastal and near-coastal areas between Perth and

North West Cape, morphological variation suggests that two subspecies may be recognisable (Sands 1986). The southern form, restricted to coastal areas between Perth and the Moore river, has a history of decline associated with urban development and is considered vulnerable (New and Sands 2002, Sands and New 2002). An obligate myrmecophile, it has a narrow host plant range and is restricted to remnant bushland. A microdistribution and autecological study at a single site found that early successional habitats in recently burnt or otherwise disturbed areas had both higher host plant and butterfly densities and were preferred for oviposition (Dover and Rowlingson 2005, Dover et al. 2008).

Of the three other taxa, *Antipodia dactyliota anaces* is more widespread than originally believed and of no conservation significance, *Jalmenus inous* is restricted to coastal and near coastal dunes and considered data deficient (Sands and New 2002), and *Theclinesthes hesperia* is now considered conspecific with the more widespread *Theclinesthes albocincta* (R. Eastwood, Griffith University, pers. comm.).

1.3 Methodology

1.3.1 Sampling methods

Ecology is often defined as the study of the distribution and abundance of organisms, but the methods with which to census them are far from standardized or complete. Sampling and monitoring programs for animal populations and communities have been established throughout the world and estimating the number and abundance of species present in a given area is crucial for conserving and managing biodiversity (Colwell and Coddington 1994, Boulinier *et al.* 1998). Two important sources of variation must be considered in the design of sampling programs (MacKenzie *et al.* 2002). Firstly, because many areas are too large to be surveyed completely, smaller areas must be selected in a manner that permits inference to the entire area of interest. Secondly, few animals are so conspicuous that they will always be detected when present and failure to detect a species at a site does not necessarily imply that it is absent (Elton 1927, Davies and Smith 1997, MacKenzie 2005, MacKenzie *et al.* 2006). Assessing the adequacy of sampling regimes and the adequacy of species lists is important to avoid bias and ensure correct inference (Abbott 1983, Kery 2002, Dorazio *et al.* 2006, Kery and Plattner 2007).

1.3.2 Estimating occupancy, abundance and species richness

The usual approach to determining the occurrence and abundance of species within a site is to identify and tally each individual using a standardized method. In most studies, counts of species observed (the number seen, heard, trapped, or otherwise detected) are used to estimate an index of abundance. This provides information on the presence of species within a site, an estimate of species richness and a count of the number of individuals observed, but it is important to be aware of the limitations inherent in these estimates (Boulinier *et al.* 1998, MacKenzie *et al.* 2002, MacKenzie *et al.* 2003, Tyre *et al.* 2003, Bailey *et al.* 2004, MacKenzie 2005). The major problem with simple counts is that species vary widely in their detectability. While the presence and abundance of large or conspicuous species may be estimated quite accurately, many more species are small, inconspicuous or cryptic (MacKenzie *et al.* 2002). Over the past 25 years the need to investigate, quantify and compensate for variations in detectability has been increasingly recognized (Buckland *et al.* 1993, Colwell and Coddington 1994, MacKenzie *et al.* 2006).

1.3.2.1 Detectability

Detectability is the probability that a species is observed at a site, given that it is present. To quantify detectability it is necessary to take repeated samples of the site, either spatially or temporally. Multiple samples of the same locations within the site are preferred because these eliminate potential confounding of temporal and spatial variation in detectability. Assuming that the species does not temporarily emigrate from the site and that its detectability is constant during the sampling period, the probability of detection is estimated by the proportion of repeated samples in which the species is recorded. For a given detectability p, the overall probability P that a survey regime consisting of n samples will detect the species at the site (i.e. record it in one or more samples) is $P = 1 - (1 - p)^n$. For species with high detectability ($p > 0.8$) three repeated samples are sufficient to ensure a high likelihood of observing it on one or more occasions ($P > 0.99$); at moderate detectability ($p > 0.5$) six samples are needed to obtain $P > 0.98$ (Figure 1.1; (Tyre *et al.* 2003)). To test hypotheses about changes in species richness using data from counts of species, it must be assumed either that all species are detected (which is not true in most biological samples), or that detectability is the same for all species. Quantifying detectability is one means to determine the accuracy of a sampling regime.

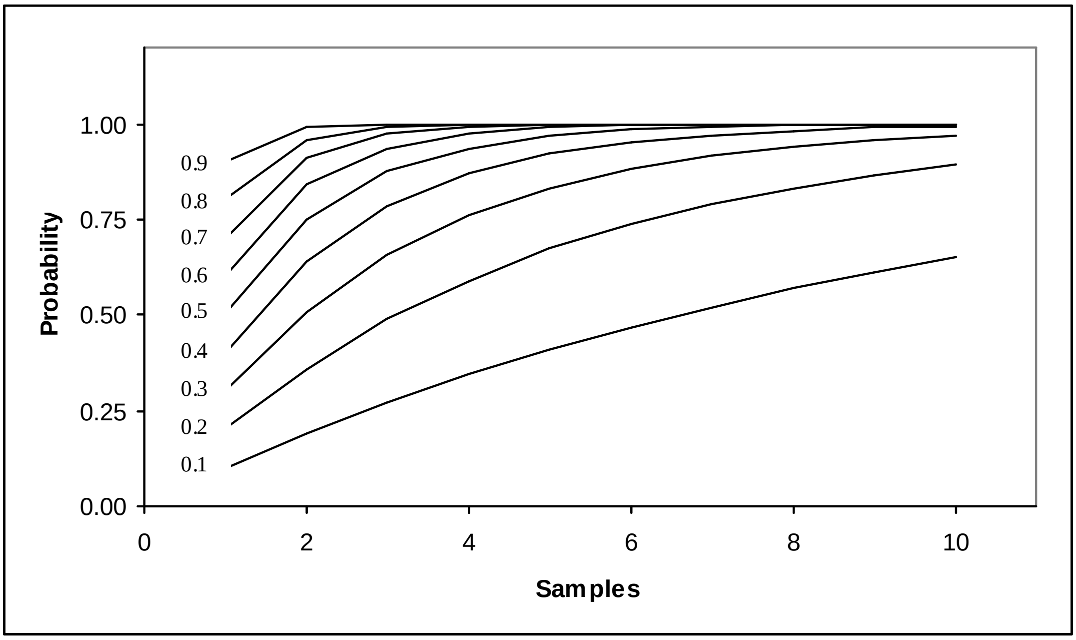

Figure 1.1. Overall probability (*P*) of observing a species on one or more occasions using a sampling regime of 1–10 repeated samples, at varying levels of detectability (*p*) between 0.1 and 0.9.

1.3.2.2 Occupancy

The most basic problem in censusing habitat fragments is to determine if a particular species is present. Failures to observe species that are in fact present introduces ‘false negative’ errors. In modelling the effects of habitat characteristics on species presence and richness, these errors can introduce bias or alter those effects determined to be important (Tyre *et al.* 2003). To resolve this problem either species detectability must be accounted for explicitly or a sufficient number of samples must be taken to obtain accurate estimates of site occupancy. For the former, methods based on mark–release–recapture (MRR) estimate site occupancy by taking into account species that were not recorded but the presence of which could be inferred from the pattern of their observed occurrences. However, until recently these methods were seldom used in biodiversity studies despite warnings that the assumption of equal detectability among species is generally false and unequal species detection probabilities can invalidate the results of hypothesis tests (Boulinier *et al.* 1998, MacKenzie *et al.* 2006).

1.3.2.3 Abundance

Methods used to estimate the abundance of animals are frequently expensive of time and effort. The MRR method is widely accepted as the best means of estimating an animal's true abundance but considerable resources are needed to sample sufficient numbers of individuals to obtain accurate estimates. For this reason MRR is often used for detailed experiments or small-scale investigations, but not in large-scale monitoring programs. In these, simpler methods are used that provide an index of abundance – typically by counting individuals with a standardized sampling regime (MacKenzie *et al.* 2006). While this provides a count of the number of individuals observed, variation in detectability between different species affects the relationship between the index and true abundance. Relative changes in the index are nonetheless useful indicators of changes in abundance, but may not be comparable between species.

1.3.2.4 Species richness

Estimates of site species richness are compiled from individual estimates of site occupancy, and so may compound any errors generated by low or variable detectability. The enormous number of studies that model the relationship between the species richness and habitat characteristics of isolates show varying regard to this problem. On one hand, species lists compiled for each isolate may be taken at face value and any possible errors simply ignored, being consigned to the 'residual' or 'error' variation not explained by the fitted model. This approach is likely to be reasonable if the level of error is small, such as when species detectability is high or when sufficient numbers of repeated samples are taken to obtain high overall detectability (Tyre *et al.* 2003). On the other hand, explicit estimates of detectability can be incorporated into the model, but more complex models require more data to obtain reliable estimates (Stevens 1992, Hosmer and Lemeshow 2000, Vittinghoff *et* *al.* 2005). In practice it is necessary to trade off additional model complexity with the pragmatics of model fitting.

1.3.2.5 Relationship between occupancy, detectability and abundance

Determining the presence of a species at a site only requires the observation of a single individual, so increased abundance typically has a positive effect on detectability. Intuitively, common species are easier to detect than rare ones simply because there are more individuals available to be observed. Abundance-induced heterogeneity in detection probability is most likely to be important when populations are small and will diminish in importance as population size increases (MacKenzie *et al.* 2006). Thus for reasonably abundant species detectability may be approximately constant.

As abundance varies spatially, the detectability of a particular species is likely to vary between sites. Similarly, for species that are seasonal in appearance detectability is likely to vary with temporal changes in abundance. In temperate regions, butterflies often show such seasonal patterns because although individuals are present throughout the year, the flying period of the adults is strongly seasonal, and standard survey methods only record adults.

1.3.3 Comparison of sampling methods

1.3.3.1 Introduction and aims

In research and monitoring studies sampling is used to assess both the abundance and diversity of butterflies, but methods vary world-wide. Many are based on the ‘standard’ monitoring protocols developed from the early work of Pollard and others (Pollard 1977, Pollard and Yates 1993). This method uses transects placed along existing landscape features (originally paths and rides in Britain) that are walked by an observer at regular (typically weekly) intervals, recording all butterflies seen within a ~5 m wide corridor and up to 5 m ahead. The width of the corridor varies according to local conditions, although 5 m is considered standard. Transect length is fixed for each site but varies between sites in relation to the extent of the area sampled. Suitable sampling times and weather conditions are also standardized. Butterfly monitoring schemes in Britain and Europe use such standard sampling to measure changes in abundance and distribution over time. I assessed regional and other variation in sampling methods to determine if a comparable ‘standard’ existed for research studies that assess butterfly diversity and to develop an appropriate methodology for use in south-west Western Australia, based on the experiences of other researchers.

1.3.3.2 Methods

I examined the methods used by 32 studies that assessed butterfly diversity published between 1977 and 2005. Studies of a single or a few closely related species were excluded, as in these methods were often species-specific. Studies were selected at random and represent a large fraction of such studies published during the period. For each study the following details were recorded: general location; survey method (transect, plot- or point-based area search, baiting or trapping); the frequency, number and duration of surveys; where applicable, transect dimensions and route; allowable weather conditions (temperature, cloud cover and wind speed); and time of day when sampling was conducted.

1.3.3.3 Results

Most studies were conducted in temperate areas, particularly North America (13) and Europe (10), with three in Africa, three in South and Central America, two in Australia and one in Asia (Table 1.1). In several cases not all of the survey details were reported. Most (22) used strip transects and nine used area searches, occasionally with supplementary baiting or trapping, particularly in the tropics; the remaining study used trapping alone. The frequency, number and duration of surveys varied considerably. Eight of the transect- and plot-based studies sampled one or more times per week but twice as many sampled at intervals of 1.5 to 3 weeks, usually at fortnightly intervals. The remainder sampled once each month or less frequently. In temperate areas most studies sought to sample the majority of the butterfly flight period, which is seasonal, and the number and duration of surveys reflected the length of this period.

Table 1.1. Sampling methods used by 32 studies that assessed butterfly biodiversity published between 1977 and 2005. An entry or prefix of "?" indicates the information was not stated or unclear, respectively. An entry of "Pollard standard" indicates transects 5m wide × 5 m ahead, sampled between 0945 and 1545 hr, temperatures >13 °C and with >60% sun between 13–17 °C, no rainfall, and wind <5–6 m sec^{-1} (<18–22 kmh).

Study	Location	Survey method	Frequency, number and duration of surveys	Transect dimensions (width × ahead)	Transect route	Weather conditions and time of day
(Baz and Garcia-Boyero 1995)	Spain	Fixed time area searches	1 / 15 days over 4 months	N/a	?	?
(Bergman et al. 2004)	Sweden	Variable length transects	5 times over 3 months	10m × 5m	Random	Predominantly sunny, >17 °C, wind < 20kmh
(Bramble et al. 1999)	Pennsylvania, USA	Area searches	7 times over 3.5 months	N/a	N/a	Sunny, warm days, >9am, no wind
(Brown and Freitas 2000)	Brazil	Area searches, baiting and trapping	N/a	N/a	Paths and roadsides	Not rainy
(Caldas and Robbins 2003)	Brazil	Fixed time and length transects	~ 16 times over 11 months	?Unbounded	Paths and roadsides	Sunny >90% of time, >18 °C
(Clausen et al. 2001)	Denmark	Variable length transects	1 / week over 3 months	Pollard standard	Hedgerows, road verges and random	Pollard standard
(Cowley et al. 2000, Cowley et al. 2001b, Cowley et al. 2001a)	Wales	Fixed length transects	1 / 2 weeks over 6 months	Pollard standard	Random	Pollard standard
(Fleishman et al. 1998, MacNally et al. 2003)	Nevada, USA	Variable length transects	1 / 2 weeks over 3.5 months	100m × ?50 m	Hiking trails or roadsides	Sunny skies, moderately warm temperatures, light winds

Study	Location	Survey method	Frequency, number and duration of surveys	Transect dimensions (width × ahead)	Transect route	Weather conditions and time of day
(Fleishman et al. 2001)	California and Nevada, USA	Variable length transects	1 / 2 weeks over 3.5 months	100m × 50m	Usually trails or roadsides	Sunny skies, moderately warm temperatures, light winds
(Grill and Cleary 2003)	Greece	Fixed length transects	1 / 10 days over 4 months	10m × 5m	?Random	?Pollard standard
(Hamer et al. 2003)	Borneo	Baited traps	85 times over 3 yr	N/a	N/a	N/a
(Hill 1988)	E Australia	Variable length transects	1 / month over 1 yr	5m × 10m	?	Sunny days, 1030–1430, light winds
(Hill et al. 1992)	NE Australia	Fixed time area searches	6 times over 18 months	N/a	N/a	Sunny days, light winds
(Huntzinger 2003)	Oregon and California, USA	Fixed length transects	5–6 times over 2 months	20m × 10m	Random	Clear days, 1000–1500
(Keller and Yahner 2002)	Pennsylvania, USA	Fixed length transects	1 / month over 4 months	20m × ?10m	Historic railroad bed and roadsides	Between 0900 and 1530 >15 °C wind <15kmh
(Krauss et al. 2003)	Germany	Variable length transects	5 times over 3–4 months	Pollard standard	Random	Pollard standard
(Kremen 1992)	Madagascar	Fixed time and length transects	2 times over 2.5 months	10m × ?5m	Trails and stream banks	Sunny conditions, 1000–1400
(Kremen 1994)	Madagascar	Fixed time area searches and baiting	5 times over 1 month	Unbounded, using binoculars	N/a	Good weather

Study	Location	Survey method	Frequency, number and duration of surveys	Transect dimensions (width × ahead)	Transect route	Weather conditions and time of day
(Lawrence and Samways 2002)	South Africa	Fixed time area search	10 / 39 days	N/a	N/a	Cloud cover <30%, 1000–1100
(Munguira and Thomas 1992)	England	Fixed length transects	1 / week over 3.5 months	2m × ?5m	Road verges	Pollard standard
(Panzer 2002)	Illinois, Indiana and Wisconsin USA	Variable length transects, fixed time point counts	?1 over 2 months	?Pollard standard	Random	?
(Pollard 1977)	Monk's Wood, England	Fixed length transects	3 / week over 5 months	Pollard standard	Rides or paths	Pollard standard but 1045–1545
(Ricketts et al. 2002)	Colorado, USA	Area searches	8–10 times over 2 months	N/a	N/a	?
(Rudolph and Ely 2000)	Texas, USA	Fixed length transects	1 / month over 8 months	?Pollard standard	?	Cloud cover <15%, 25– 32 °C, 0900 – 1300, wind < 20kmh
(Saarinen 2002b, a, Saarinen and Jantunen 2002)	Finland and Russian Karelia	Fixed length transects	1 / 2 weeks over 2 months	Pollard standard	Field boundaries	Cloud cover <30%, 21–24 °C in afternoon, 0910–1810
(Simonson et al. 2001)	Colorado, USA	Area searches	4 times over 3 months	N/a	N/a	Sunny conditions, >17 °C, 0930–1600, calm to light winds
(Swengel 1996, 1998b, a, Swengel and Swengel 2001)	Illinois, Iowa, Minnesota, Missouri, North Dakota and Wisconsin, USA	Fixed length transects	1–4 visits in each of 4 years	Unbounded, using binoculars	?	Cloud cover <30%, weather recorded (with 'good' conditions >16 °C), wind <25kmh

Study	Location	Survey method	Frequency, number and duration of surveys	Transect dimensions (width × ahead)	Transect route	Weather conditions and time of day
(Thomas 1983)	England	Variable length transects	1 / 5 days	4–6m × 5m (for different taxa)	?	Pollard standard
(Wood and Gillman 1998)	Trinidad	Fixed length transects and baiting	2 / day over 4 weeks	Pollard standard	?	Not raining, 0830–1030 and 1530–1700
(Yahner 1996)	Pennsylvania, USA	Fixed time area searches	3–4 times over 2 months in 2 years	N/a	Random	Not raining, >20 °C, not windy
(Yahner 1999)	Pennsylvania, USA	Fixed length transects	7 times over 4 months	17m × ? and 30m × ?	Forest and agricultural edges, roadsides	Temperature >15 °C, 0900–1530, wind <15–20kmh
(Yahner 2001)	Pennsylvania, USA	Fixed length transects	7 times over 4 months	50m × ?	Roadsides	Temperature >15 °C, 1000–1700, wind <15–20kmh

At least half of the transect-based studies used routes that followed existing features: field and forest edges, stream banks, hedgerows, tracks, trails, paths, rides and roads. In six cases transect routes were randomly placed but in the remainder the method of transect placement could not be determined. There was considerable variation in transect width – about half used the standard 5 m width (mostly in Europe) but the majority used widths of 10–100 m or were unbounded. The variations in transect width were usually adopted in response to vegetation type – in forests or along forest edges, transect width was sometimes less than 2.5 m either side of the observer, whereas in open habitats transect width was often 10 m or more. In some cases species identification at these greater distances was facilitated by the use of binoculars. The distance ahead of the observer in which individuals were recorded varied less frequently, deviating from the usual 5 m in seven studies.

Transect lengths were rarely reported and the fraction of each site sampled could be determined only twice (Hill 1988, Bergman *et al.* 2004). However, many studies did not sample discrete areas such as habitat remnants and many transect-based studies (14) in such areas set a fixed time and/or length for transects. The remainder used variable length transects, typically in proportion to site area.

Eleven studies conducted sampling between 0945–1545 hr but others used non-standard times to suit local conditions – such as in northern Europe, where summer day lengths are long, or in the tropics, where daily activity is longer. Weather conditions considered suitable to conduct surveys varied considerably. Acceptable temperatures were predominantly 15–21 °C, but varied regionally: in Britain, northern Europe and the northern USA threshold temperatures (13–17 °C) were lower than elsewhere (18–25 °C). Cloudiness and temperature adjudged suitable for sampling were often interrelated, with greater cloud cover tolerated at higher temperatures. At low temperatures (<17 °C) cloud cover of more than 30% was generally considered unsuitable for sampling. The maximum tolerated wind speed only exceeded Pollard’s (1977) prescription (<18–22 kmh) in one study.

1.3.3.4 Discussion

The high proportion of studies conducted in Europe and North America no doubt reflect the resources available for research in these regions and the historical interest in butterflies in Britain and Europe. Relatively few studies were conducted in Australia and elsewhere.

Strip transects were the predominant method of assessing diversity in both temperate and tropical regions. In the tropics and sub-tropics, where high diversity required the capture of many individuals to enable identification, more surveys, extended sampling times or additional methods (baiting, trapping) were used to obtain more complete species lists (Sparrow *et al.* 1994). The additional effort required to identify tropical taxa reduces the efficiency of the transect method, although incomplete data and data collected by inexperienced observers were still representative of total diversity (Baz and Garcia-Boyero 1995, Caldas and Robbins 2003).

Pollard’s (1977) proposed standard transect width of 5 m, chosen to correspond with the boundaries of rides and paths in England, was widely adopted in Europe but there was little consistency elsewhere. The constraint of recording only up to 5 m ahead of the observers was more widely adopted than any standard transect width.

Transects were rarely placed randomly, although for statistical reasons this is usually preferred in sampling. Constraints on transect routes were the availability and location of paths, the nature of the vegetation, the speed at which transects could be conducted and the potential to damage remnant vegetation by sampling off existing paths. Another reason given for this bias was that open areas and edges, including artificial environments such as roadsides, cleared corridors and field margins, represent important habitat elements that are favoured by some species (New 1991, Munguira and Thomas 1992, Yahner 1996, Bramble et al. 1997, Thomas and Hanski 1997, Yahner 1999, Saarinen 2002b, Wahlberg et al. 2002, Dover and Rowlingson 2005, Forrester et al. 2005, Saarinen et al. 2005). Although randomly placed transects may fail to sample these, basing them only on such features may introduce bias by oversampling species that favour them. In either case, bias may be introduced and some species may be overlooked.

In temperate regions, including southern Australia, many butterfly species have well-defined flight periods of between one and a few months, and the total flight period for all species is typically 3 to 4 months (Pollard and Yates 1993, Pullin 1995, Braby 2000). A sampling frequency of 1–4 times / month has been the norm in these areas. Most researchers have knowledge of the local butterfly fauna and I inferred from my examination of the literature that generally, the number of surveys was not usually determined *a priori*, but a practicable survey frequency was chosen first, then the number of surveys was tailored to fit the length of the flight season.

Only three studies (Kremen 1992, Sparrow *et al.* 1994, Caldas and Robbins 2003) examined the effect of sampling frequency on species richness estimates: frequencies of 1.5, two and six surveys / month all underestimated true species richness with the shortfall proportional to the size of the fauna. Two further evaluations of the transect method published after my review of the literature examined the effect of survey frequency and sampling fraction (proportion of area sampled) on the completeness of species lists (Birrer *et al.* 2005, Collier *et al.* 2006). In Switzerland, a regime of 4–7 surveys at monthly intervals using transects 2.5 km long and 5 m wide within 1 km^2 areas (sampling fraction of 1.25%) detected 66–70% of taxa. In South Australia, fortnightly or monthly surveys of three urban remnants using 10 m wide transects detected 69–82% of the fauna. Sampling fractions were 0.3, 1.9 and 3.4% and the proportion of the fauna detected each year increased correspondingly (69 and 75%, 80 and 80%, 82 and 76%).

Weather conditions suitable for temperate Europe and North America were inappropriate in warmer areas such as the tropics. However, weather conditions are considered to be minor considerations in sampling. In Britain, the week of recording had the greatest effect on counts and in comparison the effects of time of day, weather and observer were relatively small (Pollard and Yates 1993).

1.3.3.5 Conclusion

A “world standard” methodology for assessing butterfly species diversity is a desirable objective – without it, there is no prospect of collating and synthesising quantitative data. But such a standard is not feasible, given the large differences between temperate and tropical regions. A standard for temperate areas is possible, with slight variations to suit local conditions. Strip transects placed using existing features such as walk paths, roads, fire breaks or powerline rights-of-way may introduce bias in those species detected and estimates of their abundance. Theoretically, randomly placed transects should be preferred but particular features, including those of human origin, often constitute flight areas and provide nectar or other resources and may be the only places where some species congregate. The effect of transect placement has not been investigated.

A standard width for strip transects has the advantage of providing comparability between surveys in different areas (Pollard 1977); however, in many studies practical issues dictated the width used. A 10 m width (5 m either side of the observer) was used most frequently and was presumably feasible in the majority of regions – given the wide acceptance of counting butterflies up to 5 m ahead of the observer. To determine species lists of habitat isolates it is usual to adjust transect length to the area of the study site; in any case, fixed-length transects are impractical if small remnants are included in a regional survey. Closer investigation of sampling fraction is needed to assist in designing effective survey regimes.

The number of surveys, sampling frequency and sampling fraction needed to adequately inventory a given site is an unresolved question prior to the commencement of sampling – the only guiding principle in determining an appropriate number of surveys is that larger sites and sites with a more diverse fauna or more varied habitats require greater survey effort. The number and duration of surveys required is dependent on the survey frequency and the length of the flight season.

Precise prescriptions for the time of day and weather conditions in which to conduct surveys were relatively minor considerations in conducting surveys. What constitutes suitable sampling conditions for a particular region varies considerably, and threshold conditions need to be determined parochially.

1.3.4 Modelling species presence, abundance and richness

Many studies investigate the effects of environmental factors on the local occurrence, abundance or total number of species present within isolates such as islands and habitat fragments. To assess the relative importance of these factors statistical models are constructed using a set of predictor variables chosen from those known or hypothesized to affect the outcome (Vittinghoff *et al.* 2005). For example, it is well known that the area of an isolate often affects species presence and total richness so this should be examined in such models. Similarly, the pattern of species occupancy in isolates reflects site characteristics, isolation and anthropogenic disturbance, so measures of these should also be included. Disentangling these effects can be difficult, however, as they may be interrelated in complex ways (Russell *et al.* 2004).

1.3.4.1 The species–area relationship

The species–area relationship, the most widespread pattern in ecology, has generated debate since Arrhenius proposed the first explicit functional model (Arrhenius 1921, Gleason 1922, Arrhenius 1923b, a, Gleason 1925, Connor and McCoy 1979, He and Legendre 1996, Lomolino 2000). The power and exponential functions of the relationship are generally considered to be the most widely applicable, but several alternatives have been proposed and little theory exists to indicate which is to be preferred (Tjörve 2002). The appropriate methodology to compare the alternatives is also unclear and has generated much debate (Williamson *et al.* 2001, 2002, Fattorini 2006, Whittaker and Fernández-Palacios 2007). The usual approach to fitting these functions has been to find an appropriate transformation to linearize the relationship for computational convenience (Whittaker and Fernández-Palacios 2007), but this has also been the subject of debate (Wright 1981, Fattorini 2006). Almost a century of fitting species–area curves has failed to produce agreement on which function is best model of the relationship.

1.3.4.2 Incorporating other covariates

In empirical studies the ‘pure’ species–area relationship must be accounted for so that the effect of other factors on species number, such as habitat or environmental characteristics, may be distinguished (Arrhenius 1921, Connor and McCoy 1979, Schoener and Adler 1991, Rosenzweig 1995). In such studies the relationship between species number and area is ‘factored out’ so that the effects of other variables can be estimated and a suitable link function must be chosen so that these relationships are not masked or biased.

1.3.4.3 Interactions between covariates

As mentioned previously (section 1.1.1.8), few studies have examined the importance of interactive effects on patterns of species distribution and abundance.

The importance of such interactions is widely understood, but quantitative assessment of interactive effects is often overlooked or rudimentary. Including interactions between effects is a standard feature of model construction (Hosmer and Lemeshow 2000, Vittinghoff *et al.* 2005), but has been a neglected area of species–habitat modelling (Russell *et al.* 2004).

1.4 Study species

Approximately 60 species of butterflies occur in south-western Australia (Table 1.2) and several studies have documented their distribution in conservation reserves and on offshore islands, particularly in the south-west region (Williams *et al.* 1992a, 1993, 1995, 1996; Williams 1997; Williams and Powell 1998, 2006). Although most species are restricted to remnant bushland, several species breed facultatively or predominantly on introduced plants or weeds that are common throughout the urban matrix. They depend, therefore, to a greater or lesser extent on remnant bushland to sustain populations within the region. The species were therefore divided into two groups of taxa: one comprising species that breed entirely or predominantly on plants restricted to bushland remnants (termed ‘resident species’); and another group of species known to breed throughout the urban matrix, or that breed on plants not present within the remnants, together with other species that are recorded as introduced, regular migrants or vagrants (‘non-resident species’). For each species, I took a conservative, precautionary approach so that each was only classified as non-resident if objective information was available that the species comprised self-sustaining populations outside of bushland areas, or was a known migrant or vagrant. For example, *Zizina labradus* breeds on native and introduced legumes and occurs in both bushland and urban areas, but there is no evidence that the populations in urban areas are self-sustaining. In contrast, *Vanessa kershawi* breeds primarily on the exotic and widespread weed *Arctotheca calendula*, which occurs commonly on roadsides, in gardens and on vacant land, and is also known to be migratory – it was therefore deemed to not rely upon bushland to sustain populations within the study region.

For most species the distinction between resident species restricted to bushland remnants (native species that only breed on native plants that are not urban weeds) or non-resident species (introduced species that breed on introduced plants) was clear-cut. For the remainder, several were then allocated to the non-resident category if they bred only on introduced weeds within the study region, or if the species account in Braby (2000) contained either of the terms ‘migrant’ or ‘vagrant’. To complete the classification, additional local information was obtained from Hay et al. [1994]. For *Heteronympha merope*, *Geitonuera minyas* and *Delias aganippe* they state, respectively: “…sometimes colonise areas of gardens left fallow for grasses”; “…one of the more common butterflies of woodland areas around Perth”; and “…plentiful inland, although uncommon along the coast”. In the case of *Delias aganippe,* the usual mistletoe host plants of this species (particularly *Amyema miquelii*) are very rare or absent from bushlands in the study area, resulting in a classification of ‘non-resident’. Notably, if the study were conducted in inland areas, this species would be classified as ‘resident’. Overall, the classification of species used in the thesis differs only slightly from the only other Australian study (Braby and Edwards, 2006) that classified species into ‘resident’ or ‘non-resident’ in bushland. These differences arise because of local variation in the availability of the their host plants.

Because day-flying moths have habits similar to those of butterflies it is common practice to include these in surveys. The most notable of these are the sun-moths (*Synemon* spp., Castniidae), conspicuous day-flying moths often confused with butterflies (Douglas 2004). With only 43 recognized Australian species (of which 23 have been formally described) they are a small group in comparison with butterflies, although 24 species are known from the south-west bioregion, almost half the number of native butterfly species (Anonymous 1993, Edwards 1997a, b). One species, *Synemon gratiosa*, has a distribution restricted to the Swan Coastal Plain within the Perth metropolitan region and is listed as endangered (Burbidge 2004) but little is known about the others, many of which are poorly collected (Edwards 1997a). Any other day-flying moths that were encountered during the surveys were included, but they were not specifically targeted. The group is therefore likely to be under-sampled in this study.

Table 1.2. Butterflies recorded from south-west Western Australia (Sw WA) and the Swan Coastal Plain (SCP) bioregion (Braby 2000). In each region taxa are classified as either: native (n); introduced (i); self-introduced (s); migratory (m); or vagrant (v). Species of the SCP are classified as either resident (r1: breeding exclusively on native plants and restricted to remnant bushland; r2: breeding on both native and introduced plants, but predominantly restricted to remnant bushland; r3: myrmecophageous on native ant species and restricted to remnant bushland) or non-resident (nr1: introduced or native species breeding exclusively on introduced plants in the study region; nr2: rare migrants or vagrants within the study region; nr3: native species breeding on both native and introduced plants, but known to be highly vagile (i.e. migratory or vagrant) and not restricted to remnant bushland). Host plant(s) with the suffix * are or include species introduced to the SCP.

Taxon	Sw WA	SCP	Resid-ence	Voltin-ism	Flight period in region	Major host plant(s)
Butterflies						
Exometoeca nycteris Meyrick 1888	n			uni	Oct-Nov	
Trapezites sciron sciron Waterhouse & Lyell 1914	n	n	r1	uni	Sept-Nov	*Lomandra caespitosa*
T. atkinsi Williams, Williams & Hay 1998	n			uni	Oct-Nov	
T. argenteoornatus (Hewitson 1868)	n	n	r1	uni	Sept-Nov	*Acanthocarpus preissii*
T. waterhousei Mayo & Atkins 1992	n			uni		
Anisynta sphenosema (Meyrick & Lower 1902)	n	n	r2	uni	Mar-May	Various grasses*
Hesperilla donnysa albina Waterhouse 1932	n	n	r1	bi	Sept-Nov, Mar-Apr	*Gahnia trifida*
H. donnysa galena Waterhouse 1927	n			uni		
H. chrysotricha chrysotricha (Meyrick & Lower 1902)	n	n	r1	uni?	Sep-Nov	*Gahnia trifida*
Motasingha dirphia (Hewitson 1868)	n	n	r1	uni	Oct-Nov	*Phlebocarya ciliatum*
M. trimaculata occidentalis Moulds & Atkins 1986	n	n	r1	uni	Oct-Nov	Unknown (native sedge)
Antipodia dactyliota (Meyrick 1888)	n			uni		
Anisynta albovenata albovenata (Waterhouse 1940)	n			uni		
A. albovenata fuscata (Parsons 1965)	n			uni		
Croitana croites (Hewitson [1874])	n	n	r1	uni	Sept-Oct	Native grasses
Mesodina cyanophracta Lower 1911	n	n	r1	uni	Oct-Dec	*Patersonia occidentalis*
M. hayi Edwards & Graham 1995	n			uni		
Taractrocera papyria agraulia (Hewitson 1868)	n	n	r2	multi	Sept-Apr	Various grasses*
Cephrenes augiades sperthias (C Felder 1862)	i	i	nr1	multi	Sept-May	Introduced palms*
C. trichopepla (Lower 1908)	i	i	nr1	multi	Sept-May	Introduced palms*

Taxon	**Sw WA**	**SCP**	**Resid-ence**	**Voltin-ism**	**Flight period in region**	**Major host plant(s)**
Papilio demoleus sthenelus Macleay 1826	n	m	nr2			
Catopsilia pomona pomona (Fabricius 1775)	s	s	nr1	multi	Apr-Jun	*Cassia fistula**
Eurema smilax (Donovan 1805)	m	m	nr2			
E. hecabe hecabe (Linnaeus 1758)	m					
Belenois java teutonia (Fabricius 1775)	m	m	nr2			
Delias aganippe (Donovan 1805)	n	n	nr2	multi	Sept-May	
Peiris rapae rapae (Linnaeus 1758)	i	i	nr1	multi	All year	
Geitoneura klugii (Guerin-Meneville [1830])	n	n	r2	uni	Nov-Dec	Various grasses*
G. minyas (Waterhouse & Lyell 1914)	n	n	r2	uni	Sept-Oct	Various grasses*
Heteronympha merope duboulayi (Butler 1867)	n	n	r2	uni	Nov-Dec, Feb-Apr	Various grasses*
Acraea andromacha andromacha (Fabricius 1775)	v					
Junonia villida calybe (Fabricius 1787)	n	n	nr3	multi	Sept-May	Unknown, *Plantago* sp.*
Vanessa kershawi (McCoy 1868)	n	n	nr3	multi	Sept-May	*Arctotheca calendula**
V. itea (Fabricius 1775)	n	n	nr3	multi	Sept-May	*Parietaria debilis*
Danaus chrysippus petilia (Stoll 1790)[1]	n	n	nr1	multi	Sept-May	*Gomphocarpus fruiticosa**
D. plexippus plexippus (Linnaeus 1758)	i	i	nr1	multi	Sept-May	*Gomphocarpus fruiticosa**
Acrodipsas brisbanensis (Miskin 1884)	n	n		uni		
Hypochrysops ignitus oliffi Miskin 1889	n			uni		
H. halyaetus Hewitson 1874	n	n	r1	uni	Oct-Nov	*Jacksonia sternbergiana* and *Daviesia divaricata*
Ogyris oroetes apiculata (Quick 1972)	n	n		multi?		
O. amaryllis meridionalis (Bethune-Baker 1905)	n	n	r1	multi?	Oct-Nov, Feb-Apr	Mistletoes
O. otanes arcana Williams & Hay 2001	n			multi		
O. otanes sublustris Williams & Hay 2001	n			multi		
O. idmo idmo (Hewitson 1862)[2]	n	n	r3	variable	Nov-Dec	Myrmecophageous
O. subterrestris petrina Field 1999	n			multi		
Jalmenus icilius Hewitson [1865]	n	n	r1	uni or bi	Oct-Dec	*Acacia saligna*
J. inous inous Hewitson [1865]	n	n	r1	uni or bi	Oct-Dec	*Acacia saligna* and *Daviesia divaricata*
J. inous notocrucifer Johnson, Hay & Bollam 1992	n			uni		
Candalides cyprotus cyprotus (Olliff 1886)	n	n	r1	uni	Sept-Oct	Unknown native plant
C. hyacinthinus simplex (Tepper 1882)	n			uni		

Taxon	Sw WA	SCP	Resid-ence	Voltin-ism	Flight period in region	Major host plant(s)
C. hyacinthinus gilesi Williams & Bollam 2001	n			uni		
C. acastus (Cox 1873)	n	n	r1	multi?	Sept-Nov, Mar-Apr	*Cassytha* spp.
C. heathi heathi (Cox 1873)	n	n	r1	uni	Oct-Dec	Unknown
Nacaduba biocellata biocellata (C & R Felder 1865)	n	n	r2	variable	All year	*Acacia* spp.*
Theclinesthes miskini miskini (Lucas 1889)	n	n	r1	multi	Sept-May	*Acacia saligna*
T. albocincta (Waterhouse 1903)	n			uni		
T. hesperia hesperia Sibatani & Grund 1978	n	n	r1	uni	Sep-Dec	*Adriana quadripartita*
T. hesperia littoralis Sibatani & Grund 1978	n			uni		
T. serpentata serpentata (Herrich-Schaffer 1869)	n	n	r1	uni?	Oct-Nov	*Atriplex* and *Rhagodia* spp.
Neolucia agricola occidens (Waterhouse & Lyell 1914)	n	n	r1	uni	Sept-Nov	*Jacksonia sternbergiana* and *Daviesia divaricata*
Lampides boeticus (Linnaeus 1767)	n	n	nr3	multi		Various legumes*
Zizina labradus labradus (Godart [1824])[3]	n	n	r2	multi	All year	Various legumes*
Day-flying moths						
Synemon sp. (Perth) (E.D. Edwards pers.comm.)	n	n	r1	uni	Sep-Dec	Various sedges
S. gratiosa Westwood 1877	n	n	r1	uni	Mar-Apr	*Lomandra hermaphrodita* and probably *L. maritima*
Pollanisus cuprea Walker 1854	n	n	r1	uni or bi	Aug-Nov	*Hibbertia hypericoides*
Hecatesia thyridion Feisthamel 1839	n	n	r1	multi?	unknown	*Cassytha* spp.
Periscepta polysticta[4] (Swinhoe, 1892)	n	n	r1	uni	unknown	*Hibbertia* spp.

[1]: Now *Danaus petilia* (Stoll, 1790) (Lushai et al. 2005).

[2]: Now *Ogyris idmo* (Hewitson, 1862) (Braby and Douglas 2008).

[3]: Now *Zizina otis labradus* (Godart [1824]) (Yago et al. 2008).

[4]: Now *Periscepta butleri* (M.F. Braby pers. comm.).

1.5 Study area

The capital of the state of Western Australia, Perth is Australia’s fourth largest city (population 1.5 m) and houses 75% of the state’s population (Australian Bureau of Statistics 2008). The city is located on the Swan Coastal Plain beside the Swan River, bounded in the west by the Indian Ocean and in the east by the low coastal Darling escarpment. The suburban area extends up to 125 km north–south and 50 km inland, occupying 5400 km^2. The region has a Mediterranean-type climate with warm, dry summers (Dec–Feb average 29 °C maximum and 17 °C minimum temperature, 49 mm rainfall) and mild winters (Jun–Aug average 18 °C maximum and 9 °C minimum temperature, 490 mm rainfall) (Bureau of Meteorology 2008). The vegetation and climate of the region make it prone to frequent bushfires that have shaped the biological landscape and continue to be important for the preservation and conservation of the native biota (Abbott 2003, Abbott and Burrows 2003). Of the original *Banksia* and *Eucalyptus* open woodlands that dominated the coastal plain prior to European settlement only 18% remains as fragments of remnant ‘bushland’, surrounded by suburban development (Government of Western Australia 2000).

With the population of the city expected to double within 50 years, increasing pressure will be placed on the mineral and biotic resources of the region, particularly the limited water resources. Coupled with declining rainfall and increased temperatures resulting from climate change, this led Australian *Scientist of the Year* Dr. Tim Flannery to predict that Perth would become the world’s first ‘ghost metropolis’, the residents being forced to abandon the city due to lack of water (BBCNews 2007). While successive urban planning schemes and initiatives implemented to decrease per-capita water consumption and to increase water supplies are likely to resolve this problem (Kennewell and Shaw 2008), human-induced impacts on remnant bushland and the native species it protects will continue and increase.

1.6 Study objectives and thesis structure

1.6.1 Study objectives

The aim of this research is to review and adapt existing methods of assessing and modelling biodiversity of butterflies and day-flying moths in south-west Western Australia, and to determine those factors affecting their presence, abundance and species richness in urban habitat fragments. I sought to resolve the following questions about the ecology and conservation of butterflies and day-flying moths in urban habitat remnants:

(1) What methods and survey regime are needed to assess diversity and abundance of butterflies in remnants?

(2) How do individual species vary in their phenology and detectability?

(3) How should total species number be modelled in relation to site area and other characteristics?

(4) How do the patterns of species occurrence relate to habitat characteristics and their interactions?

(5) What implications do the answers to these questions have for conservation and management of butterfly populations in urban habitat fragments?

1.6.2 Thesis structure

I initially investigated the efficiency of the strip transect method to assess diversity of butterflies and day-flying moths in habitat fragments (chapter 2). I then used this method to sample 46 patches of remnant bushland in the Perth metropolitan region of the Swan Coastal Plain bioregion (chapter 3). After reviewing methods to analyse such species–area–habitat data (chapter 4), I determined the effects of site characteristics and connectivity on the presence, abundance and species richness of butterflies and day-flying moths within isolates (chapter 5). The main results of each study and how these affect our understanding of the ecology and conservation of butterflies and day-flying moths within isolates are reviewed in the General Discussion (chapter 6).

Chapters 2–5 are individual papers either published (chapter 2), in press (chapters 3, 4) or in review (chapter 5). Each is therefore self-contained with a list of references cited within the paper. References cited in chapters 1 and 6 are listed after chapter 6. Each chapter is formatted according to the style of the relevant journal.

Chapter 2 – Assessing diversity of diurnal Lepidoptera in habitat fragments: testing the efficiency of strip transects

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Abstract

Species richness is the most widely used measure of biodiversity, but the relationship between the observed and true numbers of species present in a study site is not always investigated. A field study at 27 habitat remnants was used to measure the effectiveness of a survey regime for assessing species richness of butterflies and day-active moths in south-west Western Australia. Observed species richness was compared to known species richness and to statistical estimates of true species richness, and the bootstrap was found to be the best predictor of true richness. A regime of 10m-wide walk transects sampled on six occasions at two-weekly intervals during the austral spring (mid September to mid December) gave an almost complete inventory of resident species for each site (approximately 87% of the fauna detected), consistent with two previous studies that have assessed sample completeness in temperate areas. The abundance of diurnal lepidoptera showed large temporal variation over the flight season, and varied to a lesser extent with time of day and temperature, but not with cloud cover or wind speed. Transect route and sampling frequency were the most important considerations in devising a survey regime: transects placed off tracks detected both more species and more individuals per unit length. The fraction of the site area sampled was relatively unimportant, and even low sampling fractions of 1–2% may be adequate if the number and frequency of surveys is sufficient. The design of future surveys would be facilitated if sampling fraction was routinely reported and examined in relation to sample completeness.

Keywords: Butterflies; day-flying moths; estimating species richness; sample completeness; sampling fraction.

Introduction

Estimating species diversity of an area by means of surveys is a fundamental task in biogeography, ecology and conservation biology. Although the purposes of such surveys are diverse (e.g. biodiversity assessment, comparison of experimental treatments, assessing effects of habitat characteristics, management or disturbance, or population monitoring), designing an effective survey strategy is essential to obtain reliable results and use resources efficiently. Survey regimes to inventory species diversity are increasing, particularly within habitat fragments, as more conservation agencies seek to document baseline data on biodiversity against which to assess temporal change or change in relation to management practice. Species richness is a widely used measure of biodiversity, but the relationship between the observed and true values of species richness is not always investigated (Watson 2003, Kery and Plattner 2007). Some species will not be detected even though they are present at a site, a fact that is commonly overlooked (Mackenzie *et al.* 2003). This imperfect detection produces underestimates of site occupancy, an important index of the current state of a population, and a crucial factor in defining conservation priority. Even low rates of false negatives (the failure to detect a species which is present) introduce bias that can confound models of the spatial pattern of biodiversity, and have a significant and detrimental effect on habitat occupancy models (Rosenzweig 1995, Tyre *et al.* 2003). If the false negatives are related to site characteristics then systematic errors may be introduced, possibly leading to erroneous conclusions (Verner 1985, Watson 2003). Thus, failure to verify the accuracy of a survey regime may have a significant and detrimental impact on subsequent conclusions (MacKenzie *et al.* 2003, Tyre *et al.* 2003, MacKenzie *et al.* 2004, MacKenzie 2005).

To overcome this impediment, abundance- or incidence-based data can be used to estimate true species richness by extrapolating species accumulation curves or by non-parametric methods (Colwell and Coddington 1994). These estimates are more accurate than observed species richness, but may still be imprecise or biased (Palmer 1990, Chiarucci *et al.* 2003, Brose and Martinez 2004, Walther and Moore 2005). The methods vary in accuracy depending upon factors such as the species abundance distributions (Colwell and Coddington 1994) and species mobility (Brose and Martinez 2004), and the best performing estimators vary between data sets (Brose *et al.* 2003). The efficacy of the various estimators has most often been tested with simulated data, as empirical studies rarely record total species richness (Walther and Moore 2005).

The precision and efficiency of the methods used to assess the diversity of butterflies has seldom been examined (Kery and Plattner 2007). The predominant sampling method is the strip transect: a pre-determined route through the study site that is traversed at intervals during the flight season (Douwes 1976, Pollard 1977). The transect is divided into sectors, so that is effectively a set of contiguous plots, and all individuals within a defined distance from the observer(s) are identified and tallied. Transect length may be fixed (e.g. Caldas and Robbins, Cowley *et al.* 2001a, 2001b; Saarinen 2002a, 2002b; Saarinen and Jantunen 2002) or variable (Thomas 1983, MacNally and Fleishman 2002, Panzer 2002, Krauss *et al.* 2003). Originally devised to monitor the abundance of butterflies, the method is now used widely to inventory butterflies in remnant habitat. However, the considerations that apply to survey strategies for assessing abundance also apply generally to assessing species richness. To devise a survey regime a number of parameters must be defined: transect route, width and length; number, frequency and timing of surveys; and time of day and weather restrictions. The strip transect method is also used widely to inventory other taxa, notably birds (Rosenstock *et al.* 2002).

The aim of this study was to measure the effectiveness of the strip transect method for assessing species richness of butterflies and day-active moths in south-west Western Australia and to quantify its level of precision. Specifically, three questions were addressed: (i) in obtaining species lists to a prescribed level of accuracy, what is the optimal combination of transect length, number, timing and frequency of surveys?; (ii) should transects be conducted using existing tracks and walk paths, or be placed randomly?; and (iii) what constitutes acceptable weather conditions for conducting surveys?

Methods

Strip transects were placed in 27 habitat remnants within the Swan Coastal Plain bioregion (Thackway and Cresswell 1995), south-west Western Australia. This region has a Mediterranean-type climate with a pronounced summer drought and is prone to frequent fires (Hopper and Gioia 2004). Vegetation at the sites was predominantly low open woodland or low open forest dominated by *Banksia* or *Eucalyptus,* although some contained wetland and sedgeland vegetation, coastal heathland or estuarine-fringing vegetation (Beard 1990). Most sites were selected from a comprehensive review of remnant vegetation within the Perth metropolitan region (Government of Western Australia 2000); full details of the sites are given by Williams (2009).

The Australian butterfly fauna is well documented (Braby 2000): 56 species occur within the south-west region, of which 10 are introduced, occasional migrants or vagrants. Of the native species, 28 have been recorded within the study area. The majority of these (20 species) are univoltine or predominantly so, with a single annual generation of adults restricted to spring, and only one species has an exclusively autumn-flying generation. The day-active moth fauna is less well-studied, and the number of taxa within the study region is unknown. The most notable are the sun-moths (*Synemon* spp., Castniidae), conspicuous day-active moths that are often confused with butterflies. With only 45 Australian species they are a small group in comparison with butterflies, although 24 of these species are known from the south-west region, almost half the number of native butterfly species (Edwards 1997a, 1997b). One species has a distribution restricted to the study region: the univoltine, autumn-flying species *Synemon gratiosa*, which is listed as endangered (Burbidge 2004). However, little is known about the others, many of which are poorly collected (Edwards 1997a). For butterflies, taxonomy follows the standard works of Braby (2000); for day-flying moths taxonomy follows Common (1990) and Edwards (1997b).

At each site a fixed-route transect was established to sample variation in vegetation type, structure and regeneration age since the last fire. Transect length varied with site area, ranging from 190 to 5,100 m, and smaller sites typically had shorter transects but a higher sampling fraction (the fraction of the site area sampled by the strip transect). Full details of the sampling methods are provided by Williams (in press). As a pilot study, one remnant was sampled intensively on 36 days over a 58 day period between late October and mid December 2001, and in 2002 five remnants were sampled on 7–13 occasions from mid October to late December, and in March 2003. In spring 2003, all of the remnants were sampled at fortnightly intervals on six occasions from mid September to late December, and twice between late February and early April 2004.

In all analyses, species that are vagrants, migrants, or introduced to the region were excluded, a standard approach used by previous studies (Hill 1987, Braby and Edwards 2006). This division is equivalent to the concept of ‘matrix’ and ‘island’ species (Pollard and Yates 1993): ‘matrix’ (non-resident) species are typically highly dispersive, common, occur in both remnant habitat and intervening areas, and are of little conservation concern; ‘island’ (resident) species typically have low dispersal rates, are local or uncommon, and are restricted to remaining suitable habitat patches.

To assess the completeness of the species lists for each site, observed resident species richness was compared with known species lists and with estimates of species richness predicted using statistical extrapolation. As only one butterfly and one moth species are known to fly exclusively in autumn, and abundances in autumn were very low, only the data from the spring surveys was used in this analysis. To determine the best extrapolation method for these data the approach suggested by Colwell and Coddington (1994, p.107) was used: the predictions of a number of methods were compared with known inventories. Accurate species lists could be determined for three sites, based on the collections of the Western Australian Museum, the Western Australian Department of Environment and Conservation, and the records of amateur collectors. Amateur collectors tend to be biased, in that they are more prone to overlook common, easily detected species, but this bias is useful in detecting rare species. Nine extrapolation methods that have been shown to provide good results were compared: two that use abundance data (ACE, Chao–1) and seven that use site occupancy data (ICE, Chao–2, jack–1, jack–2, bootstrap, MM runs and MM means). Details of these estimators are given by Colwell and Coddington (1994) and Colwell (2005). Estimates were calculated using the EstimateS software package (Colwell 2005) and compared with known values using both absolute and relative measures of accuracy (the mean square error, *MSE* = sum of squared errors, and scaled *MSE*, *SMSE* = sum of squared relative errors, respectively; Walther and Moore 2005).

At four sites the off-track surveys were compared with adjacent, paired sectors of equal length extracted from the longer on-track surveys, on the 33 sampling occasions when both transect types were conducted. Average counts for each species, and for the total number of individuals, were compared by two-way analysis of variance (ANOVA) using the SAS statistical package (SAS Institute 2006). Logarithmic transformation ($\log(x+1)$) was necessary to satisfy the assumptions underlying ANOVA of approximate normality and homoscedasticity of residuals.

The effects of site, sampling period, time of day, weather conditions and the number of observers on counts and on the number of species detected were analysed using a general linear model. Each survey was allocated to one of nine sampling periods, corresponding to the half-monthly intervals from mid September to late December, or to the first or second half of March. The time of day at the mid-point of each survey was allocated to one of 12 half-hourly intervals. Average temperature during each transect was allocated to one of 11 classes (2°C intervals above 15°C), wind speed into 5 classes (5 km/h intervals), and cloud cover to the nearest okta. Weather data (hourly air temperature, wind speed and 3 hourly cloud cover) were obtained from the Bureau of Meteorology Perth metropolitan recording station, located less than 20 km from all of the study sites. Counts were logarithmically transformed, and species richness square-root transformed, to satisfy the assumptions underlying the model.

Results

In total, the survey regime comprised 660 km of walk transects and sampled 14,605 individuals. I recorded 33 butterfly and three day-flying moth species (23 resident and 13 non-resident) with individual site richness varying between zero and 25 species; only five butterfly species known from the region were not detected. Full results of the surveys are detailed in Williams (in press).

Comparison of the alternative methods of predicting resident species richness showed that the bootstrap estimator was the most accurate, having the lowest absolute and relative measures of error (Table 1). Of the other estimators, Chao–2 was of comparable accuracy to the bootstrap, but all except the bootstrap produced occasional anomalous predictions that were in error by 20% or more of true richness. Although the bootstrap predictions underestimated true richness on average by 0.4 species, this was not significantly different from zero (95% confidence interval = –0.4, 1.2). Repeated sampling at the three sites over 2–3 years produced consistent estimates (range 78–100%) and averaged 88% of the known of species richness (Table 2). Assuming the total number of resident species predicted to occur at the remaining sites is accurate, the sampling regime detected 87% of the fauna (range 75–99%). The estimated fraction of species detected at each site was positively related to the number of observed species ($R^2 = 0.33$, $P = 0.003$) and to log(site area) ($R^2 = 0.32$, P = 0.03), and negatively but weakly related to sampling fraction (R^2 = 0.11, P = 0.10; Fig 1). Thus, the estimated proportion of species detected was generally lower in small, species-poor sites that had higher sampling fractions.

Table 1. Species richness of resident butterflies and day-active moths in spring at three sites with known species lists, compared with estimated richness using statistical extrapolation. Absolute (*MSE* = mean square error) and relative (*SMSE* = scaled *MSE*) measures of accuracy are given for each method, with smaller values indicating greater precision.

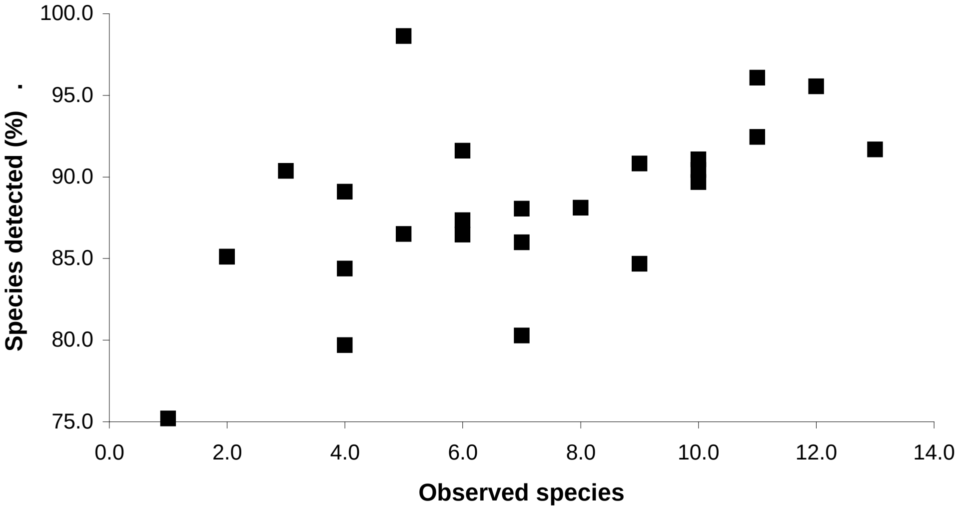
Site	**Koondoola**			**Warwick**		**Cottonwood**		***MSE***	***SMSE***
Known resident species	**13**			**12**		**9**			
Year	2001	2002	2003	2002	2003	2002	2003		
Surveys	36	10	6	5	6	4	6		
Estimator									
S obs	11	13	12	10	11	8	7	2.14	0.018
ACE	11.5	17.5	12.0	11.5	11.3	8.4	7.4	3.79	0.025
ICE	11.5	14.7	12.3	13.7	11.4	10.8	8.3	1.84	0.015
Chao 1	11.0	16.0	12.0	10.3	11.0	8.0	7.0	3.26	0.024
Chao 2	11.0	14.4	12.0	12.4	11.0	8.8	8.5	1.19	0.008
Jack 1	12.0	15.7	12.8	13.2	11.8	10.3	7.2	2.09	0.017
Jack 2	12.9	17.4	12.4	15.2	10.9	11.1	8.7	5.01	0.035
Bootstrap	11.5	14.2	12.6	11.4	11.7	9.1	8.0	0.79	0.006
MM Runs	10.7	14.4	14.9	32.5	16.5	16.1	15.0	76.89	0.600
MM Means	10.9	14.7	14.7	13.0	15.2	10.6	11.2	4.19	0.033

Table 2. Observed, known and predicted butterfly and day-active moth fauna using statistical extrapolation, at 26 remnant bushland sites on the Swan Coastal Plain, south-west Western Australia.

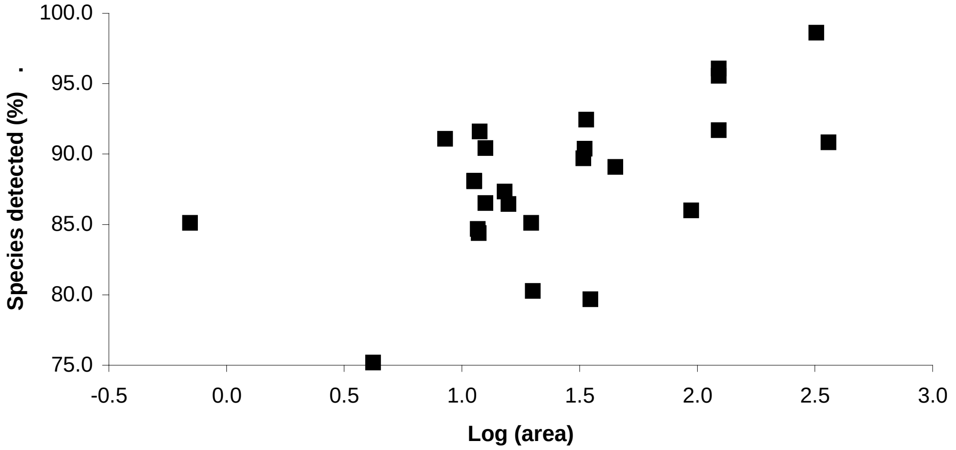
	Observed			Known		Predicted	
Site	Total species	Non-resident species	Resident species	Resident species	Resident species detected (%)	Resident species	Resident species detected (%)
Bold Park	15	5	9			9.9	91
Cottonwood	13	4	9	9	100	9.9	91
Cottonwood 2002			8		*89*		
Cottonwood 2003			7		*78*		
Errina Rd	15	4	10			11.0	91
Fred Samson	8	3	5			5.8	87
Harry Sandon	7	4	1			1.3	75
Hillview	4	2	2			2.4	85
Kensington	3	3	0			-	
Kings Park	11	5	5			5.1	99
Koondoola	25	11	13	13	100	13.1	100
Koondoola 2001			11		*85*		
Koondoola 2002			13		*100*		
Koondoola 2003			12		*92*		
Landsdale	10	4	6			6.9	86
Marangaroo	16	5	10			11.2	90
Mt Henry	10	3	6			6.6	92
Point Resolution	1	1	0			-	
Shenton	5	2	2			2.4	85
Shepherds Bush	9	3	6			6.9	87
Signal Hill	4	4	0			-	
Star Swamp	12	4	7			8.1	86
Trigg E	6	2	3			3.3	90
Trigg N	13	6	7			8.7	80
Trigg S	10	5	4			4.5	89
Trigg W	6	2	4			4.7	84
Wal Hughes	2	2	0			-	
Warwick	20	7	11	12	92	11.2	98
Warwick 2002			10		*83*		
Warwick 2003			11		*92*		
Warwick N	15	3	10			11.1	90
Warwick SE	17	5	11			11.9	92
Warwick SW	13	3	9			10.6	85
Wireless Hill	9	4	4			5.0	80
Total / *average*	36	13	23		*88*		*87*

Figure 1. Proportion of the estimated resident species richness detected in relation to (a) observed species richness, (b) site area, and (c) fraction of the site sampled.

(a)



(b)



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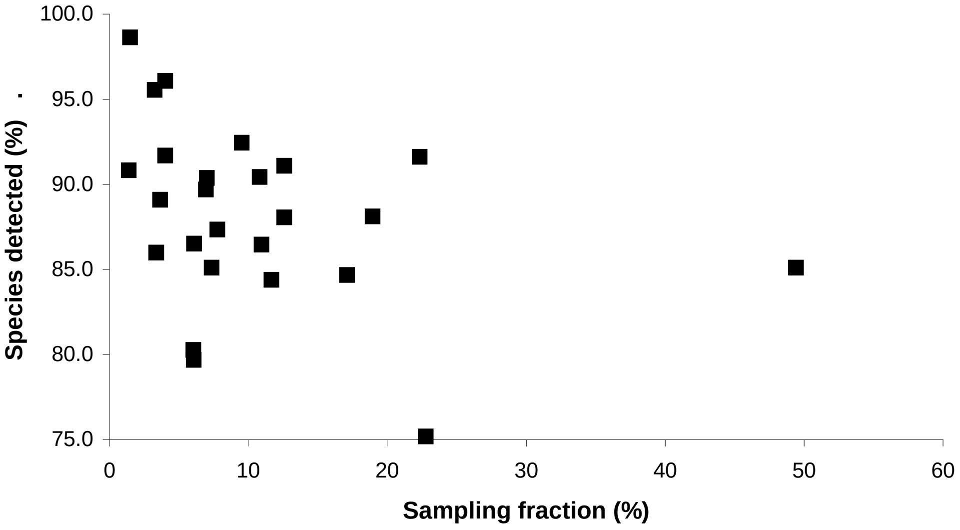


Comparison of species richness and counts between transect types showed that off-track routes generally detected both more species and individuals (Table 3). Four species were detected only off tracks, and one only on tracks, although three of these cases were singletons. Three species showed statistically significant differences in counts between transect types, with more individuals detected off tracks in each case. The overall density of individuals varied substantially between sites, but overall density off tracks was approximately twice that on tracks.

Sampling period and site had significant effects on both counts and the number of species detected, with sampling period having the largest impact (Table 4). There was a pronounced peak in density of both individuals and species in November and, other than the very low counts in the autumn surveys, counts in late December yielded the fewest individuals (Fig 2). Mean density of individuals was significantly lower before 1000 h and after 1430 h (Fig. 2; mean density between 1000 and 1430 h = 0.39 individuals per 100 m of transect, outside this period mean density = 0.16 individuals per 100 m; P = 0.05 by *post-hoc* single degree-of-freedom contrast). Temperature, weather conditions and the number of observers did not significantly affect either counts or the number of detected species. Counts were reasonably consistent between 20 °C and 32 °C; outside this range they were more variable.

Table 3. Number of individuals observed per 100m (means and standard errors) for on- and off-track transect surveys of diurnal lepidoptera at four sites on the Swan Coastal Plain, south-west Western Australia (* Significant difference between on- and off-track surveys by 2-way ANOVA, *P*<0.05).

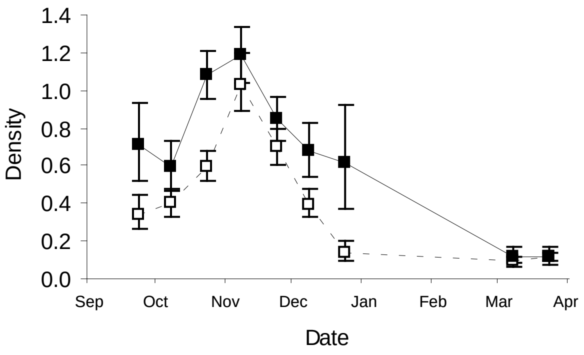
		Cottonwood		**Koondoola**		**Landsdale**		**Warwick**	
	Survey type	Off	On	Off	On	Off	On	Off	On
	Number of surveys	3	3	18	18	8	8	4	4
	Survey length (m)	717	710	929	949	273	313	760	758
Trapezites sciron	Count	0	0	2	0	0	1	0	0
	Mean	0.00	0.00	0.01	0.00	0.00	0.04	0.00	0.00
	se	0.00	0.00	0.01	0.00	0.00	0.04	0.00	0.00
Motasingha trimaculata and *M. dirphia**	Count	7	0	6	0	0	0	0	0
	Mean	0.33	0.00	0.04	0.00	0.00	0.00	0.00	0.00
	se	0.33	0.00	0.02	0.00	0.00	0.00	0.00	0.00
*Mesodina cyanophracta**	Count	8	1	111	30	2	0	2	0
	Mean	0.37	0.05	0.66	0.18	0.09	0.00	0.07	0.00
	se	0.23	0.05	0.13	0.04	0.09	0.00	0.04	0.00
Taractrocera papyria	Count	0	0	0	0	0	0	1	0
	Mean	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
	se	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Geitoneura klugii	Count	38	10	33	45	0	0	10	3
	Mean	1.77	0.47	0.20	0.26	0.00	0.00	0.33	0.10
	se	1.09	0.17	0.05	0.05	0.00	0.00	0.17	0.06
Heteronympha merope	Count	1	0	4	0	0	0	0	0
	Mean	0.05	0.00	0.02	0.00	0.00	0.00	0.00	0.00
	se	0.05	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Hypochrysops halyaetus	Count	1	1	61	70	0	0	30	21
	Mean	0.05	0.05	0.36	0.41	0.00	0.00	0.99	0.69
	se	0.05	0.05	0.11	0.15	0.00	0.00	0.70	0.40
Nacaduba biocellata	Count	0	0	0	0	0	0	1	0
	Mean	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
	se	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Neolucia agricola	Count	1	4	55	77	0	1	0	0
	Mean	0.05	0.19	0.33	0.45	0.00	0.04	0.00	0.00
	se	0.05	0.19	0.10	0.10	0.00	0.04	0.00	0.00
Zizina labradus	Count	0	0	0	1	0	0	0	0
	Mean	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
	se	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Synemon sp. aff. *sophia**	Count	5	4	308	166	1	1	7	2
	Mean	0.23	0.19	1.84	0.97	0.05	0.04	0.23	0.07
	se	0.17	0.19	0.31	0.19	0.05	0.04	0.11	0.07
Synemon gratiosa	Count	0	0	1	1	0	0	0	0
	Mean	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
	se	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Pollanisus cupreus	Count	0	0	0	1	4	6	0	0
	Mean	0.00	0.00	0.00	0.01	0.18	0.24	0.00	0.00
	se	0.00	0.00	0.00	0.01	0.18	0.24	0.00	0.00
TOTAL*	Count	70	33	1122	688	18	21	55	28
	Mean	3.25	1.55	6.71	4.03	0.82	0.83	1.81	0.92
	se	1.80	0.57	0.84	0.44	0.30	0.29	0.90	0.46

Table 4. Analysis of variance of counts (log (x + 1) transformed) and species richness (square root transformed) of diurnal lepidoptera in 290 surveys of 27 sites, in south-west Western Australia.

		Count			Species richness		
Source	df	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Site	26	4.68	7.19	<.0001	0.113	7.73	<.0001
Sampling period	8	15.62	23.98	<.0001	0.177	12.05	<.0001
Time of day	11	1.44	2.21	0.01	0.024	1.65	0.09
No. of observers	2	0.60	0.92	0.40	0.006	0.40	0.67
Cloud cover	7	0.28	0.44	0.88	0.011	0.74	0.64
Temperature	10	0.73	1.13	0.34	0.009	0.62	0.79
Wind speed	4	0.79	1.21	0.31	0.032	2.18	0.07
Residual	221	0.65			0.015		

Figure 2. Density of diurnal lepidoptera in transect surveys in south-west Western Australia: mean number of species detected per km of transect ± standard error (closed symbols) ; and mean number of individual insects detected per 100 m of transect ± standard error (open symbols), in relation to (a) time of year (fortnightly intervals in spring and autumn); (b) time of day (half-hourly intervals); (c) cloud cover (oktas); (d) temperature (2 °C intervals); (e) wind speed (5 km/h intervals); and (f) number of observers.

(a)



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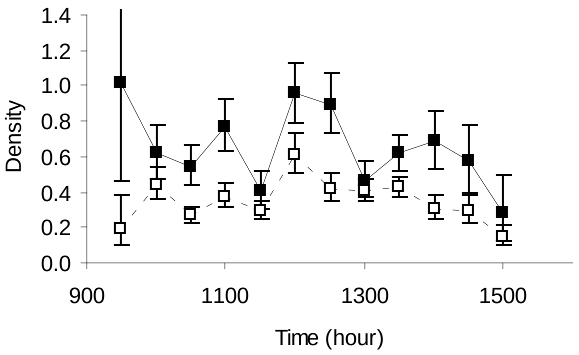

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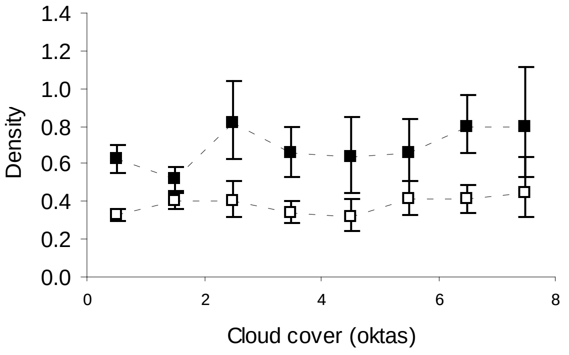

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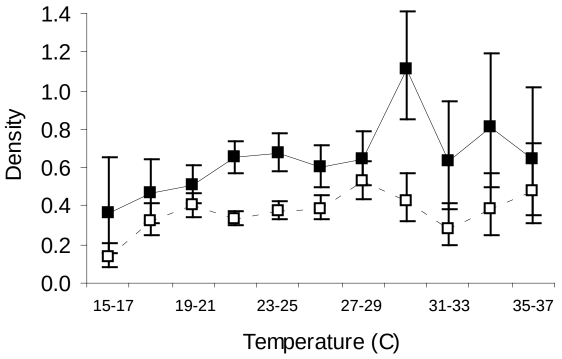
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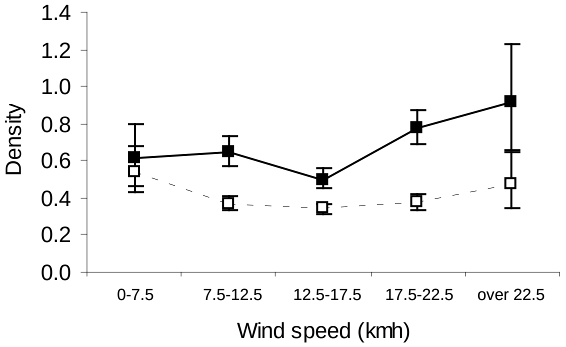
31-33
35-37
Temperature (C)

(e)


1.4
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Density
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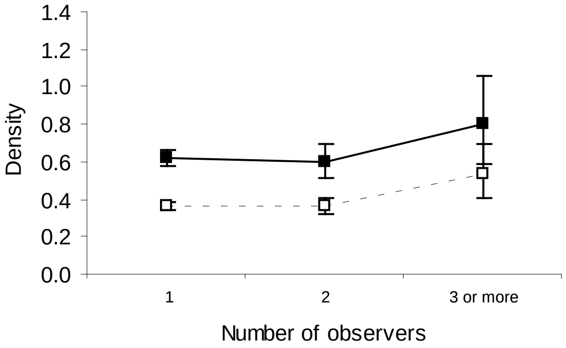
17.5-22.5
over 22.5
Wind speed (kmh)

(f)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Density
1
2
3 or more
Number of observers

Discussion

The sampling regime used in this study detected 88% of the known, and 87% of the estimated resident fauna. In contrast to its usually poor accuracy, the bootstrap was the best estimator of total species richness although performance of estimators is known to vary between data sets (Walther and Moore 2005). Only two previous studies have examined sampling adequacy for butterflies in temperate regions. In Switzerland, the Swiss Biodiversity Monitoring Scheme inventoried butterflies with seven surveys conducted over 5 months, using 2.5 km long, 5 m wide transects within 1 km^2 grid cells (i.e. a sampling fraction of 1.25%). This regime detected 66–70% of taxa present (Birrer *et al.* 2005, Kery and Plattner 2007). In South Australia, Collier *et al.* (2006) studied three urban remnants using 10 m wide transects; I calculated the sampling fraction at these sites to be 0.3, 1.9 and 3.4%. The surveys, conducted over two flight seasons, detected 75–82% of the estimated total fauna in the first year (8–10 surveys at an average 1 monthly interval), and 69–80% of the fauna in the second year (9 surveys at fortnightly intervals). The site with the smallest sampling fraction had the lowest proportion of the fauna detected each year (69 and 75%); whereas the other two sites were similar (80 and 80%, 82 and 76%). In both of these studies the figures for actual and expected total species included migratory, vagrant and introduced species, and it could be expected that the figures for resident species detected were higher. Combining the results of all three studies suggests that at sampling fractions above about 1%, monthly surveys detected 65–80% of the fauna and fortnightly surveys increased this to 75–90%.

The lack of any positive relationship between the fraction of resident species detected and sampling fraction appears counter-intuitive. It might be expected that increased sampling fractions should detect a greater proportion of the species present, although this may not necessarily follow for mobile species such as butterflies that have varying levels of detectability and seasonal flight periods (Brose and Martinez 2004, Kery and Plattner, 2007). The results show that sampling frequency and sampling fraction need to be considered together: once sampling fraction is adequate, effort is better allocated to more frequent surveys. In a comparable study of birds, Watson (2003) showed that increased site visits were more productive than extended sampling times, and this is likely to apply equally to butterflies.

Watson (2003) also discussed the issues relating to fixed- and variable-area sampling in habitat patches: if sampling area within each patch is a fixed size quadrat (as is the usual practice in bird surveys, and a common practice in surveys of butterflies), the quadrat becomes the focus, not the patch. This prevents hypotheses being framed in terms of the patch characteristics, such as area or number of habitats, as the quadrats sample a fixed area and a fixed number of habitats that may not be reflective of the patch area or the number of habitats within the patch. However, it is almost invariably the patch that is of interest, not the quadrat. Some practical problems also arise if the sample area is fixed. In this study, the smallest patch was 0.7 ha and if fixed-area sampling was used, this would limit transect length to 700 m in all other patches: for the largest site, this would result in a sampling fraction of 0.2%. In sampling isolated remnants, fixing transect length across all sites may result in over- or under-sampling of small and large remnants respectively. If species richness increases with area, which is usually the case, this would result in substantial bias.

Using only existing tracks introduced bias in which species were detected and affected estimates of their relative abundance. Numerous studies have shown that many butterfly species favour open areas, such as tracks or early successional habitats (New 1991, Thomas and Hanski 1997, Dover and Rowlingson 2005), open habitats, habitat edges and artificial environments such as roads, cleared corridors under powerlines and field margins (Munguira and Thomas 1992, Yahner, 1996, 1999; Bramble *et al.* 1999, Wahlberg *et al.* 2002, Saarinen 2002a, Saarinen *et al.* 2005, Forrester *et al.* 2005). In contrast, this study found no evidence of any species that favoured tracks, and more species and individuals were detected in undisturbed vegetation.

Three interrelated factors, time of day, weather conditions and time of year, are known to affect the activity of diurnal lepidoptera (Pollard 1977) and this was also found to be the case in this study. Time of year had a large impact on counts but, within broad limits, weather, time of day, and the number of observers had minor or negligible effects. This accords with the findings of Pollard, Elias and Skelton in Monk’s Wood, England (Pollard and Yates 1993) who showed that the week of recording had the greatest effect on counts and in comparison the effects of time of day, weather and number of observers were relatively small. In England, northern Europe and the northern USA threshold temperatures (usually 13–17 °C, e.g. Pollard

1977, Bergman *et al.* 2004, Clausen *et al.* 2001, Kraus *et al.* 2003, Yahner 1999, 2001; Keller and Yahner 2002, Swengel 1996, 1998a, 1998b; Swengel and Swengel 2001) are considerably lower than elsewhere (typically 18–25 °C, e.g. Caldas and Robbins 2003, Rudolph and Ely 2000). The results of this study accord with these findings, and conducting surveys between 19 °C and 33 °C produced consistent counts.

The observed number of species may be a misleading indicator of true species richness unless sampling adequacy is confirmed. This study found that even low sampling fractions were adequate to detect the majority of species, and that the number and hence frequency of surveys is more likely to be a critical factor in maximizing species detection. A practical approach to compiling species lists is to set sampling effort above some minimum fraction of the site area, and to sample all of the habitats present, including those resulting from disturbance. The sampling effort should be greatest in more species-diverse areas; in this study the relatively small fauna was adequately inventoried with six site visits and sampling fractions of 1.3% or greater. To attain a defined level of sampling adequacy, proportional sampling or the use of results-based stopping rules (Soberón and Llorente 1993, Colwell and Coddington 1994, Watson 2003) may be a more valuable method of increasing the efficiency of surveys. Comparisons between studies and the design of future surveys of remnant habitat would be facilitated if sampling fraction was routinely reported and examined in relation to sample completeness.

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Chapter 3 – Butterflies and day-flying moths in a fragmented urban landscape, south-west Western Australia: patterns of species richness

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Abstract

Surveys of butterflies and day-flying moths were conducted at 46 bushland remnants in the Swan Coastal Plain, Western Australia, between 2001 and 2005. A total of 17 075 individuals were recorded, representing 35 butterfly and 5 day-flying moth species. Individual site species richness varied between one and 27 species. Two main groups of taxa were identified: (i) species that are reliant on remnant native vegetation for breeding and are entirely or predominantly restricted to remnant bushland (resident species or urban avoiders, 27 taxa); and (ii) species that now breed primarily on introduced plants and disperse readily through the urban matrix, but which also visit remnant bushland and sometimes breed there (non-resident species or urban adapters, 13 taxa). Estimated species detectability varied widely both between species and seasonally, but for most taxa was consistent across the three years of the study. Peak detectability was strongly related to observed abundance, something that is well known (intuitively), but has rarely been demonstrated (quantitatively). Only one listed endangered species was recorded, the graceful sun-moth (*Synemon gratiosa*) which was observed in low numbers at six sites. Several species were encountered less frequently, although these have populations outside the region. Few of the surveyed remnants were considered to have an intact butterfly fauna; it is inferred that the majority had lost some or all of their original resident species. The reliance of many species on specific host plants, and the ability of some to adapt to introduced weeds, are important factors in their persistence within remnants. These bushland remnants are effectively habitat 'islands' for butterflies and day-flying moths, and the few remaining species-rich bushlands are therefore of regional importance for conservation of this group. This paper serves as a baseline study against which to monitor any future changes to the butterfly fauna of these remnants.

Key words: Butterfly fauna, Moth fauna, Conservation, Detection probability, Fragmented landscapes, Site occupancy, Urban ecosystems.

Introduction

Patches of remnant vegetation are now common features in urban and rural landscapes throughout the world. Faunal populations in these fragments are isolated, and the resources necessary for breeding and reproduction may have been altered, potentially causing decline and local extinction of some species. Like other organisms, butterflies are increasingly dependent on remnant vegetation for survival, especially in urbanized areas (Shapiro and Shapiro 1973, Ruszczyk and De Araujo 1992, Blair 1999, Connor *et al.* 2002, Newland 2003, Brown and Freitas 2004). The urban area of the Perth Metropolitan region in south-west Western Australia is an example of such a disturbed landscape, with fragments of remnant vegetation varying in size, time since isolation and vegetation condition. The intervening urban matrix contains few resources for many of these species and may present a substantial barrier to dispersal.

The need to conserve invertebrate animals (Ponder and Lunney 1999) has only been recognized relatively recently (New 1991). The reason for this increased conservation concern is simple: invertebrates are the most important component of the world fauna, both in numbers of species and biomass. As one of the best known and recognisable groups of invertebrates, butterflies have been a flagship for invertebrate conservation. Studies to systematically monitor butterflies for the purpose of conservation commenced in Britain in the 1960s (Pollard and Yates 1993) and the information collected has proven to be important not only for conserving individual species of butterflies, but has also provided insights into temporal changes in habitat and climate, particularly those caused by changes to land use practices and global warming (Warren *et al.* 2001). The threats to butterflies are generally the same as for other fauna: habitat destruction or alteration; changes to management practices; isolation of remnant habitat; pollution and use of chemical insecticides and herbicides; climate change; and in some cases overcollecting or trade in specimens (New 1991; Pollard and Yates 1993; Beaumont and Hughes 2002).

In Australia, several studies have documented the conservation status of individual species or genera (New 1993; Kitching *et al.* 1999; Braby 2000), and a major review of the Australian fauna was conducted by Sands and New (2002). Although substantial distributional data on Australian butterflies has been amassed, such data do not provide unbiased estimates of changes in abundance or distribution. In evaluating the conservation needs of Australia's butterflies, Sands and New (2002) censused expert opinion as a means of identifying threatened taxa. They cited the lack of systematic surveys in conservation reserves and the lack of a national database as the major impediments to establishing the conservation status of many species, recommending that State conservation agencies accept the responsibility of undertaking such surveys as a critical first step in advancing understanding of butterfly conservation in Australia. A major shortcoming in identifying threatened butterflies is the lack of quantitative data to enable objective assessment of population declines (New and Sands 2003).

More than four hundred species of butterflies are recorded from Australia and the taxonomic inventory is about 90% complete, making butterflies the best known insect group (Braby 2000). Approximately 60 species of butterflies occur in south-western Australia and several studies have documented their distribution in conservation reserves and on offshore islands, particularly in the south-west region (Williams *et al.* 1992a, Williams *et al.* 1993, Williams *et al.* 1995, Williams *et al.* 1996, Williams 1997, Williams and Powell 1998, 2006). The distribution and conservation status of butterflies in south-western Australia is thus relatively well known in comparison with other regions of Australia. Of the 133 butterfly taxa (species and subspecies) recorded from Western Australia, Sands and New (2002) recommended that two be listed as endangered, neither of which occurred in the south-west bioregion. However, a further 11 taxa were considered data deficient.

Because day-flying moths have habits similar to those of butterflies it is common practice to include these in surveys of butterflies. The most notable of these are the sun-moths (*Synemon* spp., Castniidae), conspicuous day-flying moths that are often confused with butterflies. With only 45 recognized Australian species they are a small group in comparison with butterflies, although 24 of these species are known from the south-west bioregion, almost half the number of native butterfly species (Anon. 1993; Edwards 1997a, b). One species, *Synemon gratiosa*, which has a distribution restricted to the Swan Coastal Plain within the Perth metropolitan region, is listed as endangered (Burbidge 2004) but little is known about the others, many of which are poorly collected (Edwards 1997a). However, as a group they are relatively well known in comparison with other moths (ACT Government 1998, Douglas 2003, Douglas and Marriott 2003, Marriott 2004, Braby 2005). In Victoria, where eight sun-moth species occur, only one is considered secure and five are listed as threatened taxa under the

Flora and Fauna Guarantee Act 1988 (Douglas and Marriott 2003, New *et al.* 2007, Gilmore *et al.* 2008).

Although observed species richness is a widely used measure of biodiversity it provides only an estimate of true species richness, because detectability varies between species. Most studies fail to observe some species at some sites, often because particular species are difficult to detect or have seasonal patterns of presence or observability (MacKenzie *et al.* 2002). Butterflies often show such seasonal patterns because although individuals are present throughout the year, the flying period of the adults is strongly seasonal, and standard survey methods only record adults. Failure to account for this imperfect detection may cause misleading results and mask the true patterns of species richness (MacKenzie 2005, Kery *et al.* in press). Detectability provides a crucial link between species counts and true species numbers, but has rarely been estimated for insects (Kery and Plattner 2007). Recently developed statistical methods enable the probability of detecting a species to be quantified and true species richness to be estimated (Boulinier *et al.* 1998; MacKenzie *et al.* 2002, MacKenzie 2005).

Identification of priority taxa for conservation relies upon objective data and claims about changes in the abundance of butterflies, and potential causes, remain unresolved until these data are obtained. The aim of this study is to obtain quantitative data on the species richness, abundance and detectability of butterflies and day-flying moths in urban remnants on the Swan Coastal Plain in the Perth metropolitan region, providing baseline data to examine any future changes in distributions and abundance.

Methods

Forty-six bushland remnants in the Swan Coastal Plain in the Perth Metropolitan region were targetted for surveys. Four sites were selected based on their known importance for butterflies (Koondoola bushland and three sites at Warwick), one because it is a large inner suburban remnant (Kings Park), and the remainder were either selected at random from the *Bush Forever* study (Government of Western Australia 2000) (37 sites) or added opportunistically (4 sites). The south-west region has a Mediterranean-type climate with a pronounced summer drought and is prone to frequent fire (Hopper and Gioia 2004). Vegetation at the sites was predominantly low open woodland or low open forest dominated by *Banksia* or *Eucalyptus*, and some sites contained wetland and sedgeland vegetation or coastal heathland (Beard 1990). All of the sites are within 35 km of Perth, the major urban centre in Western Australia, which has a population of 1.5 million, and they ranged in area from 0.7 to 362 ha (Fig. 1). Several of the sites comprised fragments that were separated by cleared areas or roads, were joined by narrow corridors of disturbed remnant vegetation, or had parts subjected to different management practices, and these were treated separately.

At each site one to three strip transects were established, positioned to sample as many vegetation and habitat types as possible, including any recently or long unburnt areas. Although transects were predominantly restricted to existing walk tracks and fire breaks, to protect the native vegetation from trampling and reduce the spread of weeds and fungal pathogens, parts of some transects traversed the bushland. Each transect was divided into sectors approximately 100 m long, with boundaries that coincided with prominent features, such as crossroads or changes in habitat type. Each sector was measured to 1 m accuracy.

During the main butterfly flight season in the Austral spring, between late September and mid December, each transect was walked at fortnightly intervals. Two additional surveys were conducted between late February and early April, corresponding with the flight periods of two species that fly only in autumn (*Synemon gratiosa* and *Anisynta sphenosema*). Phenological data for individual species is provided by Braby (2000, 2004). Some additional surveys, as part of other projects, were also conducted at some sites. Thus, although most sites were sampled on five to six occasions during spring and twice during autumn, some sites had considerably more surveys (Table 1). A survey regime of six spring transects conducted at fortnightly intervals has been found to give an almost complete species list for sites in this region, detecting 85% of spring-flying species (Williams 2008). Sites were sampled between 2001 and 2005, but predominantly between September 2003 – April 2004 and September 2004 – April 2005.

Figure 1. Location of sites surveyed for butterflies and day-flying moths in the Swan Coastal Plain, Perth metropolitan region, south-west Western Australia. Each site is identified by the number in Table 1. The total extent of each site is depicted, not the remaining native vegetation; the bushland area of each site is given in Table 1.

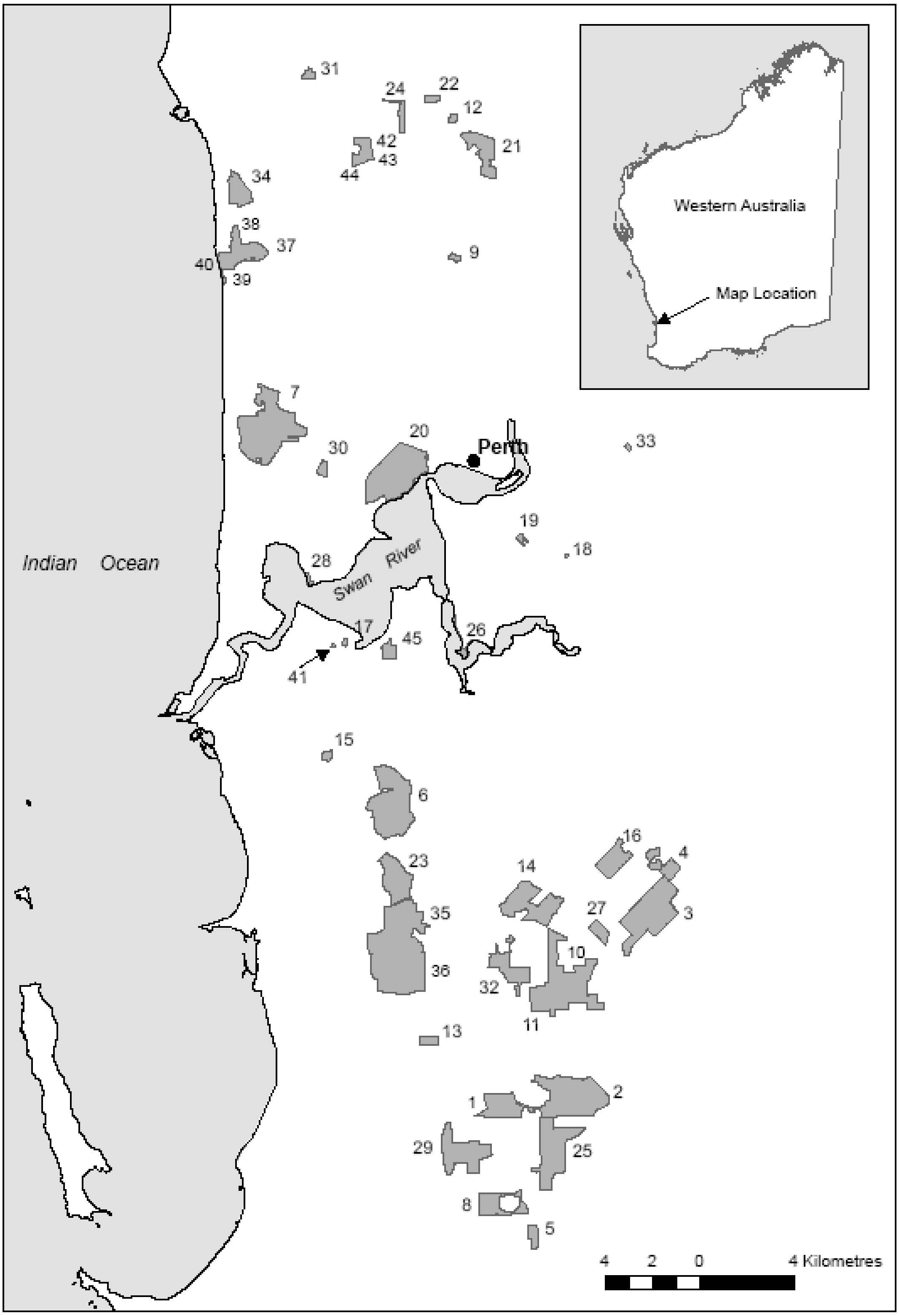

Table 1. Site name and survey details for each site. Bush Forever site number refers to Western Australian Government (2000), which contains detailed information for each site. NR = Nature Reserve.

Site number	Site name	Bush Forever site number	Area of remnant vegetation (ha)	No. surveys on tracks (spring / autumn)	Length of transect(s) on tracks (m)	No. surveys off tracks (spring / autumn)	Length of transect(s) off tracks (m)
1	Anketell Road E	347	288.0	6 / 2	2561	6 / 2	537
2	Anketell Road W	347	92.5	6 / 2	2699		
3	Anstey/Keane	342	311.6	6 / 2	2115		
4	Balannup	413	76.6	6 / 2	1861		
5	Banksia NR	353	32.3	6 / 2	2640		
6	Bibra Lake	244	27.4	6 / 2	2320		
7	Bold Park	312	361.7	5 / 2	5095		
8	Casuarina Prison	273	116.9	6 / 2	2380		
9	Cottonwood	43	11.3	10 / 5	714	3 / 0	717
10	Denis de Young N	344	40.8	6 / 2	1424	6 / 2	189
11	Denis de Young SW	344	78.6	6 / 2	961	6 / 2	340
12	Errina Road	493	8.5	6 / 2	1070		
13	Frankland	-	26.3	6 / 2	1480		
14	Fraser Road SE	390	71.8	6 / 2	1687		
15	Fred Samson	59	12.6	6 / 2	769		
16	Harrisdale swamp	253	98.4	6 / 2	1748		
17	Harry Sandon	226	4.2	6 / 2	957		
18	Hillview	-	0.7	6 / 2	191	6 / 2	155
19	Kensington	48	9.1	6 / 5	1035		
20	Kings Park	317	320.8	6 / 2	4810		
21	Koondoola	201	123.5	52 / 6	4044	17 / 1	929
22	Landsdale	199	15.8	6 / 2	1459	6 / 2	273
23	Little Rush Lake	256	4.3	6 / 2	1655		
24	Marangaroo	328	32.8	6 / 2	2281		
25	Modong NR	348	242.0	6 / 2	371	6 / 2	324
26	Mt Henry	227	11.9	6 / 2	2060	6 / 2	598
27	Piarra NR	262	35.8	6 / 2	1187	6 / 2	216
28	Point Resolution	221	3.3	5 / 2	900		
29	Sandy Lake	270	201.4	6 / 2	3962		
30	Shenton	218	19.7	7 / 2	1450		
31	Shepherds Bush	39	15.2	6 / 2	1184		
32	Shirley Balla swamp	263	103.9	6 / 2	2296		
33	Signal Hill	-	3.3	6 / 2	849		
34	Star Swamp	204	94.4	4 / 2	3194		
35	Thomsons Lake N	391	58.2	6 / 2	2190		
36	Thomsons Lake S	391	308.5	6 / 2	2052		
37	Trigg E	308	33.3	5 / 2	2336		
38	Trigg N	308	20.0	5 / 2	1210		
39	Trigg S	308	44.9	5 / 2	1641		
40	Trigg W	308	11.8	5 / 2	1379		
41	Wal Hughes	-	1.5	6 / 2	257		
42	Warwick N	202	12.6	13 / 5	1363		
43	Warwick SE	202	33.8	11 / 5	2852	11 / 5	369
44	Warwick SW	202	11.7	11 / 5	1242	4 / 0	760
45	Wireless Hill	336	35.2	6 / 2	2144		
46	Yangebup Lake	256	23.4	6 / 2	2164		

Sampling was conducted between 0945 and 1500 hr on days with fine weather and forecast maximum temperatures above 21° C. At each site, the direction of traverse and starting time varied for each survey. Each transect was walked at a steady pace and all butterflies and day-flying moths observed within a rectangle 5 m to either side of and ahead of the observer(s) were identified and counted. Any species seen outside this range, detected outside the designated sampling time, or recorded from the site by other observers, were included as incidental sightings. The butterfly fauna of this region is well documented and most species are easily identified by experienced observers. Two species (*Motasingha dirphia* and *M. trimaculata*) that are difficult to distinguish were recorded as the more common *M. trimaculata*, unless *M. dirphia* was positively identified; this is the conventional approach described by Pollard and Yates (1993). The spring-flying sun-moth *Synemon* sp. (Perth) may also consist of two very similar species, neither of which is currently described (E. D. Edwards, pers. comm.). For butterflies, taxonomy follows the standard works of Braby (2000, 2004); for day-flying moths taxonomy follows Common (1990) and Edwards (1997b). Voucher specimens were retained only for those taxa where taxonomic uncertainty exists.

Several species breed exclusively or facultatively on introduced plants or weeds that are common throughout the urban matrix: for example, *Vanessa kershawi* often breeds on the widespread weed *Arctotheca calendula,* which occurs commonly on roadsides, in gardens and on vacant land. Table 2 has therefore been divided into two groups of taxa: one comprising species that breed entirely or predominantly on plants restricted to bushland remnants (“resident species”); and another group of species known to breed throughout the urban matrix, or that breed on plants not present within the remnants, together with other species that are recorded as introduced, regular migrants or vagrants by Braby (2000) (“non-resident species”). This division is consistent with previous studies of Australian butterflies by Hill (1987) and Braby and Edwards (2006).

Data analysis

Species detectability was determined using proportion of area occupied (PAO) modelling (Mackenzie *et al.* 2002; Mackenzie 2005). This is a likelihood-based method of estimating species detection probabilities and proportion of sites occupied using repeated sampling surveys at each site. The method is an extension of mark–

recapture modelling, treating the “detection history” of a species at each site as analogous to a capture–recapture history. The detection history is a sequence of 1s and 0s representing detections and non-detections, respectively. In fitting this model, the same assumptions of closed-population capture–recapture modelling apply: (i) the community of species is closed to changes in site occupancy during the period of the study (i.e. no colonization or local extinction); (ii) species are identified correctly; and (iii) the probability of detecting a species at any site is independent of the probability of detecting the species at all other sites. The PAO model estimates two parameters: the probability that a site is occupied (ψ) and the probability of detecting the species at a site, given that it is present (p).

Both parameters may be modelled as a function of site- or time-specific covariates (e.g. site occupancy may vary with site area, and detection probability may vary with survey date). Because many butterfly species are known to have highly seasonal flight periods, models with time-dependent detection probabilities were thought *a priori* to be likely candidate models. To estimate these seasonal models, each survey was allocated to one of eight time periods: six in spring (half-monthly periods from mid September to mid December) and two in autumn (late February to mid March, and mid March to early April). These periods were chosen based on the fortnightly sampling regime, which commenced in mid to late September, so site typically had at least one survey conducted within each time period. Four alternative time-dependent models were considered for each species: (i) a null model (*null*) with species presence and detection probability constant over time ($\psi(.)$, $p(.)$); (ii) a time period-dependent model (*season*) with p varying between time periods but constant over each sampling year ($\psi(.)$, $p(t)$); (iii) a time and season-dependent model (*season*year*) with p varying between each time period and between years ($\psi(.)$, $p(t*y)$; and (iv) a survey-specific model (*survey*) with p varying between every survey, irrespective of time period ($\psi(.)$, $p(s)$). As the area of remnant sites may also affect species presence and persistence, for the best-fitting time-dependent model an additional area-dependent model (*area*), with probability of site occupancy varying in relation to log(site area), was also tested ($\psi(A)$, p). Thus, models were fitted to account for any area- or time-dependent pattern in the detection histories of each species.

All of the species observed at four or more sites were analysed over the three seasons 2002/3–2004/5, when each site was surveyed 6–8 times (41 sites, over one season) or 12–19 times (five sites, over two seasons). It was not possible to fit models for species occurring at fewer than four sites because data were too sparse. The models were fitted using the program PRESENCE, and alternative models compared using AIC values and the best model (lowest AIC) chosen. The Akaike weight for this model, *w*, was also determined. Values of *w* vary between 0 and 1, corresponding to the weight of evidence in support of each model within a set; a value > 0.9 indicates a clearly superior model (Burnham and Anderson 2002). The alternative models were developed *a priori* to compare factors known or thought to influence species presence and detectability, and it is important to stress that the model selected as "best" may not include other important factors that influence occupancy or detection and is only the best within the set of five candidate models examined.

Results

A total of 17 075 individuals were recorded, comprising 35 species of butterflies and 5 species of day-flying moths, with the observed number of each species varying between 1 and 5 458 (Table 2). Only four of the resident butterfly species known from this region were not recorded in this study: *Jalmenus inous*, *Candalides cyprotus*, *C. heathi* and *Theclinesthes hesperia* (information based on the insect collection of the Western Australian Department of Environment and Conservation). For the total 1 001 km covered in the surveys, this represented an average density of 17.1 individuals / km, although total abundance was strongly seasonal: in autumn only 211 individuals were recorded for 220 km of survey (1.0 individual / km) compared with 21.6 individuals / km in spring.

Table 2. Counts of butterflies and day-flying moths recorded in 46 bushland remnants, south-west Western Australia. Taxa marked * are introduced to the south-west region. A table entry of * denotes an incidental sighting, indicating that the species was seen outside of the standard survey transect, detected outside the designated sampling time, or recorded from the site by other observers.

	Site number																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Resident butterflies																							
Trapezites sciron												19									49	1	
Trapezites argenteoornatus							7																
Anisynta sphenosema	3	4			2					4										18			
Hesperilla donnysa																							
Hesperilla chrysotricha			1																				
Motasingha trimaculata									8		1										44		
Motasingha dirphia																					1		
Croitana croites																							
Mesodina cyanophracta	1		2	1	1			2	15		1	9	1								449	3	
Taractrocera papyria	2	1		7	2	2	14			2	2	2	6		2	3				3	8		
Geitoneura klugii	63	22		20	53	10	180	34	81	3	82	12	8	17	27	21				192	738		1
Geitoneura minyas	60	1			42	49	435	4		1	1				55	7				145			11
Heteronympha merope	22			2	2	1	30	11	1	1	2				1	3				8	12		
Hypochrysops halyaetus									19			8									1005		
Ogyris amaryllis																	4						
Ogyris idmo																					5		
Candalides acastus		5	16	1			2						2	1									
Nacaduba biocellata		1			1		8			1		2						3	*		16	2	
Theclinesthes miskini		1					3																
Theclinesthes serpentata							2														*		
Neolucia agricola	1	3			5			7	15		1	3				1				9	1226	6	
Zizina labradus	1		1	4			4	3	4			8	2	2	2		1				21		4
Resident day-flying moths																							
Synemon sp. (Perth)					2			13	16			7		1							2178	5	
Synemon gratiosa												1									5	*	
Pollanisus cuprea	38	15	1	1	52			35	3			10	16	14			1	1	*		133	33	
Hecatesia thyridion																							
Periscepta polysticta	3	2						2			2												
Resident species	**10**	**10**	**5**	**7**	**10**	**4**	**10**	**9**	**9**	**6**	**8**	**11**	**6**	**5**	**5**	**5**	**3**	**2**	**2**	**6**	**16**	**7**	**3**
Non-resident butterflies																							
**Cephrenes augiades*																					*		
**Cephrenes trichopepla*																					1		
Papilio demoleus																					*		
**Catopsilia pomona*																					*		
Belenois java																				*			
Delias aganippe							3										1				13		
**Pieris rapae*	2	12	2		3	8	16	2	16	2	4	20	6	3	10		25	3	7	7	72	26	14
Junonia villida			2									4							5		2		
Vanessa kershawi	54	8	22	22	29	8	19	18	29	6	32	31	10	13	2	10	4	3	3	192	4633	28	2
Vanessa itea							1		1												3		
Danaus chrysippus																							
**Danaus plexippus*						2							1							1	1	*	1
Lampides boeticus		10			1		2	1	24			7	2		1		1			1	347	1	1
Non-resident species	**2**	**3**	**3**	**1**	**3**	**3**	**5**	**3**	**4**	**2**	**2**	**4**	**4**	**2**	**3**	**1**	**4**	**2**	**3**	**5**	**11**	**4**	**4**
Total number of species	**12**	**13**	**8**	**8**	**13**	**7**	**15**	**12**	**13**	**8**	**10**	**15**	**10**	**7**	**8**	**6**	**7**	**4**	**5**	**11**	**27**	**11**	**7**

Table 2. (continued).

	Site number																						
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	Total
Resident butterfly species																								
Trapezites sciron	3																		2	2	1			**77**
Trapezites argenteoornatus														19		7	5							**38**
Anisynta sphenosema				2					5			6								*			1	**45**
Hesperilla donnysa			1			1					4													**6**
Hesperilla chrysotricha																								**1**
Motasingha trimaculata	2	1									1									2				**59**
Motasingha dirphia																								**1**
Croitana croites														3		2	1							**6**
Mesodina cyanophracta	6	1																	1	8	2			**503**
Taractrocera papyria			14	1		9	1	1	1		4	2			2				1	5	2		1	**100**
Geitoneura klugii	32	19	25	19		100	11	20	8		21	44	16		5	3	1		71	57	18	11	2	**2047**
Geitoneura minyas	17		31			97		19	16		187	531	35										63	**1807**
Heteronympha merope				1		12			2		1	8			2				8	4	2			**136**
Hypochrysops halyaetus	14																		9	14	64			**1133**
Ogyris amaryllis			12																					**16**
Ogyris idmo																								**5**
Candalides acastus									3					1			3							**34**
Nacaduba biocellata	1	1	1	1		2			4						1				2	1	1		1	**50**
Theclinesthes miskini																1			1		1			**7**
Theclinesthes serpentata																								**2**
Neolucia agricola	3	5		1		7		2			9	1	10		2				3	8		1		**1329**
Zizina labradus						3			44			1	2	33	1	1						1	2	**145**
Resident day-flying moths																								
Synemon sp. (Perth)	37	12				1		11			3				9				9	19	13	8		**2344**
Synemon gratiosa	3						1												1	25				**36**
Pollanisus cuprea	6	5	2	1		1		1				4	1						7	17	2	1		**401**
Hecatesia thyridion									1															**1**
Periscepta polysticta						2																		**11**
Resident species	**11**	**7**	**7**	**7**	**0**	**11**	**3**	**6**	**9**	**0**	**8**	**8**	**5**	**4**	**7**	**5**	**4**	**0**	**12**	**13**	**10**	**5**	**6**	**27**
Non-resident butterflies																								
Cephrenes augiades																								**0**
Cephrenes trichopepla																			*					**1**
Papilio demoleus																								**0**
Catopsilia pomona																								**0**
Belenois java																								**0**
Delias aganippe																1								**18**
Pieris rapae	20	1	18		24	3	1	11	8	21	32	7	1	152	42	17	35	7	16	25	16	12	33	**762**
Junonia villida	1														2	1				2				**19**
Vanessa kershawi	26	16	20	4		27	17	4	15	4	13	12	13	2	4	2	2	1	18	39	20	12	9	**5458**
Vanessa itea										1											2			**8**
Danaus chrysippus	1		2			1					1				1	1				1				**8**
Danaus plexippus		1				2			1			1	3		1							1		**16**
Lampides boeticus	4					3		1		1	14	1	7		5					4		4	2	**445**
Non-resident species	**5**	**3**	**3**	**1**	**1**	**5**	**2**	**3**	**3**	**4**	**4**	**4**	**4**	**2**	**6**	**5**	**2**	**2**	**3**	**5**	**3**	**4**	**3**	**13**
Total number of species	**16**	**10**	**10**	**8**	**1**	**16**	**5**	**9**	**12**	**4**	**12**	**12**	**9**	**6**	**13**	**10**	**6**	**2**	**15**	**18**	**13**	**9**	**9**	**40**

The majority of species showed strong seasonal variation in detectability, with only six of 27 having constant *p* across all sampling periods, and four of these were non-resident, multivoltine species (Table 3). For most species the best model was one of seasonal detectability that was constant across the three years (17 species), with few showing annual variation in seasonality (four species). The best model for each species was generally clearly superior to the alternatives (i.e. $w > 0.9$), so that in most cases there was very strong support for the model chosen. Detection probabilities varied among species, but the predominant pattern was a pronounced peak in detectability during one time period. Many species were highly detectable at these peak times, and for eight detectability exceeded 0.9. However, many species were difficult to detect even at their peak flying time, and for 12 species *p* never exceeded 0.5. Comparison of each species' peak detectability with the total number of individuals observed showed a strong relationship between abundance and detection probability ($R^2 = 0.63$, $n = 27$, $p < 0.0001$; Fig. 2). After accounting for seasonal variation, area was found to be an important factor for site occupancy for five of the resident and none of the non-resident species.

Figure 2. Relationship between species detectability (*p*) and total observed number of individuals for n = 27 species of butterflies and day-flying moths, south-west Western Australia. The fitted logistic curve is $p = 1 / (1 + \exp(-3.63 + 0.906 \times \ln(\text{abundance})))$, $R^2 = 0.63$, $p < 0.0001$.

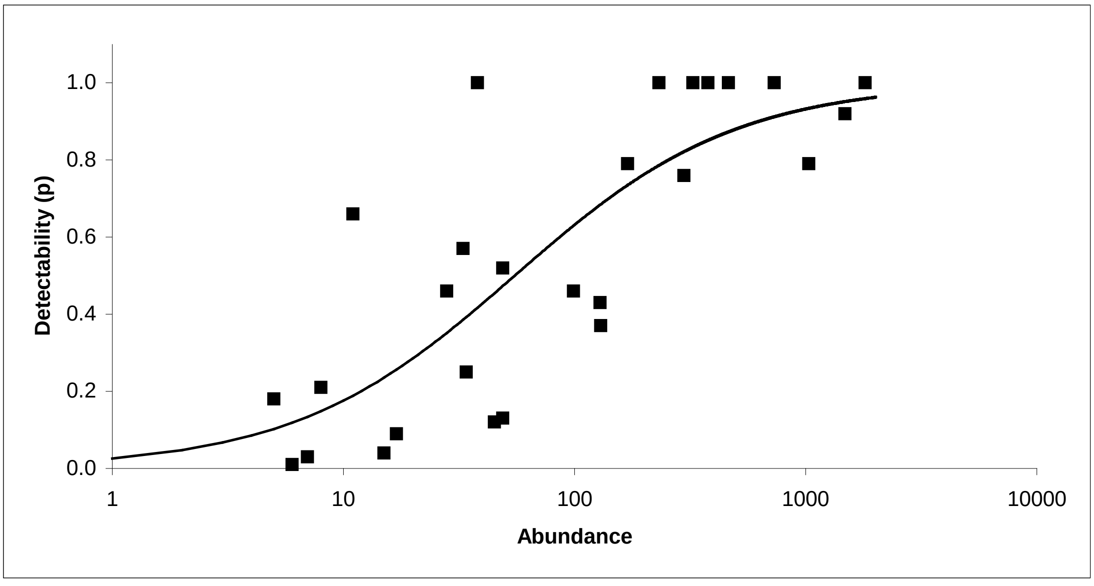

Table 3. Best fitting model of species detectability, model weight (*w*), and observed and estimated fraction of sites occupied.

			Fraction of sites occupied	
Scientific name	**Best model**	**w**	**Observed**	**Predicted (ψ)**
Resident butterfly species				
Trapezites sciron	*Season*	0.55	0.15	0.22
Trapezites argenteoornatus	*Season*	0.96	0.09	0.09
Anisynta sphenosema	*Season*	1.00	0.20	1.00
Hesperilla donnysa			0.07	
Hesperilla chrysotricha			0.02	
Motasingha trimaculata	*Season*	0.99	0.15	0.20
Motasingha dirphia			0.02	
Croitana croites			0.02	
Mesodina cyanophracta	*Season*	1.00	0.35	0.37
Taractrocera papyria	*Area, season*	0.99	0.59	0.66
Geitoneura klugii	*Area, season*	0.99	0.80	0.80
Geitoneura minyas	*Season*	1.00	0.46	0.46
Heteronympha merope	*Area, season*	0.74	0.48	0.59
Hypochrysops halyaetus	*Season*	1.00	0.15	0.15
Ogyris amaryllis			0.04	
Ogyris idmo			0.02	
Candalides acastus	*Null*	0.99	0.20	0.21
Nacaduba biocellata	*Null*	0.62	0.41	0.61
Theclinesthes miskini	*Season*	0.65	0.11	0.46
Theclinesthes serpentata			0.04	
Neolucia agricola	*Area, season*year*	0.66	0.50	0.54
Zizina labradus	*Area, season*	0.65	0.48	0.56
Resident day-flying moths				
Synemon sp. (Perth)	*Season*year*	1.00	0.37	0.46
Synemon gratiosa	*Season*	1.00	0.13	0.21
Pollanisus cuprea	*Season*	1.00	0.57	0.71
Hecatesia thyridion			0.02	
Periscepta polysticta	*Season*	0.96	0.11	0.14
Non-resident butterflies				
Cephrenes augiades			0.02	
Cephrenes trichopepla			0.04	
Papilio demoleus			0.02	
Catopsilia pomona			0.02	
Belenois java			0.02	
Delias aganippe	*Null*	0.97	0.07	0.08
Pieris rapae	*Season*year*	0.98	0.93	1.00
Junonia villida	*Null*	0.94	0.17	0.33
Vanessa kershawi	*Season*	0.78	0.98	0.98
Vanessa itea	*Null*	0.95	0.11	1.00
Danaus chrysippus	*Season*	0.81	0.15	0.38
Danaus plexippus	*Null*	0.90	0.24	0.85
Lampides boeticus	*Season*year*	0.99	0.52	0.62

Based on the predicted proportion of sites occupied, the most widespread species ($\psi > 0.80$) were *Pieris rapae, Vanessa kershawi, V. itea, Anisynta sphenosema, Danaus plexippus* and *Geitoneura klugii*, all of which are known to breed on weeds or garden plants in addition to native plants. Similarly, many of the moderately widespread species ($\psi > 0.45$) were those, which can utilise non-native plants for breeding (*Taractrocera papyria, Geitoneura minyas, Heteronympha merope, Nacaduba biocellata, Theclinesthes miskini, Zizina labradus* and *Lampides boeticus*). All of the least widespread species, those which were recorded in fewer than 4 sites and those with $\psi < 0.22$ (i.e. species predicted to occur in 10 or fewer sites), were native species restricted to native host plants or vegetation: *Trapezites sciron, T. argenteoornatus, Hesperilla donnysa, H. chrysotricha, Motasingha trimaculata, M. dirphia, Croitana croites, Hypochrysops halyaetus, Ogyris amaryllis, O. idmo, Candalides acastus, Synemon gratiosa, Periscepta polysticta* and *Delias aganippe*. The only widespread native species restricted to native host plants were *Mesodina cyanophracta* ($\psi = 0.37$), *Neolucia agricola* (0.54), *Synemon* sp. (Perth) (0.46) and *Pollanisus cuprea* (0.71).

For most species, the difference between the observed and predicted number of sites occupied was small, indicating that these taxa were reliably detected and that the observed number of sites occupied was a reliable measure of true occupancy. The largest discrepancies (a difference between observed and expected of > 0.2, or 9 sites) were for *Vanessa itea*, *Anisynta sphenosema*, *Danaus plexippus*, *Theclinesthes miskini* and *Danaus chryssipus*, all of which were species of low detectability ($p < 0.22$) and most had low observed abundance (Tables 2, 4). However, for four of these $p < 0.15$, and PAO models are known to perform poorly in such cases and likely to overestimate the fraction of sites occupied by these taxa (Bailey *et al.* 2004).

Table 4. Estimated species detectability (*p*) of each species in each sampling period. Blank entries indicate *p* = 0.

		Detectability within each time period							
	Year	**16–30 Sept**	**1–15 Oct**	**16–31 Oct**	**1–15 Nov**	**16–30 Nov**	**1–16 Dec**	**27 Feb–14 Mar**	**15 Mar–7 Apr**
Resident butterfly species									
Trapezites sciron		0.22	0.52	0.28					
Trapezites argenteoornatus		-	0.65	1.00	0.49				
Anisynta sphenosema									0.12
Motasingha trimaculata				0.29	0.46	0.34	0.13		
Mesodina cyanophracta				0.37	0.53	0.79	0.29		
Taractrocera papyria		0.46	0.36	0.42	0.30	0.10	0.06		0.04
Geitoneura klugii				0.29	0.84	0.92	0.83		
Geitoneura minyas		0.13	0.84	1.00	0.85				
Heteronympha merope					0.22	0.43	0.21		0.25
Hypochrysops halyaetus			0.22	0.73	1.00	0.33			
Candalides acastus		0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Nacaduba biocellata		0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13
Theclinesthes miskini		0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
Neolucia agricola	2002/3		1.00	0.49	0.50	0.25	0.14		
	2003/4	0.19	0.35	0.50	0.55	0.31	0.57		
	2004/5	0.15	0.62	0.60	0.11				
Zizina labradus				0.22	0.37	0.20	0.32	0.15	0.15
Resident day-flying moths									
Synemon sp. (Perth)	2002/3		0.50	0.78	1.00	0.44			
	2003/4		0.30	0.66	0.82	0.49			
	2004/5		0.36	0.57					
Synemon gratiosa								0.57	0.12
Pollanisus cuprea		0.76	0.41	0.25	0.08	0.03			
Periscepta polysticta		0.16	0.66			0.37			
Non-resident butterflies									
Delias aganippe		0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
Pieris rapae	2002/3		1.00	0.92	0.60	0.40	0.33	0.20	0.20
	2003/4	0.68	0.82	0.97	0.81	0.69	0.52		0.03
	2004/5	0.31	0.56	0.53	0.41	0.64	0.18		
Junonia villida		0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09
Vanessa kershawi		0.54	0.71	0.69	0.79	0.63	0.58	0.07	0.08
Vanessa itea		0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Danaus chrysippus					0.05		0.04		0.21
Danaus plexippus		0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
Lampides boeticus	2002/3		1.00	1.00	0.67	0.67	0.80	0.67	0.33
	2003/4		0.07	0.28	0.37	0.18	0.50	0.07	0.11
	2004/5			0.44	0.09	0.11	0.17		0.21

Koondoola bushland was the most species-rich site, and together with sites nearby (Warwick, Marangaroo, Landsdale, Cottonwood and Errina Road bushlands) had populations of many uncommon species, notably *Trapezites sciron*, *Motasingha trimaculata*, *M. dirphia*, *Mesodina cyanophracta*, *Ogyris idmo*, *Hypochrysops halyaetus*, *Theclinesthes miskini* and *Synemon gratiosa*. Another group of uncommon species, *Trapezites argenteoornatus*, *Hesperilla donnysa*, *Croitana croites*, *Theclinesthes miskini* and *T. serpentata* were restricted to three near-coastal remnants at Bold Park, Trigg and Star Swamp.

Discussion

No previous studies record butterflies from urban reserves in south-west Western Australia. Williams (1997) listed 21 butterfly species recorded from two islands offshore from the Perth metropolitan region: 14 from Rottnest Island (1 900 ha, 19 km from the mainland, 8 resident taxa) and 14 from Garden Island (1 100 ha, 2 km from the mainland, 8 resident taxa; this island is depicted in the SW of figure 1). These two islands are relatively depauperate in comparison with the mainland sites (27 resident and 35 total species in a total 3 500 ha, average 76 ha, 6.7 resident species). All but two of the species recorded from these islands were found in this study: the exceptions were the native *Jalmenus inous*, which is generally restricted to coastal habitats on the Swan Coastal Plain (Braby 2000); and the introduced *Vanessa cardui*, populations of which are thought to be only occasionally present in Australia (Braby 2000).

There are relatively few Australian studies against which to compare these results. Haywood and Wilson (2002) recorded 10 species (7 resident) in the 178 ha Penamol Conservation Park, an isolated remnant near Mount Gambier, South Australia. Collier *et al.* (2006) recorded a total of 21 butterfly species in three urban remnants in the Adelaide metropolitan region, in sites of area 51, 78 and 835 ha. Eleven of these were resident species, using the criteria adopted in this study and that of Braby and Edwards (2006). In an extensive study of fragments within an agricultural landscape, Braby and Edwards (2006) recorded the butterfly faunas of six regions of inland New South Wales; total species richness varied between 32 and 50 species. In their main study area, the Griffith district, they recorded 19 resident and 33 total species in a region of 11 000 km^2. In a series of studies of tropical and subtropical sites in Queensland, Hill (1987) recorded 41 resident and 60 total species of butterflies in the Toohey Forest, a 640 ha urban remnant near Brisbane, and 20–50 species in three other remnants (Hill 1988); Hill *et al.* (1992) recorded an average of 57 species in three point samples of 300 m^2 and 61 species in 200 m^2 at three sites within rainforest (Hill 1995). The 27 resident and 35 total butterfly species detected in this study, in a region of 3 500 km^2, is thus consistent with the other southern Australian sites, although only the study of Braby and Edwards (2006) is directly comparable on a regional scale.

Many species of butterflies are specialized herbivores, with larvae feeding on a narrow range or single species of plant (Mackay 1999, Dennis *et al.* 2004), and some specialize on particular life stages of their host plants (Krauss *et al.* 2004). Host plant quality strongly affects fecundity of phytophageous insects generally (Awmack and Leather 2002) and host plant density has been shown to affect both adult body size and abundance of *Speyria idalia (*Kelly and Debinski 1998) and the abundance of *Cupido minimus* (Kraus *et al.* 2004). The occurrence and persistence of butterfly species within isolated remnants is therefore highly dependent upon suitable host plants being present, being of sufficient quality, and occurring in sufficient numbers or density to sustain a population. Species characterized by a narrow range of larval host plants, low dispersal abilities or low population densities (traits typical of habitat specialists) are therefore more susceptible to local extinction in fragments (Krauss *et al.* 2003, Dennis *et al.* 2004). Many of the resident species identified in this study fall into this category. In contrast, the non-resident species and the species that have adopted introduced plants as hosts, demonstrate partial or total dependence on alien plants, a pattern also found in California, a comparable region with a Mediterranean-type climate (Shapiro 2002). A major objective in the management of these remnants is the control or eradication of weeds, a process that is likely to reduce the abundance of many of the non-resident butterflies and some of the resident butterfly species, but benefit the more ecologically specialized species.

Most species showed a unimodal peak in detectability during spring, corresponding to the well-known peak in butterfly abundance and species numbers in this region during October–November (Hay *et al.* 1994). This feature of butterfly phenology is common to many temperate regions (Thorne *et al.* 2006, Kery and Plattner 2007). Many species had high peak detectability so that observed site occupancy was a good measure of true presence, consistent with some previous findings that, for butterflies, observed species numbers often approximate true numbers (Dorazio *et al.* 2006; Williams 2008). However, this varies between regions and methodologies, and other studies have found that even in temperate regions as many as 30 % of species may be overlooked (Kery *et al.* in press), and this figure may be much higher in the tropics (Brown and Freitas 2000).

Although peak flight periods were generally found to be consistent across years, for logistic reasons not every site could be surveyed every year and so for some species year-to-year differences may be poorly estimated. Similarly, studies longer than three years duration will be needed to determine annual variation in species phenologies, which may be influenced by variation in weather conditions (Thorne *et al.* 2006). Abundant species were more readily detected, and the strong relationship between observed numbers and detectability ($R^2 = 0.63$) was much greater than has been found elsewhere (Kery and Plattner 2007). Species that were rare or uncommon in this study region, and which had correspondingly low detectability, may be more widespread than was observed.

The detection probability values of Table 4 may be used to quantify the number of surveys required to detect each species to a specific level of accuracy. For a site surveyed on n occasions within a time period, the probability of detecting the species in one or more surveys is 1 minus the probability that the species is missed on all n occasions. To obtain an accuracy of y % in detecting the species, the required number of surveys can be determined by solving the formula $y / 100 = 1 – (1 – \mathrm{p})^{\mathrm{n}}$. (Equivalently, the minimum number of surveys required is $\log(1 – \mathrm{y}/100)/\log(1 – \mathrm{p})$; Kery 2002). For example, the estimated number of surveys required to detect *Synemon gratiosa* with at least 95 % accuracy during the peak detectability period in late February – mid March (when $\mathrm{p} = 0.57$) is $\mathrm{n} = 4$. If surveys were to be conducted during the late March–April period, when $\mathrm{p} = 0.12$, a similar level of accuracy would require an estimated 24 surveys. These detection probabilities will therefore be of value in the design of future monitoring studies.

Site area was a determinant of site occupancy for five resident but none of the non-resident species, consistent with the definition of these groups. No pattern was apparent in body size of these species (three were small, one medium and one large) or their taxonomy (two lycaenids, two satyrids, and one hesperid). More detailed examination of the area and habitat relations of individual species will be undertaken in future studies.

Of the resident butterfly species, three patterns were observed: (i) those species that breed on plants that are common in most or all of the remnants, and so are generally widespread, although some are notably absent from sites where they would be expected to occur; (ii) species that appear to have expanded their distribution into disturbed or degraded sites, by adopting introduced host plants, and are now widespread; and (iii) species that are local, uncommon, or which show idiosyncratic distributions.

Taxa in the first group are *Mesodina cyanophracta* (on the Swan Coastal Plain this butterfly breeds exclusively on the widespread native plant *Patersonia occidentalis*), *Motasingha trimaculata* (on *Phlebocarya ciliatum* and *Lepidosperma angustatum*), *Candalides acastus* (on *Cassytha* spp.), *Nacaduba biocellata* and *Theclinesthes miskini* (on *Acacia* spp., especially *A. saligna*), *Neolucia agricola* (on *Daviesia divaricata* and *Jacksonia sternbergiana*), and *Polanisus cuprea* (on *Hibbertia* sp., probably *H. hypericoides*). Detailed information for each plant species is provided by Marchant *et al.* (1987) or at http://florabase.dec.wa.gov.au/. Because they breed on widespread plants this explains why these taxa are still extant in many remnants. *Pollanisus cuprea* in particular seems able to persist in even very small and otherwise species-poor remnants such as Harry Sandon, Hill View and Kensington bushlands, so its absence from many other bushlands is curious, but may be the result of sampling bias (see below). However, it may be possible that other species in this group have become locally extinct in some sites. For example, *Mesodina cyanophracta* is notably absent from Kensington bushland, where *P. occidentalis* is abundant (358 plants / ha, data not shown).

Conversely, species in the second group are now widespread as a result of adapting to introduced host plants, particularly common weeds that have invaded many bushland remnants: *Anisynta sphenosema*, *Geitoneura minyas*, *G. klugii* and *Taractrocera papyria* all now breed on introduced weedy grasses as well as native grasses; and *Zizina labradus* breeds on introduced legumes. It is possible that that these species now occur in remnants they did not previously occupy, colonising either before or after the remnant became isolated. The evidence for this assertion is particularly strong in the case of *Geitoneura minyas*, which is able to breed on the common bushland weeds *Ehrharta* spp. (veldt grasses, Hay *et al.* 1994). In many of the sites where it was recorded, *G. minyas* occurred in large numbers. It was the most common species in eight remnants, with densities as high as 70 individuals / 100 m of transect in bushland to the north of Thomsons Lake Nature Reserve (data not shown). These high densities were observed to coincide with swards of veldt grass. Despite the large sampling effort at Koondoola bushland, *G. minyas* was never recorded there, nor at Warwick, Errina Road, or Landsdale bushlands, all of which are relatively species-rich but have low densities of veldt grasses (pers. obs.).

For species in the third group, any past changes in distribution cannot be inferred with confidence. *Trapezites sciron* is both local and uncommon, and although its usual food plant (*Lomandra caespitosa*) is quite widespread, it does not always occupy apparently suitable habitat (Fisher 1978, 1984, Williams *et al.* 1992, Hay *et al.* 1994). Similarly, two species (*Ogyris idmo* and *Hypochrysops halyaetus*) have obligate ant associations and occurred patchily in what appears to be otherwise suitable habitat. In the case of *H. halyaetus* the host plant (*Jacksonia sternbergiana*) is both common and widespread, and was observed in the majority of remnants, but *H. halyaetus* does not occur south of the Swan River. Similarly, most of the day-flying moths fall into this group, although their ecology is poorly known. Of the least widespread species detected, *Hesperilla chrysotricha* is restricted to dampland habitats and *Croitana croites* to coastal heathland, but neither of these habitats were common in the study sites; *Hecatesia thyridion* is crepuscular and likely to be have been under-sampled; and *Motasingha dirphia* is difficult to identify unless captured, as noted above. Similarly, another four resident species that were recorded at few sites have specific habitat preferences that were not common in the study sites: *Trapezites argenteoornatus* and *Theclinesthes serpentata* (coastal heathland), *Hesperilla donnysa* (dampland), and *Ogyris amaryllis* (fringing estuarine vegetation). Similarly, of the four taxa known from the region but not detected in this survey, three (*Jalmenus inous*, *Candalides heathi* and *Theclinesthes hesperia*) are largely or completely restricted to coastal heathland within the study region, while the other (*Candalides cyprotus*) is both local and uncommon and has rarely been recorded on the Swan Coastal Plain.

The first and third groups are similar to the ‘urban avoiders’ of Koh and Sodhi (2004) – species that are dependent of remnant vegetation and are predominantly monophagous, although many of the urban avoiders in this study were biphagous. The second group, corresponding to 'urban adapters', are often cosmopolitan and typically oligo- or polyphagous.

Synemon gratiosa, the only species that is currently listed as endangered, was recorded at six of the sites; all except Shenton bushland are in close proximity. Very few individuals were recorded, and at two sites only single individuals were seen (the incidental recording at Landsdale is based on the observations of P. Robertson). Only one other extant site is known for this species, at Whiteman Park (3 km NE of Koondoola bushland), where two specimens were collected in March 1997 (Anon 1997a). The only other site where the species had been recently recorded, at Neerabup 13 km NNW of Landsdale bushland, was cleared soon after its discovery (Anon 1997b). The low abundance and generally low detectability suggests that four or more surveys are needed during the peak flying period to ensure it is detected. The largest population recorded in this survey was at Warwick bushland and this site should be given priority for protecting this species pending further studies to increase knowledge of this species' biology and conservation needs. Many of the sites where this species was detected were in close proximity, and searches to detect additional populations should examine other remnants near the known sites – in particular, Underwood Avenue bushland, a 32 ha remnant 500 m north of the Shenton bushland, should be surveyed. Another species of local conservation concern is *Ogyris idmo*. The population of *O. idmo* at Koondoola bushland is thought to be one of only two extant populations on the Swan Coastal Plain; three other populations at Carramar, Australind and Jandakot have been extirpated as a result of habitat destruction (A. A. E. Williams, A. Atkins and M. Powell pers. comm., respectively).

One potential bias in this survey is the possible failure to detect species that fly in early September, or in late March – early April. Two taxa, *Pollanisus cuprea* and *Anisynta sphenosema*, may be subject to this bias: only 8% of the 401 *P. cuprea* were recorded in October or later; and no individuals of *A. sphenosema* were recorded before 24 March (data not shown). Thus *P. cuprea* may be slightly under-detected, and *A. sphenosema* is likely to be have been missed in many of the sites north of the Swan River, where no surveys were conducted in early April.

As the richest site, and the largest containing many of the less common species, Koondoola bushland is an important site for conservation within this region. Many of the smaller sites, or those with degraded vegetation, had small faunas. Four or fewer resident species were recorded from Bibra Lake, Harry Sandon, Hillview, Kensington, Little Rush Lake, Point Resolution, Shenton, Signal Hill and Wal Hughes bushlands.

Many of the urban vegetation remnants in this study appear to have lost species of butterflies and day-flying moths that were likely to have been present previously. Unfortunately, there are insufficient historical data to confirm these local extinction events. Many taxa still occupy all or most of the sites that contain their host plants, and these taxa seem to be relatively resistant to disturbance. Indeed, some taxa have adapted to breed on alien plants, and are probably more abundant and widespread now than in the past. Efforts to reduce and eliminate alien weeds are likely to impact these butterflies. A few of the larger sites, notably Koondoola, Warwick and Trigg bushlands, have an apparently intact butterfly fauna and contain several rare species, and are therefore of regional conservation significance. The majority of the least widespread taxa were those restricted to coastal heathland and further surveys to better determine the conservation status of these butterflies are needed. Ongoing conservation of butterflies in these remnants also requires further studies to determine whether the remaining populations of resident butterflies are viable, and the role of local and regional environmental factors on species richness and abundance. Future projects to re-establish butterflies and day-flying moths in previously occupied sites, using translocations, will rely on the few remaining species-rich sites as sources.

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Chapter 4 – Species–area functions revisited

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See statement of contribution (Appendix).

Abstract

Aim Numerous functions have been proposed to describe the species–area relationship but despite almost a century of curve fitting there is little agreement on which is best. We aimed to rationalize the list of proposed functions and discuss appropriate methodology for fitting and comparing the alternatives.

Location Data from the British Isles were used for model comparisons.

Methods Sixteen functions that have been proposed as models of the species–area relationship were compared algebraically and reformulated into a consistent format. Each was parameterized to enable their use as link functions to model the combined effects of area and other factors (covariates) on S (species number). Using data on the number of plant species on 41 British islands, we examined the effects of ignoring important covariates on the choice of the best fitting function. The methods used in some recent studies that compared alternative functions were examined.

Results Many of the 16 species–area functions are special cases of others, some are identical, and two arose as a result of transcription errors. The 16 functions were reduced to a set of nine general functions. The empirical comparison showed that including covariates in addition to area resulted in a different best-fitting function, and that different functions identified different covariates as important. Previous studies that have compared alternative functions suffered from three shortcomings: (1) too much emphasis was placed on maximising goodness-of-fit between S and A (area), ignoring the effects of other factors; (2) most made implicit or untested assumptions about the distribution of S; and (3) some repeated the mispractice of using R^2 to compare models with different numbers of parameters or differing error distributions.

Main conclusions The generalized linear model is a framework with which to fit alternative species–area functions and the information-theoretic approach provides one suitable method with which to compare their fit. Ignoring the effects of important covariates may result in an incorrect choice of the best-fitting function. The choice of function may also affect which covariates are found to be important. Determining an appropriate statistical model with which to relate species number to area and other covariates requires careful consideration of many issues, not just the functional relationship between species number and area.

Keywords

AIC, logistic, beta-P, Chapman–Richards, EVF, generalized linear model, Morgan–Mercer–Flodin, MONOD, negative exponential, Weibull.

Introduction

The species–area relationship, the closest thing to a rule in ecology, has generated debate since Arrhenius proposed the first explicit functional model (Arrhenius, 1921, 1923a, b; Gleason, 1922, 1925; Connor & McCoy, 1979; He & Legendre, 1996; Lomolino, 2000). This debate has been an important stimulus in ecology and many theories have been proposed to explain the causes of the relationship. These seek to explain the relationship in terms of species abundance distributions (Preston, 1962), species dynamics (MacArthur & Wilson, 1967; Matter *et al.*, 2002), the spatial distribution of individuals (Arrhenius, 1921, 1923a; Coleman *et al.*, 1982; Williams 1995; Picard *et al.* 2004), some combination of these (Coleman, 1981; He & Legendre, 2002; Martin & Goldenfeld 2006), or other mechanisms such as species–energy theory or disturbance (Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007). Another view is that the species–area relationship is simply the sum of a set of species-incidence functions (Williams, 1995; Ovaskainen & Hanski, 2003). Other theories that account for particular parts of the species–area curve, such as the ‘small island effect’, have also been proposed (Whitehead & Jones, 1969; He & Legendre, 1996; Lomolino & Weiser, 2001). Despite almost a century of curve fitting, no agreement exists on the best functional model of the species–area relationship (Connor & McCoy, 1979; Whittaker & Fernández-Palacios, 2007).

Tjørve (2003) reviewed and discussed 14 possible species–area functions and there are at least two others: those of Archibald (1949a, b) and Schoener (1976). Some of these arise from underlying theoretical models whereas others simply have a convenient shape. The power function (usually estimated by linear regression of the logarithm of species number, $\log S$, on the logarithm of area, $\log A$) and exponential function (S vs $\log A$) have been the most widely used models of the relationship, but there is no consensus that these are anything other than functions of convenience that provide good empirical fit (Connor & McCoy, 1979; Fattorini, 2006a). Although the number of proposed functions has burgeoned, none has been found that is best in all studies (He & Legendre, 1996; Scheiner, 2004; Fattorini, 2006a; Stiles & Scheiner, 2007).

Determining an appropriate form for the relationship is important for two reasons. First, a particular form may arise from an underlying theoretical model and the shape of the curve in empirical data may thus affirm the consequences of a model or discriminate between alternatives (Connor & McCoy, 1979; Lomolino, 2000; Williamson *et al.*, 2001). Studies by Coleman (1981), Coleman *et al.* (1982) and Matter *et al.* (2002) are examples of this process, from the development of a theoretical model to a subsequent empirical test of the predicted species–area curve. Other models, such as those that propose the existence of a small island effect, also give rise to consequences that may be tested empirically using species–area curves (Gentile & Argano, 2005; Panitsa *et al.*, 2006). Second, in empirical studies the 'pure' species–area relationship must be accounted for so that the effect of other factors on species number, such as habitat or environmental characteristics, may be distinguished (Arrhenius, 1921; Connor & McCoy, 1979; Rosenzweig, 1995). In such studies the relationship between species number and area is 'factored out' so that the effects of other variables can be estimated and a suitable function must be chosen so that these relationships are not masked or biased. Attempts to identify biodiversity 'hotspots' have shown that the choice of species–area function is of critical importance because different functions produce conflicting results (Veech, 2000; Ulrich & Buszko, 2005; Fattorini, 2006a, b). While such 'species-number games' (Whittaker & Fernández-Palacios, 2007) may be of little interest to many ecologists, appropriate methods are essential to disentangle the effects of area and other factors on species number.

Scheiner (2003, 2004) clarified the variety of methods used to construct species–area curves and provided a classification into four main types. These include curves that arise from nested samples of increasing size (Type I), from contiguous or non-contiguous samples of fixed size (Type II and Type III), and from the classic species–area relationships of isolates (Type IV). Curves of Types I–III are strictly increasing because they are constructed from larger combinations of the same areas, whereas Type IV curves are unconstrained because larger isolates may contain fewer species than other, smaller isolates. Type I–III curves use increasing but nested areas, usually to estimate an asymptote. Other classifications have been proposed but all distinguish true island species–area relationships (ISARs) from species accumulation curves (Whittaker & Fernández-Palacios, 2007). In our study we consider all of the functions proposed as models of the species–area relationship, but examine only the methods used to fit these to ISARs. For data arising from nested samples it is necessary to adjust the modelling process to account for the non-independence of samples and the possible overdispersion that may result, a subject beyond the scope of this study.

Our aims are: (1) to compare the 16 functions proposed as models of the species–area relationship; (2) to discuss appropriate methods for fitting and comparing these functions; and (3) to conduct an empirical comparison of alternative functions for modelling the relationship between species number, area and other explanatory variables.

The functional models of the species–area relationship

Of the 16 species–area functions we examined, many are alternate forms or special cases of others. Simple algebra can be used to demonstrate this, resulting in 14 functions of nine general types (see Appendix S1 in Supporting Information). The functions are summarized in Table 1 and the relationships between them are discussed below. Although these functions have been tabulated previously, they have not always been stated correctly, in their simplest form, or in a way that reveals the similarities between them. There has also been some confusion in the names applied to these functions, with the terms 'logistic function' and 'cumulative Weibull function' each being used to describe two alternatives. The functions are of two broad types: those that never reach an upper limit (linear, power and exponential functions) and those with an upper asymptote (the remainder). Of the latter, the asymptote may be fixed at the number of species in the 'source pool' (the logistic and extreme-value functions) or estimated as a parameter. The size of the source pool (*P*) is the number of species in the regional biota from which the species observed in each individual area are derived. Table 1 lists each function with its most commonly used name in ecological studies, or in cases where this is unclear with a proposed standard name.

Table 1. The functional formulae proposed as models (link functions) of the species–area relationship. *S* indicates species number, *A* area, *P* the size of the species source pool, and *a*, *b*, *c* and *d* are fitted parameters; MMF is the Morgan–Mercer–Flodin function and EVF is the cumulative extreme-value function. The parameter *a* is an upper asymptote, except for the rational function, for which *a* is the lower, and *b/c* the upper asymptote. Functions that are specific forms of a general type are distinguished by a code based on the group number, ordered from the least to most general form. Functions that have arisen from misstated forms of other functions have been excluded.

Code	Function name	Parameters	Formula	Reference
0	Linear	2	$S = b + cA$	Connor & McCoy (1979)
1	Power	2	$S = bA^{c}$	Arrhenius (1921)
2	Exponential	2	$S = b + c\log A$	Gleason (1922)
3a	Logistic	2	$S = P / (1 + bA^{-c})$	Archibald (1949b)
3b	MONOD	2	$S = a / (1 + bA^{-1})$	Clench (1979)
3c	MMF	3	$S = a / (1 + bA^{-c})$	Tjørve (2003)
4a	EVF	2	$S = P [1 - \exp(-bA^{c})]$	Williams (1995)
4b	Negative exponential	2	$S = a [1 - \exp(-bA)]$	Miller & Weigert (1989)
4c	Chapman–Richards	3	$S = a [1 - \exp(-bA)]^{c}$	Flather (1996)
4d	Weibull-3	3	$S = a [1 - \exp(-bA^{c})]$	Tjørve (2003)
4e	Weibull-4	4	$S = a [1 - \exp(-bA^{c})]^{d}$	Flather (1996)
5	Asymptotic	3	$S = a - bc^{-A}$	Flather (1996)
6	Rational[1]	3	$S = (a + bA) / (1 + cA)$	Flather (1996)
7	Gompertz	3	$S = a \exp [-\mathrm{b} \exp(-cA)]$	Tjørve (2003)
8	Beta-P	4	$S = a [1 - (1 + (A/b)^{c})^{-d}]$	Flather (1996)

[1] This rational function is one of the infinite number of rational functions (the ratio of two polynomial functions).

The linear, power and exponential functions. Connor & McCoy (1979) provided a detailed review of the use of these functions for species–area data, concluding that the power function was a convenient model and generally the best fitting but had no particular biological meaning. The power function has the convenient property that it is easily extended to be used in multiple regression models, to test the effects of additional factors on species number. Despite its usefulness the power function has been criticized because it is unbounded and if fitted using the usual approach of regressing log$S$ on log$A$, samples with $S = 0$ cannot be used (Connor & McCoy, 1979; Williams, 1995, 1996). A commonly applied solution to this problem is to use log(S + 1) in place of log$S$, but this is inherently flawed, precludes comparisons with many of the other models, and can be resolved by using other methods such as the generalized linear model (Russell *et al.*, 2004; Fletcher *et al.*, 2005; Vittinghoff *et al.*, 2005). The linear and exponential functions are also unbounded, easily extended for use in multiple regression models, and samples with $S = 0$ can be included, but generally do not fit species–area data as well as the power function (Connor & McCoy, 1979; He & Legendre, 1996). Both have been criticized because they may predict negative values of S at small areas (Fattorini, 2006b).

The Archibald (1949b) logistic, Lomolino (2000), Morgan–Mercer–Flodin, and MONOD functions. Archibald's (1949a, b) model of the species–area relationship is a logistic function using log$A$. The same function was proposed independently by Lomolino (2000) but in a different form (Appendix S1). In a plot of S vs log$A$, this function is sigmoidal and symmetric with an upper asymptote at P. The asymptote is thus not an estimated parameter but is determined *a priori*. However, Lomolino indicated that if P was unknown it could be estimated as an additional parameter. In this form it is identical to the Morgan–Mercer–Flodin (MMF) function. Thus the models of Archibald (1949b) and Lomolino (2000) are identical, and special cases of the MMF with one parameter (the asymptote) fixed (at P). The MONOD function and the model proposed by Schoener (1976) are also special cases of the MMF, with one parameter fixed (He & Legendre, 1996).

Tjørve (2003) listed the logistic function with A as the independent variable and cited five examples of its use. However, all of these studies used the logistic function with independent variable log$A$. The logistic function in A has not, as far as we are aware, ever been proposed as a species–area model although at least four studies subsequent to Tjørve (2003) have fitted this function (Fattorini, 2006a, b; Panitsa *et al.*, 2006; Stiles & Scheiner, 2007).

The extreme-value function (EVF), the cumulative density function of the Weibull distribution (with 3 parameters), and the negative exponential function. The EVF model (Williams, 1995) is based on the cumulative density function of the extreme-value distribution with dependent variable S and independent variable log$A$. It is sigmoidal, asymmetric about the point of inflection (the point at which the curvature changes from upward to downward; Trexler & Travis, 1993), but otherwise similar to the logistic model. Tjørve (2003) misstated the EVF as having independent variable A rather than log$A$, and at least two subsequent studies (Panitsa *et al.*, 2006; Stiles & Scheiner, 2007) have fitted the function in this form. Like the model of Archibald (1949b) the EVF has an upper asymptote at P and hence only two estimable parameters, although Tjørve (2003) stated the function with P replaced by a parameter. In this latter form the EVF is identical to the cumulative density function of the Weibull distribution (with three parameters, as in Tjørve (2003)). Thus the EVF is a special case of the Weibull-3 with one parameter (the asymptote) fixed (at P). The negative exponential model is also a special case of this Weibull function (Tjørve, 2003) and of the Chapman–Richards function (in both cases with one parameter fixed).

The cumulative density function of the Weibull distribution (with 4 parameters), asymptotic, rational, Chapman–Richards, Gompertz, and cumulative beta-P functions. Most of these functions were tested by Flather (1996) as possible models of species accumulation. All have an upper asymptote that is estimated as a parameter. Unlike all other species–area functions the asymptotic, rational and Gompertz also have non-zero lower asymptotes, at $(b – a)$, a and ae^{-b}, respectively. The rational function used by Flather (1996) is just one of the infinite number of possible rational functions (a rational function is the ratio of two polynomial functions).

Including additional variables

Of the 14 functions, only four (power, exponential, logistic and EVF) have been used as the basis of multiple regression models. This is most likely because they can be fitted using standard linear or logistic regression methods. For the remaining functions, how factors other than area could be incorporated has not been considered. So that these functions could be compared (see empirical comparison, below), we extended (‘parameterized’) each to permit the inclusion of additional factors (covariates). This was done in a way consistent with the parameterization of the power, exponential, logistic and EVF models (see Appendix S2). However, no such consistent parameterization was found for the rational and beta-P functions.

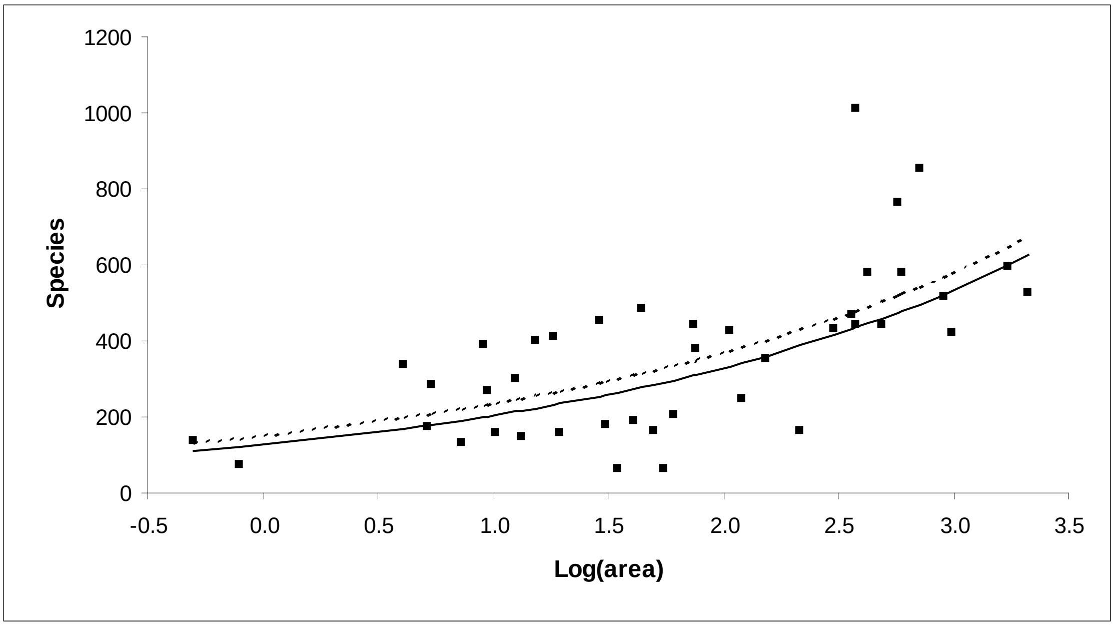
Fitting species–area functions

An aspect that has often been overlooked in comparisons of species–area models is the methodology used to fit them. Except in the case of the power function, previous studies have almost invariably used the method of least squares and ordinary linear or non-linear regression with *S* as the dependent variable. Underlying this method is an implicit assumption that the distribution of *S* is normal. In practice this means that in a plot of *S* vs log*A* the scatter of the points around the regression line (the residuals or errors) are assumed to arise from a normal distribution with mean zero and constant variance (homoscedasticity). In the case of the power function fitted by regressing log*S* on log*A*, the same assumptions are made about log*S*. Using the method of least squares to fit these functions is convenient because it is a simple process and the usual R^2 (or an adjusted-R^2) statistic may be used to choose the best model (but see Burnham & Anderson, 2002). However, the method is not appropriate if the distributional and homoscedasticity assumptions are not met. How well the data conform to these assumptions can be assessed with standard tests (Fry, 1993).

The method of least squares is only one means available to fit species–area functions. The logistic and EVF models, for example, typically or explicitly assume that *S* has an approximately binomial distribution (Williams, 1995). Other distributions for *S* such as the Poisson are also possible (Russell *et al.*, 2004). An appropriate framework for fitting functions with these distributions is that of the generalized linear model. This framework also encompasses the method of least squares and so enables comparisons of models assuming normal, binomial or Poisson distributions. As for the models that assume a normal distribution for *S*, the assumption of a binomial or Poisson distribution may be assessed with appropriate tests (Hosmer & Lemeshow, 2000; Russell *et al.*, 2004). An additional issue not encountered for normally distributed data is the need to quantify any overdispersion in these models (Richards, 2008). Unlike the normal distribution, which has independent mean and variance parameters, the variances of the binomial and Poisson distributions are determined by their means. Data are referred to as overdispersed if the observed variance is greater than that expected given the estimated mean, usually by a factor of two or more (Lindsey, 1999). A full discussion of the importance of overdispersion in modelling ecological data is given by Richards (2008). Causes of overdispersion may include the use of an inappropriate functional relationship or the absence of important covariates from the model. A benefit of using the generalized linear model is that it facilitates comparisons of alternative species–area functions because all are fitted using a consistent methodology.

That the method chosen to fit each model is an important issue is illustrated by an example using the power function. This may be fitted as $\log S = \log a + b\log A$ using ordinary linear regression, or using the non-linear form $S = aA^b$ and either ordinary non-linear, or Poisson regression (Candy, 1997; Russell *et al.*, 2004; Richards, 2008). Although the link function (i.e. power function) is identical, using alternative distributional assumptions may yield different parameter estimates and predicted values (Fig. 1). Although few authors consider the distribution of S explicitly, in every case an assumption is made about this distribution when fitting a particular model. Only after this assumption has been confirmed should goodness-of-fit be compared between models (Vittinghoff *et al.*, 2005). Determining which distributional assumption is the most appropriate for modelling a particular data set relies on knowledge of the process generating the data and can be assessed with standard diagnostic tools. In the example, these tests indicated significant lack-of-fit for the power function using log transformation and linear regression (Shapiro–Wilk statistic, $W = 0.92$, $P = 0.01$) and Poisson regression (Pearson $\chi^2 = 68.2$, $P < 0.01$), but not for the power function fitted with non-linear regression ($W = 0.95$, $P = 0.07$). In the absence of an *a priori* model or consideration of additional covariates the best-supported model for these data was therefore the power function with normal errors.

Figure 1. The relationship between species richness of plants (S) and island area ($\log_{10}A$) in the British Isles, excluding the island of Britain (see Johnson & Simberloff, 1974; McCoy & Connor, 1976). The power function was fitted using log-transformed data and linear regression ($\log S = 4.837 + 0.209 \times \log A$, $R^2 = 0.40$, solid line), non-linear and Poisson regression (both $S = \exp(4.975) \times A^{0.203}$, $R^2 = 0.45$, dashed line). However, these R^2 statistics do not provide a valid comparison between the models because one predicts $\log S$, assuming S is lognormally distributed, and the others predict S, assuming a normal or Poisson distribution. The squared correlations between the actual and predicted values of S are almost identical ($R^2 = 0.4514$, 0.4515 and 0.4515, respectively), but the predictions using log transformed data are lower, on average, by 38 species (11%). Results are essentially unchanged if Britain ($\log_{10}A = 5.4$, $S = 1666$) is included.



Comparing species–area functions

Comparing alternative species–area functions, which may have different numbers of parameters and different assumed distributions for S, also requires an appropriate framework. In the case of models with the same number of parameters and the same error distributions comparisons are straightforward. For example, if a normal distribution for S is specified then the R^2 statistic can be used to compare fits. Similarly, models that assume a binomial or Poisson distribution may be compared using the log-likelihood statistic. Comparison of models assuming the same distributions but having different numbers of parameters is also relatively straightforward as a statistic that accounts for the variation in parameter numbers may be used, such as an adjusted R^2 statistic or Akaike's information criterion (AIC). However, comparing models that differ both in distribution and in the number of fitted parameters is less straightforward, and rarely encountered in the ecological literature (Loehle, 1990; Candy, 1997; Burnham & Anderson, 2002). The information-theoretic approach is one method that enables such comparisons and this is now used widely in ecology (Burnham & Anderson, 2002; Stiles & Scheiner 2007; Richards, 2008). Fitting the alternative models using the generalized linear model and comparing them using the information-theoretic approach provides a suitable framework with which to compare species–area functions empirically.

Model comparison using the information-theoretic approach relies on a statistic that takes into account both the distribution and the number of fitted parameters. Typically AIC is used but there are several alternatives. Lower values of AIC indicate better fit, while taking into account model complexity. Although adding more parameters will increase fit, this does not guarantee a better model (He & Legendre, 1996; Stiles & Scheiner, 2007). For example, the negative exponential function, as a special case of the Chapman–Richards function, cannot fit better (have higher R^2), but may be a more parsimonious model (have lower AIC) because it has fewer parameters. Rather than apply a strict hypothetico-deductive approach using significance tests to select a particular model as best, the evidence in support of each model can be summarized by calculating the difference between the AIC value for model i and that of the best-fitting model (i.e. $\Delta_i = \mathrm{AIC_i} - \mathrm{AIC_{min}}$) and a set of weights (Akaike weights, w_i) that compare the models within a set. These weights represent the relative likelihood of each model, and are calculated as $w_i = \exp(-\frac{\Delta_i}{2}) / \sum_{i=1}^{n} \exp(-\frac{\Delta_i}{2})$. Values of w_i vary between 0 and 1, corresponding to the weight of evidence in support of a candidate model within a set; a value > 0.9 indicates a clearly superior model (Burnham and Anderson 1998). All models with $\Delta_i < 6$ should be considered for inference, whereas models with $\Delta_i > 10$ can be safely discounted. Also, more complex forms of the same model should only be considered if they fit better (i.e. have lower AIC), to avoid fitting unnecessarily complex models (Richards, 2008).

It should be noted that caution is needed in calculating AIC for models with different distributions as many statistical software programs omit terms from the likelihood equation and report incorrect values of the log likelihood. For the same model and data, reported AIC values may differ between programs and even between different procedures within the same program. To make comparisons across distributions any missing terms must be added to the reported likelihood to obtain the correct value (Shono, 2001; Burnham & Anderson, 2002: p. 317).

An empirical comparison of species–area functions

This analysis illustrates a method of fitting and comparing alternative functional models of the species–area relationship, with different numbers of parameters and different assumed distributions of S, using the generalized linear model and the information-theoretic approach.

Methods. The relationship between the number of plant species on 41 British islands and area (A), elevation (E), number of soil types (ST), degrees north latitude (L) and distance from Britain (D) was modelled using the species–area link functions of Table 1 and the parameterizations of Appendix S2. These data were taken from Table 1 of Johnson & Simberloff (1974), excluding the island of Britain (see McCoy & Connor, 1976).

Data analysis. As this is a small dataset, with the number of samples less than 40 times the number of parameters, the bias-adjusted statistic $\mathrm{AIC_c}$ was used to compare models (Burnham & Anderson, 2002). Two predictor variables (elevation and distance from Britain) that were positively skewed were log-transformed to improve the linearity between the response and explanatory variables to meet the assumptions of linear modelling. Correlations between the explanatory variables revealed significant collinearity between log(area), log(elevation), and the number of soil types ($R = 0.44$–0.86, $P < 0.01$), and between latitude and log(distance from Britain) ($R = 0.68$, $P < 0.01$), but not between latitude and log(area) ($R = 0.02$, $P = 0.89$). Variance inflation factors, which indicate the extent of collinearity between predictors, were all < 4, well below the problematic threshold of 10 (Glantz & Slinker, 2001). All of the potential predictors were significantly correlated with S ($|R| = 0.46$–0.66, $P < 0.01$), validating their inclusion as potential predictors. As in many species–area studies this dataset is not large enough to fit a valid model containing all of the covariates and their interactions. Therefore, a preliminary model using only main effects was constructed by determining the best-fit (lowest $\mathrm{AIC_c}$) model from all possible subsets.

A final model set was then determined by incorporating any interactions between the main effects that improved fit. Models were fitted using the SAS procedures REG, NLIN, and GENMOD (SAS Institute Inc., 2006). Log likelihood values (*LL*) for models assuming a normal or lognormal distribution were calculated from the residual sums of squares (*RSS*) using the formula

$$LL = -\frac{n}{2}\left[\log(2\Pi) - 1 - \log\left(\frac{RSS}{n}\right)\right].$$

For models assuming Poisson, binomial or lognormal distributions these log likelihood values and those reported by the SAS procedure GENMOD were corrected by adding $-\sum_{i=1}^{n}\log(S_i!)$, $\sum_{i=1}^{n}\log\binom{P}{S_i}$, or $-\sum_{i=1}^{n}\log(S_i)$, respectively. The size of the regional source pool was set to $P = 1666$, the number of species in Britain, although using $P = 1750$ (the approximate number of plant species in the United Kingdom) did not affect the outcome. Prior to including a model in the final set, its validity was assessed. Residuals were tested to determine if they conformed with the distribution assumed for each model using the Shapiro–Wilk test of normality or the Pearson chi-squared test of overdispersion.

Results. For species number related to area alone, seven models showed adequate fit and were included in the final set (Table 2). The other models (linear, log-transformed power, power with Poisson errors, logistic, EVF, asymptotic, rational and Gompertz) showed significant lack-of-fit to their assumed distributions or failed to converge to a solution (Weibull-4 and beta-P functions; Appendix S3). The power function with normal errors was the best-fitting, but for several others $\Delta_i < 6$. The negative exponential function was discounted as a potential model because $\Delta_i > 10$. Estimated asymptotes were highly variable or had large confidence intervals, and most were substantially lower than the total number of species in the archipelago.

Table 2. Comparison of alternative species–area functions as models of the number of plant species in the British Isles, excluding the island of Britain (data from Johnson & Simberloff, 1974; *n* = 41). Models with significant lack of fit (i.e. not meeting the distributional assumption underlying the model) have been excluded (see Appendix S3). For each function, lower values of the small-sample form of Akaike's information criterion (AIC_c) and its difference from the best-fitting model (Δ_i), and higher values of the Akaike weight (w_i) indicate a model with more support. Squared correlations (R^2) between observed and predicted values of *S* are given as indicators of fit but should not be used for model comparison. MMF, Morgan–Mercer–Flodin function.

Code	Function	*Rank*	AIC_c	Δ_i	w_i	R^2	Upper asymptote (95% CI)	
1b	Power, normal errors	1	536.9	0.0	0.36	0.45		
2	Exponential	3	538.7	1.7	0.15	0.43		
3b	MONOD	8	545.4	8.4	0.01	0.37	545	(437 – 652)
3c	MMF	5	538.9	2.0	0.13	0.45	1689	(-7160 – 10538)
4b	Negative exponential	9	550.7	13.7	0.00	0.37	531	(431 – 631)
4c	Chapman–Richards	2	538.0	1.1	0.21	0.47	624	(356 – 891)
4d	Weibull-3	4	538.8	1.9	0.14	0.45	901	(-1192 – 2994)

Incorporating additional covariates improved model fit substantially and one additional function (linear) was now included in the final model set (Table 3). Estimated asymptotes were considerably closer to the known value. The other models (log-transformed power, power with Poisson errors, logistic and EVF) showed significant lack-of-fit to their assumed distributions, or could not be fitted because non-linear regression failed to obtain stable estimates of their parameters (Weibull-4, asymptotic, Gompertz and beta-P functions; Appendix S4).

Table 3. Comparison of alternative species–area link functions as models of the number of plant species in the British Isles, excluding the island of Britain (data from Johnson & Simberloff, 1974; *n* = 41). Predictor variables are island area (*A*), elevation (*E*), number of soil types (*ST*), degrees north latitude (*L*) and distance from Britain (*D*). Models with significant lack of fit (i.e. not meeting the distributional assumption underlying the model) have been excluded (see Appendix S4). For the best-fitting model for each link function the selected covariates and the sign of their coefficients are listed. For each function, lower values of the small-sample form of Akaike's Information Criterion (AIC_c) and its difference from the best-fitting model (Δ_i), and higher values of the Akaike weight (w_i) indicate a model with more support. Squared correlations (R^2) between observed and predicted values of *S* are given as indicators of fit but should not be used for model comparison. MMF, Morgan–Mercer–Flodin function.

Code	Link function	Rank	AIC_c	Δ_i	w_i	R^2	Asymptote (95% CI)		Predictors
0	Linear	8	498.6	22.7	0.00	0.82			+log*E*, -*L*, *ST*, -*ST***L*, -log*E***L*
1b	Power, normal errors	5	480.5	4.6	0.06	0.87			+log*A*, -*L*
2	Exponential	1	475.9	0.0	0.61	0.89			+log*A*, -*L*, - log*A***L*
3b	MONOD	3	479.1	3.2	0.12	0.88	1497	(712 – 2281)	+log*A*, -*L*, -log*A***L*
3c	MMF	2	479.1	3.2	0.05	0.88	1356	(514 – 2198)	+log*A*, -*L*, - log*A***L*
4b	Negative exponential	4	479.7	3.8	0.09	0.88	1150	(699 – 1602)	+log*A*, -*L*, - log*A***L*
4c	Chapman–Richards	7	481.5	5.6	0.04	0.88	1117	(745 – 1490)	+log*A*, -*L*, - log*A***L*
4d	Weibull-3	6	481.4	5.5	0.04	0.87	1152	(538 – 1765)	+log*A*, -*L*

The linear function was discounted because $\Delta_i > 10$ and the Chapman–Richards, Weibull-3 and MMF were also discounted because they are more complex forms of the negative exponential and MONOD functions and did not fit better. Thus four functional models (non-linear power, exponential, MONOD, and negative exponential) were the best-fitting, but none was sufficiently distinct that it could be chosen as clearly superior. Three of these models identified the same set of factors as the best predictors of species number: log(area), latitude and their interaction (Table 3, Appendix S5). The negative coefficient for the interaction between log(area) and latitude indicates that the effects of area and latitude were not additive: increasing island area at low latitudes resulted in a greater rise in species number than at high latitudes. Thus, there is evidence that the slope of the species–area relationship within this archipelago is steeper at lower latitudes. As latitude and area were uncorrelated this cannot be a spurious effect due to collinearity between them (Vittinghoff *et al.*, 2004).

Discussion

The empirical comparison conducted here illustrates two salient points. First, some functions may fit species–area data poorly when other factors are ignored, but may be among the best if these factors are included. Based on area alone, the linear and negative exponential functions were excluded as species–area models because they failed to meet model assumptions and had poor fit, respectively. However, when additional covariates were employed both were included in the final model set. The contrasting results for the negative exponential function, which showed inferior fit to area alone but was among the best-fitting when other covariates were included, demonstrates that assessing performance using area alone does not guarantee finding the best fitting species–area function. This result is not novel: failure to include important covariates is a common source of error in model fitting (Barry & Elith, 2006). Second, alternative species–area functions may identify different covariates as important predictors. The linear link function identified an entirely different set of explanatory factors, although this model could be discounted because of inferior fit. The power function model did not support the presence of an interaction between area and latitude, although three other models did. Choice of a suitable species–area link function is therefore important in identifying the factors affecting species number.

Examination of a some recent studies that have undertaken empirical comparisons of species–area functions (Veech, 2000; Fattorini, 2006a, b; Fattorini & Fowles, 2006; Panitsa *et al.*, 2006; Stiles & Scheiner, 2007) revealed some shortcomings. Most assumed only a normal or lognormal distribution for S, examined the relationship between S and A in isolation, emphasized goodness-of-fit rather than distributional assumptions, or used incorrectly specified forms for some functions. Some compared alternative functions using R^2 even though different distributions were assumed for some models. The fact that some species–area functions are identical is apparent in the results of some of these studies: Stiles & Scheiner (2007) found that the logistic, Lomolino (2000) and MMF functions gave identical fits for a range of data sets; and

Panitsa *et al.* (2006) found that the logistic and Lomolino (2000) functions gave identical R^2 values. In these comparisons no consensus was reached as to which was the best functional form. As only area was considered as an explanatory variable this is not unexpected: in many of the studies factors other than area thought to influence S were recorded, and only when these factors had been incorporated should the various functions have been compared.

Connor & McCoy (1979) recommended the use of the power function partly because of the difficulty of comparing non-linear models. Methods to make such comparisons using the generalized linear model and information-theoretic approach are now available. To fit species–area models, methods appropriate to the distribution of S should be used (Vittinghoff *et al.*, 2005), but what this distribution may be has rarely been considered in the literature and so no agreement exists. At least four distributions have been proposed for S, either explicitly or implicitly: lognormal (e.g. Arrhenius, 1921), normal (e.g. Gleason, 1922), binomial (e.g. Williams, 1995), and Poisson (e.g. Candy, 1997; Russell *et al*., 2004). As all are members of the exponential family of distributions they may be fitted using the generalized linear model, which is commonly available in statistical software programs (Quinn & Keough, 2002). This method enables additional covariates to be incorporated and most software provides the diagnostic tools necessary to test assumptions. Any of the models in Table 1 can now be fitted to species–area data and compared within a consistent framework.

Stiles & Scheiner (2007) suggested that researchers compare multiple functions to discover the one with optimal fit. However, there are practical problems inherent in this approach. First, there are an infinite number of potential species–area functions and no reason to suppose that the ones that have been used to date fit better than any of the other possibilities. Second, for some functions it is not clear how factors in addition to area should be incorporated. Also, the process of modelling the species–area relationship alone to choose the best-fitting function and then proceeding to use this function as the basis of a model that incorporates additional covariates is theoretically unsound. Our study shows that this approach does not necessarily lead to the best fitting species–area function. The goodness-of-fit of alternative models is not the only consideration in determining which is appropriate – diagnostic tests are also needed to determine if the distributional assumptions underlying each are met (Fry, 1993). Basing the choice of species–area function only on a goodness-of-fit criterion is poor statistical practice (Hurvich & Tsai, 1990). We recommend that if researchers wish to compare the fit of alternative models, they use the generalized linear model and the information-theoretic approach. However, a considerable body of previous work suggests that the power function is unlikely to produce misleading results, provided the appropriate diagnostic tests indicate no serious departures from normality and homoscedasticity (Connor & McCoy, 1979; Rosenzweig 1995). The power function is a very good description of the species–area relationship whenever two conditions are fulfilled: (1) individuals of each species cluster; and (2) the species abundance distribution is similar to Preston's lognormal but with a higher rarity (Martin & Goldenfeld, 2006). Thus, unlike many other proposed species–area functions, the power function model has a reasonable theoretical basis.

Ideally, a suitable model for the species–area relationship should account for: (1) the actual functional relationship between species and area, based upon good theory; (2) variation in actual species numbers (in contrast to observed numbers) within areas; and (3) the observation error in counting species. Few of the currently proposed models consider (1), even fewer consider (2), and none considers (3). A model should then give the relationship between area and the number of species counted, and also account for the distribution of the deviations from the observed counts. This ideal model is likely to be based upon the probability that a particular species is present within a site, given the area of the site, any other explanatory variables, and the presence of the other species. A suitable starting point may therefore be models of species incidence that describe the relationship between individual species presence, area and other predictors (Ovaskainen & Hanski, 2003), such as the Proportion of Area Occupied models that incorporate estimates of species detectability (MacKenzie *et al.*, 2006). At present, there is a lack of good (or any) theory for many of the functional forms proposed for the species–area relationship.

An appropriate methodology for fitting species–area models should include the following steps: (1) choose a suitable link function based on good theory, including consideration of whether a model with an asymptote is appropriate; (2) select a distributional model for S; (3) include appropriate covariates (predictors) in the model fitting process; (4) fit the model paying due care to tests of assumptions; and (5) consider interactions between the covariates (Hosmer & Lemeshow, 2000; Vittinghoff *et al.*, 2005; Barry & Elith, 2006). To compare models with varying numbers of parameters or different distributions, an appropriate methodology (such as the information-theoretic approach) should be used. Although R^2 is a well-known indicator of model fit, its usefulness for model comparison is limited. Few studies have addressed all of these issues, especially the study of interactions between covariates, although Triantis *et al*. (2003) and Kallimanis *et al*. (2008) are notable exceptions, and Russell *et al*. (2004) is an examplar of good statistical practice in species–area modelling. Similarly, few studies consider the appropriate distribution for S. The Poisson and binomial distributions are under-utilized in applied ecology but provide better models of variation in count data (Richards, 2008).

That a species–area effect exists has been established by more than a century of study (Rosenzweig, 1995). Connor & McCoy (1979: p. 794) pointed out "… the power function … has been fitted to species–area data ignoring important underlying assumptions". Unfortunately, these underlying assumptions continue to be ignored. Despite the availability of better analytical techniques to compare species–area models, these have not been widely adopted or correctly applied. Together, this disregard of good statistical practice has been an impediment to progress. In the absence of an *a priori* theoretical basis for a particular model, Goodall (1952) suggested that the way forward is to achieve consensus on what functional form this relationship takes by empirical comparison of potential models with observational data. However, comparing a large number of possible functions without consistent methodology is a fruitless task. Insight into ecological processes, appropriate methodology, and careful consideration of assumptions are needed to progress the study of species–area relationships.

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Supporting Information

Additional supporting information may be found in the online version of this article. available for this article:

Appendix S1 Algebraic comparisons of alternative species–area functions.

Appendix S2 Parameterization of species–area link functions.

Appendix S3 Comparison of alternative species–area functions as models of the number of plant species in the British Isles.

Appendix S4 Comparison of alternative models of the number of plant species in the British Isles.

Appendix S5 Models of the number of plant species in the British Isles.

Appendix S1. Algebraic comparisons of alternative species–area functions

In the following, a, b, c, and d are fitted parameters, with a an asymptote and c the coefficient of area. The area of isolate i is x_i, for $i = 1, \dots, n$ isolates; S_i is the number of species in isolate i; and $P = S_{max}$ is the number of species in the source pool. Natural logarithms are used throughout.

1. Comparison of the Morgan–Mercer–Flodin (MMF), Lomolino (2000), Archibald (1949b) logistic, and MONOD functions.

The Morgan–Mercer–Flodin function (Tjørve, 2003) is

$$
\begin{aligned}
S_i &= a x_i^c \,/\, (b + x_i^c), \\
&= a x_i^c \,/\, [\, x_i^c \,(b/x_i^c + 1)\,] \\
&= a \,/\, (1 + b x_i^{-c}) \qquad (x_i^c \neq 0, \text{ since } x_i \neq 0).
\end{aligned}
$$

The Lomolino function (Lomolino, 2000) is

$$
\begin{aligned}
S_i &= S_{\max} \Big/ \left(1 + b^{\log(\frac{c}{x_i})}\right) \\
&= P \Big/ \left(1 + b^{\log c - \log x_i}\right) \\
&= P \Big/ \left(1 + \frac{b^{\log c}}{b^{\log x_i}}\right)
\end{aligned}
$$

replacing b with $b = \exp(\log b)$, and assuming $b, c \neq 0$

$$
\begin{aligned}
S_i &= P \,/\, [\, 1 + \exp(\log b \log c) \,/\, \exp(\log b \log x_i) \,] \\
&= P \,/\, (1 + c^{\log b} / x_i^{\log b})
\end{aligned}
$$

Setting $b' = c^{\log b}$ and $c' = \log b$

$$
S_i = P \,/\, (1 + b' x_i^{-c'})
$$

Hence, the Lomolino (2000) function is equivalent to the MMF, with $a = P$.

The logistic function (Archibald, 1949b) is

$$
\log\,(\, S_i \,/\, (\, P - S_i\,)\,) = k\,(\log x_i - \log x_{50})\,,
$$

k and x_{50} are fitted parameters, with x_{50} = the area at which half of the species in the source pool are present (i.e. the value of x_i such that the estimated value of $S_i = P/2$).

i.e. $\log (S_i / (P - S_i)) = \log (x_i / x_{50})^k$

i.e. $S_i / (P - S_i) = (x_i / x_{50})^k$

i.e. $(P - S_i) / S_i = (x_{50} / x_i)^k$

i.e. $P / S_i = (x_{50} / x_i)^k + 1$

i.e. $S_i / P = 1 / [1 + (x_{50}^k / x_i)^k]$

i.e. $S_i = P / [1 + x_{50}^k / x_i^k]$

Setting $b = x_{50}^{\ k}$ and $c = k$

$$S_i = P / (1 + bx_i^{-c})$$

Hence the logistic function is identical to Lomolino's (2000) function and equivalent to the MMF, with $a = P$.

The MONOD function (Clench, 1979) is

$$\begin{aligned} S_i &= a (x_i / (b + x_i)) \\ &= ax_i / [x_i (b/x_i + 1)] \\ &= a / (1 + bx_i^{-1})) \qquad \text{(since } x_i \neq 0\text{).} \end{aligned}$$

Hence the MONOD function is a special case of the MMF with $c = 1$.

2. Comparison of the EVF, cumulative Weibull function with 3 parameters, negative exponential and Chapman–Richards functions.

The cumulative Weibull function with 3 parameters (Weibull-3) is

$$S_i = a [1 - \exp(-bx_i^{\ c})]$$

The EVF (Williams, 1995) is

$$\begin{aligned} S_i &= P [1 - \exp(-\exp(b\log x_i + c))], \\ &= P [1 - \exp(-\exp(b\log x_i)\exp(c))] \end{aligned}$$

$$= \quad P\,[\,1 - \exp(-\exp(c)\exp(\log x_i^{\,b}))\,]$$

$$= \quad P\,[\,1 - \exp(-\exp(c)\, x_i^{\,b})\,]$$

Setting $b' = \exp(c)$ and $c' = b$

$$S_i \quad = \quad P\,[\,1 - \exp(-b' x_i^{\,c'})\,]$$

Hence the EVF is a special case of the Weibull-3 function, with $a = P$.

The negative exponential function is

$$S_i \quad = \quad a\,[\,1 - \exp(-b x_i)\,]$$

Hence the negative exponential function is a special case of the Weibull-3, with $c = 1$.

The Chapman–Richards function is

$$S_i \quad = \quad a\,[\,1 - \exp(-b x_i)\,]^c$$

Hence the negative exponential function is also a special case of the Chapman–Richards function, with $c = 1$.

Appendix S2. Parameterization of species–area link functions

The conventional notation $\boldsymbol{XB}$ indicates the product of a matrix of predictor variables (covariates) $\boldsymbol{X}$ and a vector of coefficients $\boldsymbol{B}$. $\boldsymbol{X} = [1, x_1, x_2, \dots, x_p]$, with p the number of covariates; S is the number of species, x_1 = area (A) or log$A$ of the n isolates, and $x_1 = [x_{1,1}, x_{1,2}, \dots, x_{1,n}]^T$. The coefficients to be estimated are $\boldsymbol{B} = [b_0, b_1, b_2, \dots, b_p]^T$, and for some functions the additional parameters a, c and d. Any restrictions on, or changes to, the parameters in Table 1 are noted. No suitable parameterization of the rational function was found.

Code	Function	Parameterization	x_{1i}	Notes
0	Linear	$S = \boldsymbol{XB}$	A	
1	Power	$S = \exp(\boldsymbol{XB})$	log$A$	
2	Exponential	$S = \boldsymbol{XB}$	log$A$	
3a	Logistic	$S = P / [\, 1 + \exp(-\boldsymbol{XB})\,]$	log$A$	
3b	MONOD	$S = a / [\, 1 + \exp(-\boldsymbol{XB})\,]$	log$A$	b_1=1
3c	MMF	$S = a / [\, 1 + \exp(-\boldsymbol{XB})\,]$	log$A$	
4a	EVF	$S = P\, [\, 1 - \exp(-\exp(\boldsymbol{XB}))\,]$	log$A$	
4b	Negative exponential	$S = a\, [\, 1 - \exp(-\exp(\boldsymbol{XB}))\,]$	log$A$	b_1=1
4c	Chapman–Richards	$S = a\, [\, 1 - \exp(-\exp(\boldsymbol{XB}))\,]^{c}$	log$A$	b_1=1
4d	Weibull-3	$S = a\, [\, 1 - \exp(-\exp(\boldsymbol{XB}))\,]$	log$A$	
4e	Weibull-4	$S = a\, [\, 1 - \exp(-\exp(\boldsymbol{XB}))\,]^{c}$	log$A$	
5	Asymptotic	$S = a\, [\, 1 - \exp(-\boldsymbol{X}\log(\boldsymbol{B}))\,]$	A	b replaced by b_1/a
7	Gompertz	$S = a\, [\, \exp(-\exp(\boldsymbol{XB}))\,]$	A	$-c$ replaced by b_1
8	Beta-P	$S = a\, [\, 1 - (\, 1 + (x_1/b_1 + x_2/b_2 + \dots)^{c}\,)^{-d}\,]$	A	

Appendix S3. Comparison of alternative species–area functions as models of the number of plant species in the British Isles

Comparison of alternative species–area functions as models of the number of plant species in the British Isles, excluding Britain (data from Johnson & Simberloff, 1974; $n = 41$). The lack of fit (P-value) was assessed by the Shapiro-Wilk test for models with normal errors, or the Pearson chi-square statistic (c); values < 0.05 indicate significant departure from the distributional assumption underlying each model. Functions prefixed * failed to converge.

Code	Function	Rank	AIC_c	Δ_i	c	Lack of fit
0	Linear	13	548.9	14.3		0.01
1a	Power, lognormal errors	3	535.9	1.3		0.01
1b	Power, normal errors	5	536.9	2.3		0.07
1c	Power, Poisson errors	15	3027.8	2493.2	68.24	0.00
2	Exponential	7	538.7	4.1		0.17
3a	Logistic	17	3164.5	2629.9	88.80	0.00
3b	MONOD	12	545.4	10.8		0.96
3c	MMF	9	538.9	4.3		0.09
4a	EVF	16	3156.8	2622.2	88.74	0.00
4b	Negative exponential	14	550.7	16.0		0.96
4c	Chapman–Richards	6	538.0	3.4		0.16
4d	Weibull-3	8	538.8	4.2		0.11
4e	*Weibull-4	10	539.9	5.3		0.11
5	Asymptotic	2	535.2	0.6		0.03
6	Rational	4	536.7	2.1		0.03
7	Gompertz	1	534.6	0.0		0.03
8	*Beta-P	11	543.7	9.1		0.25

Appendix S4. Comparison of alternative models of the number of plant species in the British Isles

Comparison of alternative models of the number of plant species in the British Isles, excluding Britain (data from Johnson & Simberloff, 1974; $n = 41$). For each link function of Table 1 the best-fitting model (lowest AIC_c) was selected from those incorporating the main effects and one-way interactions of island area, elevation, latitude, number of soil types, or distance to Britain. The lack of fit (P-value) was assessed by the Shapiro-Wilk test for models with normal errors, or the Pearson chi-square statistic (c); values < 0.05 indicate significant departure from the distributional assumption underlying each model. Functions prefixed * failed to converge.

Code	Function	Rank	AIC_c	Δ_i	c	Lack of fit
0	Linear	11	498.6	102.8		0.44
1a	Power, lognormal errors	12	510.3	114.5		0.00
1b	Power, normal errors	6	480.5	84.7		0.79
1c	Power, Poisson errors	16	1222.8	827.0	22.6	0.00
2	Exponential	2	475.9	80.1		0.25
3a	Logistic	1	395.8	0.0	23.2	0.00
3b	MONOD	4	479.1	83.3		0.69
3c	MMF	3	481.1	85.3		0.44
4a	EVF	15	611.7	216.0	26.4	0.00
4b	Negative exponential	5	479.7	83.9		0.71
4c	Chapman–Richards	8	481.5	85.7		0.69
4d	Weibull-3	7	481.4	85.6		0.57
4e	*Weibull-4	10	485.2	89.4		0.35
5	*Asymptotic	13	514.7	118.9		0.07
7	*Gompertz	9	483.7	87.9		0.20
8	*Beta-P	14	548.2	152.4		0.00

Appendix S5. Models of the number of plant species (*S*) in the British Isles, excluding Britain

Models of the number of plant species (*S*) in the British Isles, excluding Britain, using island area (*A*), elevation (*E*) and latitude (*L*) (data from Johnson & Simberloff, 1974; $n = 41$). Coefficients and associated standard errors (in parentheses) for models based on the four alternative link functions:

Power $S = \exp(b_0 + b_1 \times \log A + b_2 \times L)$;

Exponential $S = b_0 + b_1 \times \log A + b_2 \times L + b_3 \times \log A \times L$;

MONOD $S = a / [1 + \exp(-(b_0 + \log A + b_2 \times L + b_3 \times \log A \times L))]$; and

Negative exponential $S = a \times [1 - \exp(-\exp(b_0 + \log A + b_2 \times L + b_3 \times \log A \times L))]$.

Link function	***a*** ***asymptote***	***b₀*** ***intercept***	***b₁*** **log*A***	***b₂*** ***L***	***b₃*** **log*A*L***
Power, normal errors		12.3 (0.69)	0.178 (0.018)	-0.127 (0.011)	
Exponential		1472.5 (683.0)	543.1 (146.9)	-23.8 (12.0)	-8.40 (2.59)
MONOD	1496.8 (387.1)	5.97 (2.51)		-0.143 (0.0405)	-0.0133 (0.000672)
Negative exponential	1150.5 (222.6)	5.08 (1.92)		-0.122 (0.0313)	-0.0137 (0.000512)

Chapter 5 - Habitat resources determine incidence patterns and abundance of butterflies and day-flying moths in a fragmented urban landscape, south-west Western Australia

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Abstract

The creation of cities, towns and farms following European settlement of Australia has fragmented the original vegetation. Many native species that were previously widespread are now found only within isolated habitat remnants. These relictual populations are at increased risk of decline and local extinction, so identifying the factors that determine their persistence is important for ongoing management and conservation. I compared the effects of habitat area, resources (vegetation condition, density of specific host plants and density of shade trees) and site connectivity on the presence, abundance and total number of species of butterflies and day-flying moths within 46 urban habitat fragments in south-west Western Australia. Site area and vegetation condition were the dominant determinants of species presence: large sites with more high quality (undisturbed) vegetation favoured 16 of 20 native species and only one benefited from disturbance. Another nine species that were not sufficiently widespread or abundant to enable individual analysis were collectively more prevalent in larger sites. Host plant density was an important predictor of both site occupancy and abundance for all of the species for which it was assessed. Higher tree densities had positive impacts on occupancy for some species, but lower densities were associated with greater abundance of others. Increased site connectivity did not favour any species. Resource quality and quantity dominated the patterns of site occupancy, consistent with habitat resources, not metapopulation effects, determining current distribution patterns. The total number of species at each site reflected the collective responses of the individual species: increasing with area and declining with vegetation disturbance. The effects of area and vegetation quality were not simply additive: disturbance had a far greater impact on small remnants. Restoration or maintenance of high vegetation quality will be essential to maintain regional species diversity and to prevent local extinctions of butterflies and day-flying moths, especially in small remnants.

Key words: connectivity; disturbance; metapopulation; site occupancy; vegetation quality.

Introduction

Patches of remnant vegetation are now common features in urban and rural landscapes throughout the world. Populations of fauna in these fragments are frequently isolated and the resources necessary for breeding and reproduction may have been altered, potentially causing decline and local extinction of some species. A variety of threats result from human pressures on remnant vegetation – recreation, trampling of vegetation, altered fire regimes and the introduction of weeds and fungal pathogens – which cause changes in the structure and composition of plant communities and consequent loss of native fauna (New 1984, Samways 2007). The faunal assemblages that persist in fragments are the result of the operation of several factors, including the characteristics of the fragments (area, isolation, level of disturbance, and the presence of resources for individual taxa) and characteristics of the species (requirements for specific levels of resources, ability to adapt to altered conditions, vagility, colonization ability, and occurrence in nearby source areas). The intervening matrix typically contains few resources for many species and may present a substantial barrier to dispersal.

The majority of studies of habitat fragmentation have examined the responses of vertebrates and higher plants, with less emphasis on invertebrates despite their numerical predominance and importance in ecosystem functioning (New 1991, Akite 2008, McKinney 2008). Butterflies are one of the best-known invertebrate groups and where baseline data are available show marked declines in distribution that often exceed declines in other taxa: for example, half the resident butterfly species of Britain are threatened or extinct and most have reduced geographic ranges (Warren *et al.* 2001, Ewers and Didham 2006). Many species of butterflies now depend on remnant vegetation for survival, especially in urban areas (Ruszczyk and De Araujo 1992, Blair 1999, Connor *et al.* 2002, Newland 2003). The threats to butterflies are generally the same as for other fauna: habitat destruction or alteration; changes to management practices; isolation of remnant habitat; pollution and use of chemical insecticides and herbicides; climate change; and in some cases overcollecting or trade in specimens (New 1991, Pollard and Yates 1993, Beaumont and Hughes 2002, Brown and Freitas 2004). More than 400 species of butterflies are recorded for

Australia and few more are likely to be discovered, making them the best-known insect group (Braby 2000). Several studies have documented the conservation status of individual taxa (New 1993b, Kitching *et al.* 1999, Braby 2000) and a major review of the Australian fauna has been conducted (Sands and New 2002). These cite the lack of systematic surveys in conservation reserves and the lack of a national database as the major impediments to establishing the conservation status of many species. Information about the requirements of butterflies within habitat fragments is needed to conserve these remnant populations.

Two dominant paradigms have been proposed to account for insect distribution patterns (Thomas *et al.* 2001, Gripenberg and Roslin 2005, Grundel and Pavlovic 2007): in the first, site occupancy depends on sufficient quantity and quality of resources required by the larvae and adults (habitat effects); in the second, site occupancy varies over time with successive extinction and recolonization events, and depends on the isolation or connectivity of habitat patches (metapopulation effects). The two models lead to different conservation priorities: the first emphasizes the need to maintain optimal habitat within fragments, whereas the second gives priority to preserving numerous remnants that are within each species' dispersal range.

The conservation value of remnant habitat is often determined on the basis of total species number, which often reflects species–area relationships. Approaches that examine species–area relationships to determine biodiversity hotspots and priority areas for conservation overlook the fact that area *per se* may not be the only, or indeed the most important, predictor of total species number (Veech 2000, Ulrich 2003, Ulrich and Buszko 2005, Ewers and Didham 2006, Fattorini 2006, Dapporto and Dennis 2008b). Insects are often more sensitive to habitat quality than site area, and many decline rapidly after disturbance (Maes and Van Dyck 2001, Thomas *et al.* 2001, Gibb and Hochuli 2002, Dennis 2004a, McKinney 2008). Studies of insect faunas have shown that habitat area, quality, isolation and connectivity may all be important (Samways 2007); that the level of urbanization, which diminishes from the urban core to suburban areas, almost always reduces species numbers (McKinney 2008); but that responses may also be species-specific (Ewers and Didham 2006, Garden *et al.* 2006, Grundel and Pavlovic 2007, Dapporto and Dennis 2008b, McKinney 2008). Particular site attributes, including both structural elements (such as tree cover) and species-specific resources (such as host plants) are also important determinants of persistence for many butterflies and day-flying moths (Baz and

Garcia-Boyero 1995, Dover *et al.* 1997, Dennis *et al.* 2004, Krauss *et al.* 2004, Gripenberg and Roslin 2005, Kadlec *et al.* 2008). To manage and conserve fauna within fragments therefore requires knowledge of individual species responses to site characteristics and disturbance (Garden *et al.* 2006, Grundel and Pavlovic 2007). Lack of information about the resources required to sustain these isolated populations has been identified as a limiting factor in conserving fauna in urban fragments (Garden *et al.* 2006). Determining those aspects of habitat size, quality and the spatial arrangement of remnants that account for species persistence in isolated remnants is important in guiding the management and conservation of remaining faunal populations.

This study examines the effects of site area, connectivity and habitat resources on the presence, abundance and number of butterfly and day-flying moth species in urban habitat remnants, with the aims of (i) testing whether habitat quality or metapopulation effects dominate, and (ii) identifying the important factors for conservation and management of remaining populations.

Methods

Study Area

The urban area of the Perth metropolitan region in south-west Western Australia is an example of a disturbed landscape. Prior to European settlement the Swan Coastal Plain portion of the region consisted of continuous tracts of low open woodland and open forest dominated by *Banksia* and *Eucalyptus* (Beard 1990). Land clearing for agriculture and urbanization has reduced the native vegetation to 18% of its original extent, which now consists of fragments varying in size and level of disturbance (Government of Western Australia 2000). The intervening matrix consists mainly of low-density residential suburbs dominated by non-native plant species. Historically, the urban area has expanded along a north–south axis, bounded in the west by the Indian Ocean and in the east by the Darling Range, so that linear distance from the city centre is a good indicator of the time of fragmentation (Kennewell and Shaw 2008). The region has a Mediterranean-type climate with a pronounced summer drought and is prone to periodic fires (McCaw and Hanstrum 2003).

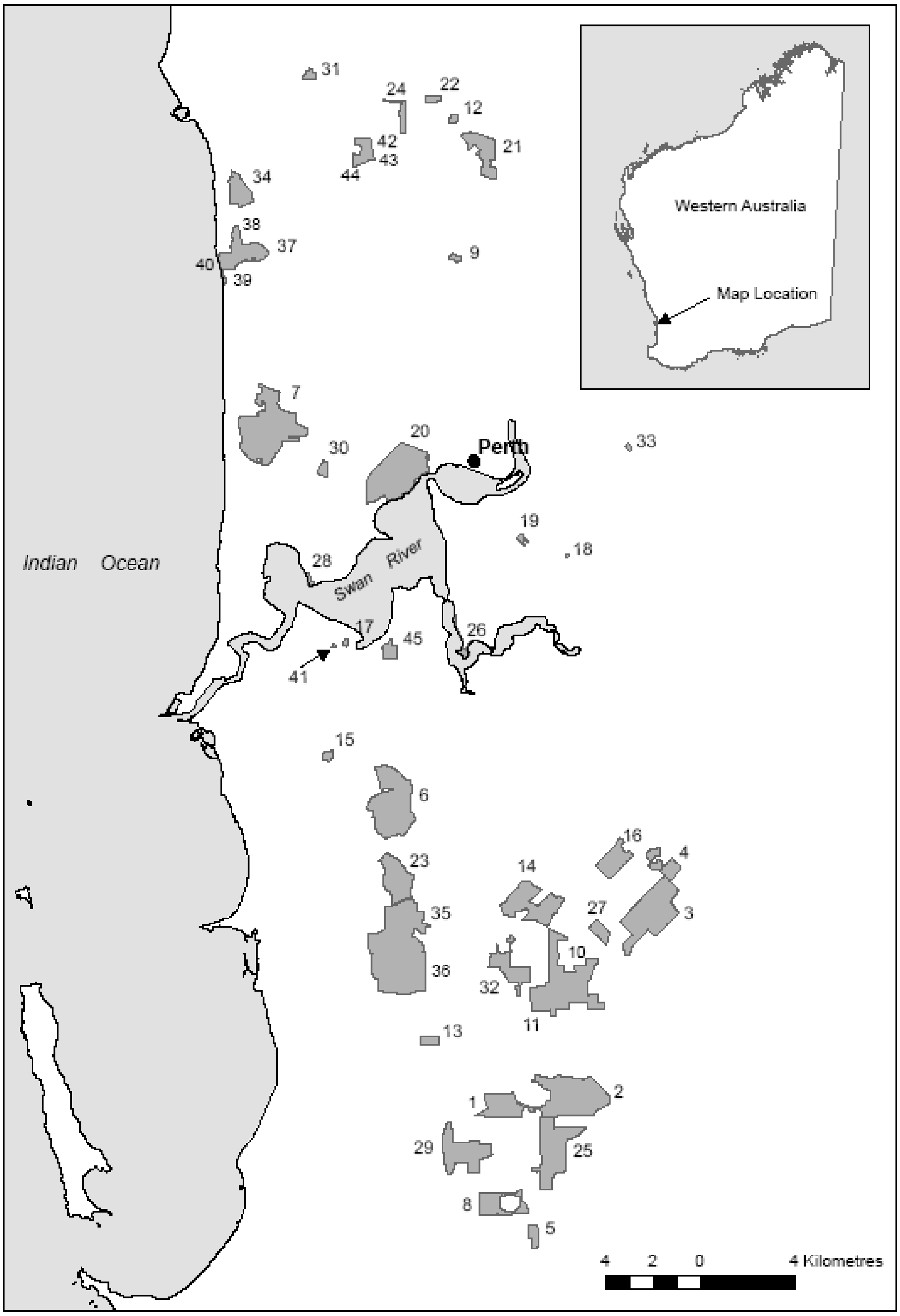
Forty-five butterfly species have been recorded for the study area (Braby 2000). Because day-flying moths have habits and resource requirements similar to those of butterflies it is common practice to include these in surveys. There are far fewer of these in the study area but the precise number of species is unknown. The most notable are the sun-moths (*Synemon* spp., Castniidae), active and conspicuous moths that are often confused with butterflies (Edwards 1997a, b). One, *Synemon gratiosa*, is listed as endangered (Burbidge 2004) but relatively little is known about the others.

Forty-six patches of remnant vegetation were selected for surveys. Four were included because they were known to have populations of the endangered *Synemon gratiosa*, one because it is the closest remnant to the urban centre, and the remainder were selected at random from a major review of the conservation values of remnant vegetation within the study area (Government of Western Australian 2000) (37 sites) or added opportunistically (4 sites). All sites were within 35 km of Perth (population 1.5 million), the major urban centre in Western Australia, and ranged in area from 0.7 to 362 ha (Appendix 1, Fig. 1). Several of the fragments were closely located, but were separated by cleared areas or roads, were joined by narrow corridors of highly disturbed remnant vegetation, or had parts subjected to different management practices, and were treated as separate sites.

Field Surveys

At each site one to three transects were established, positioned to sample as many vegetation and habitat types as possible including any recently- or long un-burnt areas. Although transects were predominantly restricted to existing walk tracks and fire breaks to protect the native vegetation from trampling and reduce the spread of weeds or fungal pathogens, parts of some transects traversed the vegetation. Transect length varied with site area, ranging from 260 to 5100 m, and smaller sites typically had shorter transects but a higher sampling fraction (the fraction of the site area sampled by the transect).

Figure 1. Location of sites surveyed for butterflies and day-flying moths in the Swan Coastal Plain, Perth metropolitan region, south-west Western Australia. Each site is identified by the site number in Appendix 1. The total extent of each site is depicted, not the remaining native vegetation; the area of remnant vegetation is given in Appendix 1.



To sample the fauna, surveys were conducted at fortnightly intervals during the two main butterfly flight periods in the Austral spring (late September – mid December, usually six surveys) and in autumn (late February – early April, two surveys), between September 2003 and April 2005. All surveys were conducted by the author, with the occasional assistance of 1 or 2 volunteers, in fine weather with forecast maximum temperatures above 21° C. This sampling regime detects over 85% of the resident fauna (Williams 2008). The butterfly fauna of the region is well documented and phenological data for each species are given by Braby (2000, 2004) and (Williams in press). Each transect was walked at a steady pace and all butterflies and day-flying moths observed within a rectangle 5 m to either side and ahead of the observer(s) were identified and tallied. Two species (*Motasingha dirphia* and *M. trimaculata*) that are difficult to distinguish in the field were recorded as the more common *M. trimaculata*; this is the conventional approach (Pollard and Yates 1993). The abundance of each species was measured by the number of individuals counted per 100 m of transect.

The species detected were divided into two groups: those that breed entirely or predominantly on native plants restricted to bushland remnants (‘resident species’); and those that are introduced, regular migrants, vagrants or which breed predominantly on introduced plants throughout the urban matrix (‘non-resident species’). This division is equivalent to the concepts of ‘island’ and ‘matrix’ species (Pollard & Yates 1993), ‘urban avoiders’ and ‘urban adapters’ (Koh and Sodhi 2004), and ‘matrix sensitive’ and ‘matrix occupying’ species (Garden *et al.* 2006). Resident (island, urban avoider, matrix sensitive) species have low dispersal rates, are local or uncommon, and are generally restricted to remaining suitable habitat patches. Non-resident (matrix, urban adapter, matrix occupying) species are highly dispersive, common, occur in both remnant habitat and intervening areas, and are of little conservation concern. This division follows the approach of previous studies of Australian butterflies (Hill 1987, Braby and Edwards 2006). Taxonomy follows Braby (2000) for butterflies, and Common (1990) and Edwards (1997a) for moths.

Site attributes

For each site several physical and habitat attributes that potentially affect species presence, abundance and the total species number were measured. Site physical attributes were area (A), two measures of site connectivity (distances to the nearest (N) and nearest larger (NL) patch of remnant vegetation), and a measure of the level of urbanization and time since isolation (the distance of the site from the urban centre (D)). Habitat resources were: the density of shade trees (T, the number of stems of *Eucalyptus, Casuarina* and *Allocasuarina* spp. > 10 cm dbh, per 100 m of transect); two measures of vegetation condition, as described below; and the density of three host plants (*Daviesia divaricata* (Dd), *Jacksonia sternbergiana* (Js) and *Patersonia occidentalis* (Po)) that are used by four butterfly species (*Mesodina cyanophracta* (Po), *Hypochrysops halyaetus* (Dd and Js), *Neolucia agricola* (Dd and Js), and *Lampides boeticus* (Js)). Host plants of other species were not recorded because they are either cryptic, difficult to identify, incompletely known, or ephemerals that were not evident during the sampling period. Tree and host plant densities were recorded on the same transects used to survey fauna.

The vegetation condition at the sites had been evaluated < 5 y prior to the surveys as part of a comprehensive study of the conservation significance of all remnant vegetation in the Perth metropolitan region (Government of Western Australia 2000). Vegetation condition at each site was scored using an objective rating scale (Keighery 1994) and the fraction of the vegetation in each of five condition classes was determined: (i) no obvious signs of disturbance (rated 9); (ii) vegetation structure intact, some disturbance affecting individual plant species, and weeds only non-aggressive species (7); (iii) vegetation structure altered, obvious signs of disturbance such as evidence of logging, grazing, repeated fires, presence of aggressive weeds, or dieback caused by fungal pathogens (5); (iv) vegetation structure significantly altered by very obvious signs of multiple disturbance, such as very frequent fires, high densities of some very aggressive weeds, partial clearing, dieback or grazing (3); and (v) as for the previous category, but vegetation structure severely impacted by disturbance and unlikely to regenerate without intensive management (1). Intermediate ratings were also used, so a typical condition assessment would be '>75% rated 5–7, <25% 1–3'. Two measures of vegetation condition were calculated: the average vegetation condition (AVC), and the fraction of high quality vegetation (HQV, the fraction rated > 5). An advantage of using the existing vegetation condition ratings was that they could then be used to make predictions of species occupancy and total species number for the total 287 vegetation remnants within the region that had been assessed.

Data analysis

The relationship between the site attributes, the incidence and abundance of each species and the number of species present was examined using logistic and linear regression models. For individual species presence and abundance, two complementary models were fitted (Fletcher *et al.* 2005): first, the relationship between species presence and the site attributes was examined using a logistic regression model; second, within the sites it occupied, the log(abundance) of each species was regressed on the same factors using linear regression. Including only occupied sites eliminated the bias that arises from a high proportion of sites having zero abundances and the need to use the arbitrary log $(x + 1)$ transformation. For the species-incidence models the complementary log-log function was used in place of the usual logit link, as this has been shown to be a more appropriate null model, although this choice has a negligible effect on results (Williams 1995). The number of resident and non-resident species at each site was modelled using the cumulative extreme-value function (EVF) model, the multiple species equivalent of the complementary log-log link function, although results using the power function model gave identical results. To improve the linearity of the relationship between the covariates and the dependent variables, positively-skewed variables were transformed for analysis: abundance, A, D, N, and NL were log-transformed; and T, Dd, Js and Po were square root transformed. Host plant densities were only included as predictors for the relevant species.

All possible subsets of the predictor variables were examined, although the maximum number of attributes included in each model was limited by the amount of data available for each species. To obtain reliable results using logistic regression approximately 10 occurrences or absences, and in multiple regression approximately 10 cases, are needed for each fitted parameter (Stevens 1992, Burnham and Anderson 1998, Hosmer and Lemeshow 2000, Burnham and Anderson 2002, Barry and Elith 2006). Therefore, for the individual species models only those taxa occurring in more than five sites were analysed and each model was restricted to an appropriate number of explanatory variables (one, if $n < 14$, or two variables for the logistic regression models, and similarly up to four variables for the linear regressions). Nine resident species that were not sufficiently widespread or abundant to be analysed individually were analysed collectively as ‘rare resident species’. A potential problem in multiple regression models is high correlation (collinearity) between predictor variables (Vittinghoff *et al.* 2005). Two measures were used to assess if high correlation necessitated removal of any of the site attributes: condition index and tolerance. A condition index > 10 or tolerance < 0.2 are indicative of problematic collinearity (Stevens 1992, Fry 1993).

The best fitting main effects models were determined using information-theoretic (IT) analysis and the relative importance of each predictor was assessed by multi-model averaging (Burnham and Anderson 1998, 2002). IT analysis and multi-model averaging is superior to other methods of identifying important predictor variables and outperforms traditional methods such as stepwise regression (Whittingham *et al.* 2006). The IT method compares a set of alternative models by calculating a likelihood weight for each (the Akaike weight, w), equal to the probability that it would be the best model were the data collected again. Values of w vary between 0 and 1, corresponding to the weight of evidence in support of a candidate model within the set; a value > 0.9 indicates a clearly superior model (Burnham and Anderson 1998). These weights were used to compute the weighted average (multi-model averaged) set of parameter estimates for each model and to identify the best supported variables. The relative importance of the individual site attributes was assessed by the Wald statistic, the ratio of parameter estimate to its standard error, with greater absolute values indicating greater importance and values > 2 corresponding to approximate statistical significance (Hosmer and Lemeshow 2000). For the total species models, the interactions between variables determined to be important main effects were also examined.

Model adequacy was assessed using the chi-squared lack-of-fit test (Hosmer and Lemeshow 2000). To assess the goodness-of-fit of the species incidence models the area under the receiver-operator characteristic curve statistic (AUC) was calculated. AUC takes values between 0.5 and 1, and an approximate guide for AUC values in terms goodness-of-fit is: values > 0.9 indicate excellent fit; > 0.8 good; > 0.7 fair; > 0.6 poor; and < 0.6 no or negligible fit (Swets 1988, Fawcett 2006). To assess the goodness-of-fit of the best fitting species abundance and total species models the usual R^2 statistic was calculated. Because of the small number of sites relative to the number of predictor variables, the small-sample adjusted form of Akaike’s Information Criterion (AIC_c) statistic was used. It is important to note that the models and attributes selected as the "best" predictors were only the best within the set examined, and may not include other important but unmeasured factors.

Results

Sites more distant from the city centre were typically larger, had better quality vegetation, lower tree densities, were less isolated from other remnants and had more resident species (Table 1). Although many of the predictors were significantly correlated they were sufficiently distinct that all could be included in the regression models (condition number = 4.0, tolerances > 0.25). For the total 702 km covered in the surveys 6540 individuals of 33 species (28 butterflies and 5 day-flying moths) were recorded (Appendices 1, 2). The other 12 butterfly species known from the study area were not detected. Most species were restricted to half or less of the fragments, with only three species (*Vanessa kershawi*, *Pieris rapae*, and *Geitoneura klugii*) occurring in more than 75% of sites. Total site species number (S_{tot}) varied from 1 to 18 species, and resident species (S_{res}) from 0 to 13. Twenty of the butterfly and all of the day-flying moth species were resident taxa and there were eight non-resident butterfly species recorded. Sufficient presence–absence data were available for analysis of 20, and abundance data for 22, of the species.

Table 1. Spearman rank correlations (above) and associated p-values (below) between site attributes, and with the number of species present. Statistically significant correlations are in bold type. Site attributes are area (A, ha), distance from the urban centre (D, km), distances to the nearest and nearest larger remnants (N, NL, km), average vegetation condition (AVC), fraction of high quality vegetation (HQV), density of *Eucalyptus*, *Casuarina* and *Allocasuarina* spp. trees (T, number of stems > 10 cm dbh per 100 m of transect), density (number per 100 m of transect) of three host plants, *Daviesia divaricata* (Dd), *Jacksonia sternbergiana* (Js), and *Patersonia occidentalis* (Po), and number of resident (S_{res}), non-resident (S_{nres}) and total (S_{tot}) species. Tolerances indicate the degree of collinearity between the site attributes.

	A	D	N	NL	AVC	HQV	T	Dd	Js	Po
A	1	**0.49**	-0.14	0.10	**0.29**	0.21	-0.19	-0.25	0.02	0.10
		0.00	0.34	0.51	0.05	0.15	0.21	0.09	0.91	0.49
D		1	**-0.34**	**-0.29**	**0.44**	**0.39**	**-0.38**	**-0.43**	-0.08	0.28
			0.02	0.05	0.00	0.01	0.01	0.00	0.60	0.06
N			1	**0.70**	-0.11	-0.24	**0.31**	**0.32**	0.15	0.13
				0.00	0.45	0.11	0.04	0.03	0.32	0.40
NL				1	-0.06	-0.16	**0.30**	**0.32**	0.16	0.07
					0.70	0.29	0.05	0.03	0.29	0.65
AVC					1	**0.89**	**-0.30**	-0.14	0.03	**0.54**
						0.00	0.04	0.35	0.86	0.00
HQV						1	**-0.34**	-0.20	-0.03	**0.57**
							0.02	0.18	0.86	0.00
T							1	**0.59**	**0.37**	-0.27
								0.00	0.01	0.07
Dd								1	0.23	**0.15**
									0.12	0.33
Js									1	-0.09
										0.57
S_{res}	**0.43**	**0.38**	-0.13	0.01	**0.48**	**0.53**	-0.03	0.19	0.18	**0.51**
	0.00	0.00	0.38	0.93	0.00	0.00	0.85	0.22	0.24	0.00
S_{nres}	0.14	-0.19	0.16	**0.38**	-0.07	0.01	**0.42**	**0.34**	**0.46**	-0.01
	0.35	0.20	0.30	0.01	0.66	0.93	0.00	0.02	0.00	0.97
S_{tot}	**0.40**	0.26	-0.09	0.11	**0.39**	**0.46**	-0.07	**0.35**	-0.23	0.17
	0.01	0.08	0.57	0.48	0.01	0.00	0.66	0.02	0.13	0.27
Tolerance	0.65	0.63	0.41	0.42	0.27	0.28	0.56	0.55	0.65	0.58

Individual species presence and abundance

Site area and vegetation condition were the dominant predictors of species presence, being identified as important for eight and seven taxa respectively, and together being identified as important for 14 of the 20 species analysed (Table 2; full results for the models are given in Appendix 3). Larger sites were positively associated with presence in all of these cases and only one species (*Geitoneura minyas*) was favoured by degraded vegetation. Collectively, the nine rare resident species were also more frequent in larger sites. All four butterfly species for which host plant density was assessed were more prevalent at sites with higher host plant densities. The density of trees was an important predictor for five species with higher tree density positively associated with the presence of four. Distance from the urban centre was positively related to the presence of only one species (*Mesodina cyanophracta*) and increased site connectivity did not increase the likelihood of any species being present. Goodness-of-fit ranged from poor to excellent, with good or better fit (AUC > 0.8) for six species. Models that included host plant density as a predictor produced the four best-fitting models (AUC 0.83–0.93).

Site area was also the dominant predictor of abundance with four species being more abundant at larger sites and three non-resident species being more abundant in smaller sites (Table 2; full results for the models are given in Appendix 4). Where it was recorded, host plant density was the also the best predictor of increased abundance. Four species were more abundant in more isolated sites and three in sites with lower tree densities. Only three species were more abundant in sites with higher vegetation quality. No species were found to be more abundant in sites with higher connectivity. Overall, 14 of the 16 resident species showed a positive response in their site occupancy or abundance to increased site area or vegetation quality.

Table 2. Factors related to site occupancy and abundance of butterflies and day-flying moths in 46 fragments of remnant vegetation, Swan Coastal Plain, south-west Western Australia. For each species, the factor(s) from the best-fitting one- or two-variable models are given, which are also the best-supported variables from multi-model averaging. For models with two or more variables the best-supported variable is stated first. Attribute codes as in Table 1. Goodness-of-fit of each occupancy and abundance model is indicated by AUC (area under the receiver–operator characteristic curve) and R^2 (coefficient of determination), respectively. Rare resident species (not individually listed) that were recorded in five or fewer sites were *Trapezites argenteoornatus*, *Hesperilla donnysa*, *H. chrysotricha*, *Croitana croites* (all Hesperiidae), *Ogyris amaryllis*, *Theclinesthes miskini*, *T. serpentata* (all Lycaenidae), *Hecatesia thyridion*, and *Periscepta polysticta* (both Noctuidae). * = introduced species.

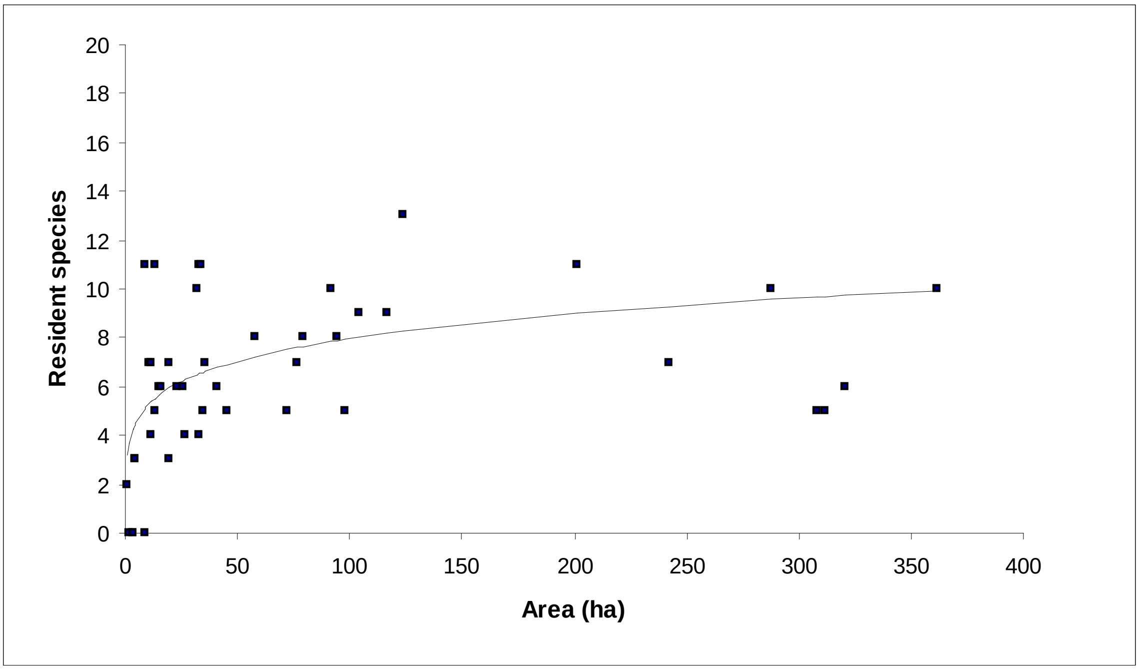
Species	Family or subfamily	Sites occupied	Total count	Occupancy	AUC	Abundance	R^2
Resident species							
Trapezites sciron	Hesperiidae	7	36	+HQV	0.78	-T	0.45
Anisynta sphenosema	Hesperiidae	9	45	+A	0.72	-D	0.52
Motasingha trimaculata	Hesperiidae	7	13	+NL	0.77	+AVC	0.34
Mesodina cyanophracta	Hesperiidae	15	79	+Po, +D	0.93	+Po, +N	0.70
Taractrocera papyria	Hesperiidae	27	96	+A, +T	0.70	-	
Geitoneura klugii	Satyrinae	37	1289	+A	0.81	+A	0.15
Geitoneura minyas	Satyrinae	21	1807	+A, -AVC	0.81	+NL, -N	0.56
Heteronympha merope	Satyrinae	21	120	+A, +T	0.78	+A	0.31
Hypochrysops halyaetus	Lycaenidae	7	104	+Dd	0.89	+(Dd+Js)	0.30
Candalides acastus	Lycaenidae	9	34	-T	0.78	+AVC	0.52
Nacaduba biocellata	Lycaenidae	17	41	+HQV	0.68	-D, -T	0.61
Neolucia agricola	Lycaenidae	23	326	+A, +(Dd+Js)	0.83	+(Dd+Js), +A	0.42
Zizina labradus	Lycaenidae	21	124	+A	0.68	-T	0.16
Synemon sp. (Perth)	Castniidae	17	206	+AVC, +T	0.75	-	
Synemon gratiosa	Castniidae	6	19	+HQV	0.63	+NL	0.28
Pollanisus cupreus	Zygaenidae	26	291	+AVC	0.77	+N, +D, +AVC	0.46
Rare resident species	9 taxa	14	75	+A	0.66	-D	0.40
Non-resident species							
*Pieris rapae**	Pieridae	43	695	N/a		-A	0.18
Junonia villida	Nymphalinae	7	16	+HQV	0.59	-A	0.59
Vanessa kershawi	Nymphalinae	45	988	N/a		-D, +A	0.19
Danaus chrysippus	Danainae	6	7	-	-	-A	0.68
*Danaus plexippus**	Danainae	11	15	+A	0.68	+D	0.23
Lampides boeticus	Lycaenidae	24	93	+Js, +T	0.92	+Js	0.22

Total species numbers

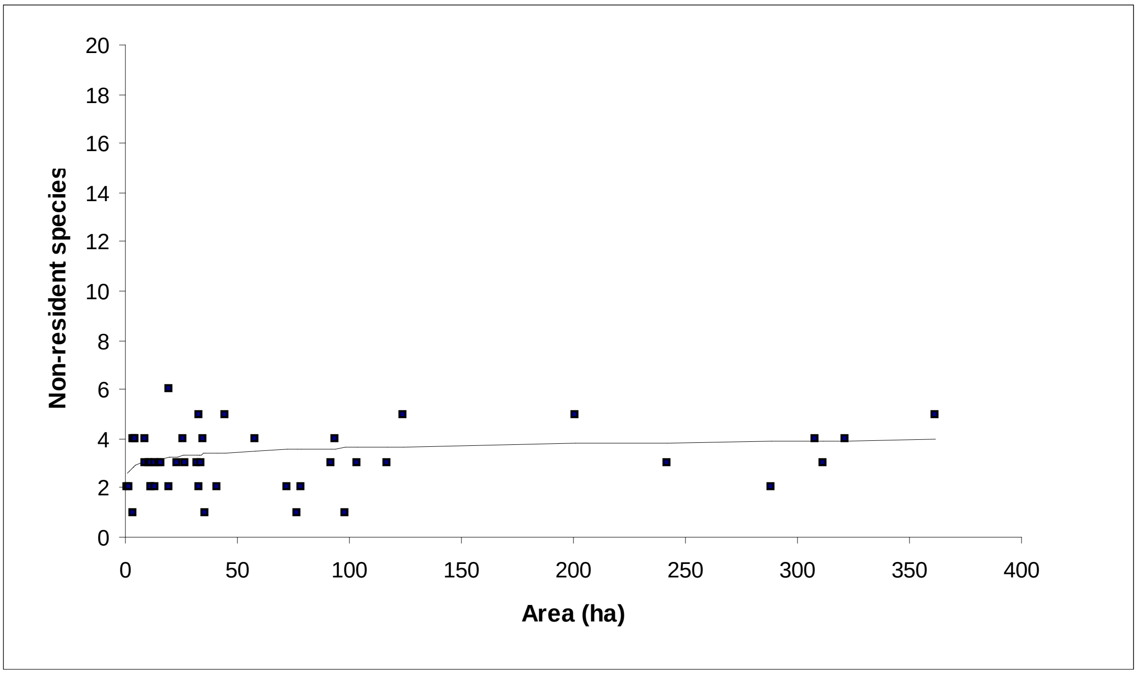
The total number of both resident and non-resident species was higher in larger sites, but for non-resident species the relationship with area was negligible (Fig. 2). The slopes of the power function species–area curves for both resident and total species number (0.19 and 0.15) were typical of the values for mainland areas (z = 0.12–0.18), not true islands (z = 0.25–0.35) (Rosenzweig 1995).

Figure 2. Species–area relationships of (a) resident, (b) non-resident and (c) all species of butterflies and day-flying moths in urban habitat fragments, south-west Western Australia. Fitted lines are for the EVF model, $S = P[1 - \exp(-\exp(-b_0 + b_1\ln(A)))]$, where P = the number of species in the regional source pool, but the power function model $S = cA^z$ gave practically identical results.
(a) $S_{res} = 32 \times [1 - \exp(-\exp(-2.19 + 0.20 \times \ln(A)))]$, $S_{res} = 3.39 \times A^{0.19}$, $R^2 = 0.27$;
(b) $S_{nres} = 13 \times [1 - \exp(-\exp(-1.49 + 0.08 \times \ln(A)))]$, $S_{nres} = 2.641 \times A^{0.07}$, $R^2 = 0.04$;
(c) $S_{tot} = 45 \times [1 - \exp(-\exp(-1.96 + 0.16 \times \ln(A)))]$, $S_{tot} = 5.942 \times A^{0.15}$, $R^2 = 0.27$.

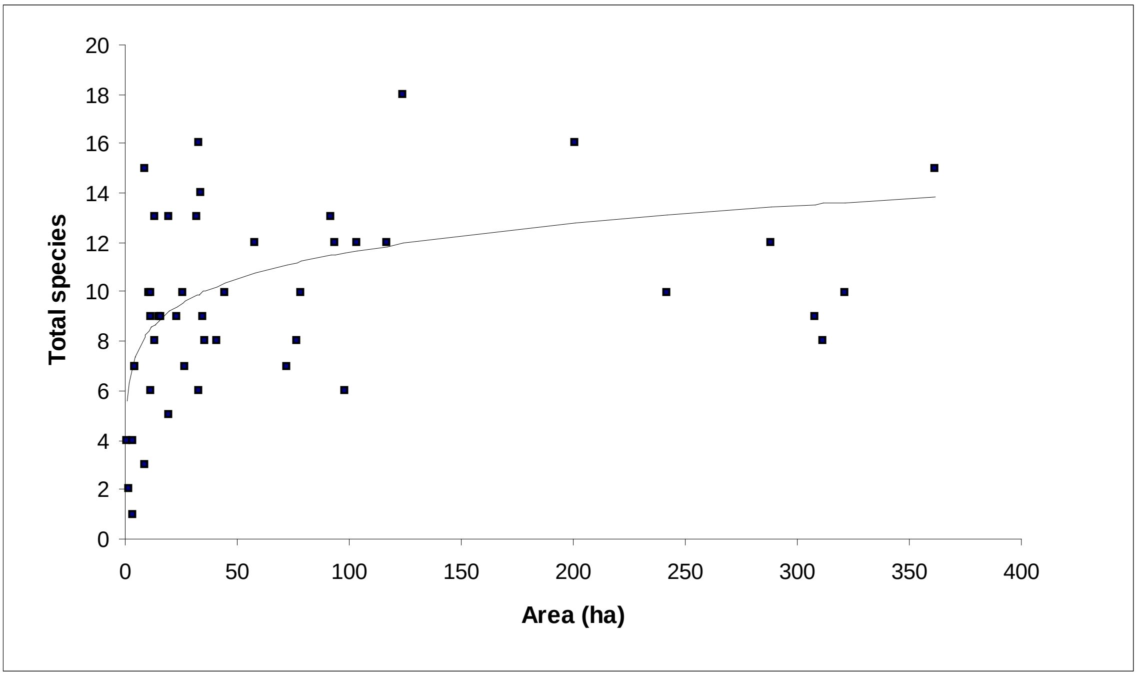
(a)



(b)


Non-resident species
20
18
16
14
12
10
8
6
4
2
0
0
50
100
150
200
250
300
350
400
Area (ha)

(c)


Total species
20
18
16
14
12
10
8
6
4
2
0
0
50
100
150
200
250
300
350
400
Area (ha)

The number of resident species increased with site area, the fraction of high quality vegetation and the density of trees (Table 3). The best fitting model for non-resident species included both area and the density of trees, although the relationship with area was weak and model fit was poor ($R^2 = 0.2$, Table 3). The chi-squared test of fit indicated that the models for both resident and non-resident species numbers were adequate ($p > 0.05$). Inclusion of interactions between these main effects resulted in a best-fitting model for resident species that included site area, HQV and their interaction; tree density was not included in this final model (Table 4). The interaction indicated that sites with low vegetation quality had steeper species–area curves with lower intercepts so that the impact of habitat degradation on the number of resident species was proportionally greater in small fragments (Fig. 3).

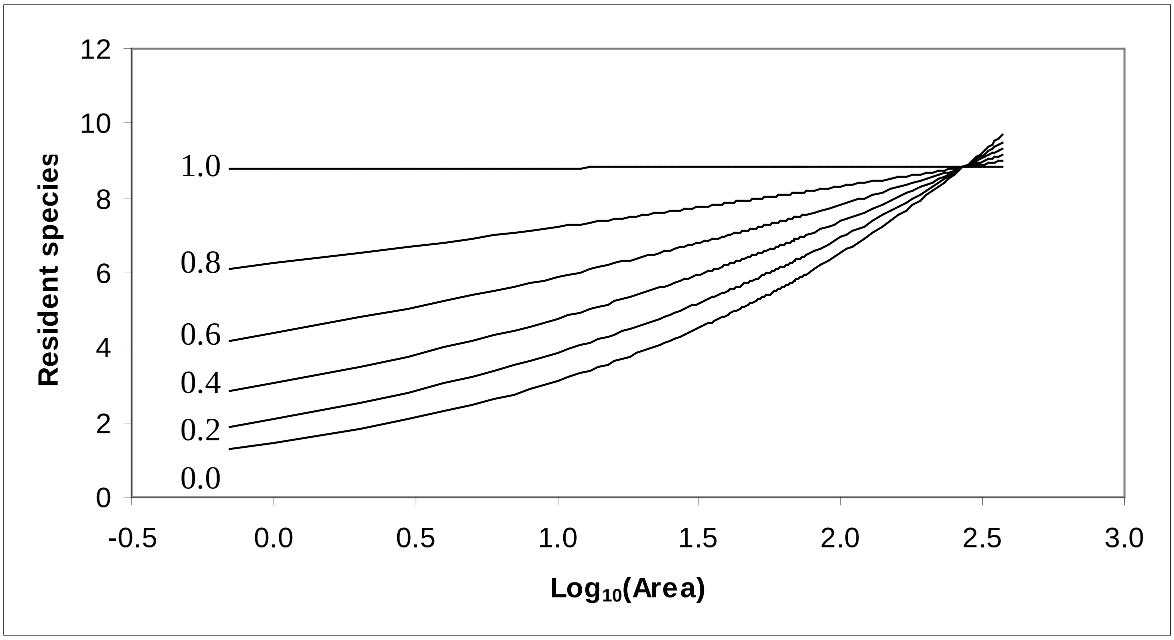
Table 3. Multi-model averaged parameter estimates and standard errors (se) of the site attributes predicting the number of butterfly and day-flying moth species in 46 fragments of remnant vegetation, Swan Coastal Plain, south-west Western Australia. The site attributes (as in Table 1) in the best fitting model are bolded.

	Resident species (AUC = 0.61, R^2 =0. 38)			Non-resident species (AUC = 0.58, R^2 = 0.20)		
	Estimate	**se**	**Wald statistic**	**Estimate**	**se**	**Wald statistic**
Intercept	**-2.93**	0.53	-6.65	-1.65	0.47	-3.53
A	**0.18**	0.05	3.83	**0.06**	0.04	1.34
D	0.07	0.06	1.07	-0.02	0.04	-0.43
N	0.00	0.01	0.02	0.01	0.02	0.46
NL	0.00	0.01	0.28	0.04	0.03	1.19
AVC	-0.03	0.03	-0.87	-0.02	0.04	-0.63
HQV	**0.95**	0.29	3.28	0.20	0.19	1.05
T	**1.18**	0.55	2.16	**1.60**	0.72	2.22

Table 4. Parameter estimates, standard errors (se) and Wald statistics for the model predicting the number of butterfly and day-flying moth species using site area, fraction of high quality vegetation and their interaction. AUC = 0.61, R^2 = 0.37.

	Resident species		
	Estimate	**se**	**Wald statistic**
Intercept	-3.09	0.34	9.20
A	0.35	0.09	3.97
HQV	1.95	0.53	3.68
A*HQV	-0.35	0.14	2.50

Figure 3. Predicted species–area curves of fragments across the range of fragment areas in this study (0.7–360 ha), with varying fractions of high quality vegetation between 1.0 (100%) and 0.0 (0%).



Discussion

This study has shown that the distribution of butterflies and day-flying moths in urban habitat fragments varies in relation to site characteristics. For resident species that rely on remnant vegetation, fragment size and the level of vegetation disturbance most often determined the patterns of incidence, abundance and the total number of species present at each site. Although the habitat relations of the rare species could not determined individually, these were also more likely to be present at larger sites. Where it was assessed, the density of host plants was also an important predictor of both site occupancy and abundance. Every resident species analysed showed a positive response in either occupancy or abundance to one or more of these factors. Tree density was important for some species but responses were idiosyncratic. Increased distance from the urban centre favoured the presence of only one species and increased site connectivity was not important for any. Site resources were thus the dominant determinants of both site occupancy and abundance of the resident species. In contrast, increased site connectivity did not increase the occupancy or abundance of any species so there is no evidence to support a metapopulation paradigm for any of these species. Removal of species that occur within the matrix is expected to increase the likelihood of detecting connectivity effects (Ewers and Didham 2006) but the lack of any such effects for the resident species indicates that they consist of predominantly relictual populations. However, the least widespread and abundant species could not be analysed individually and some species known from the region were not detected, and these may prove to be sensitive to site connectivity effects. The patterns of site occupancy in this region contrasts with butterfly faunas on true islands, which are often dominated by the effects of contemporary and historical geography on dispersal so that island isolation is a major factor affecting both island occupancy and total species number (Dennis and Shreeve 1997, Dennis *et al.* 2000, Dapporto and Dennis 2008b, Dennis *et al.* 2008). It also contrasts with several studies of mainland areas that found site connectivity to be a major factor controlling species occupancy or diversity in habitat fragments (Dennis and Eales 1997, Thomas *et al.* 2001, Krauss *et al.* 2003, Brown and Freitas 2004, Krauss *et al.* 2005, Fartmann 2006). It is, however, consistent with the increasingly recognized importance of habitat quality in explaining site occupancy in habitat fragments even for species that do exist as metapopulations (Thomas *et al.* 2001, Wahlberg *et al.* 2002, Fred and Brommer 2003, Krauss *et al.* 2004, Krauss *et al.* 2005).

Total species number integrated the responses of the individual species: area, vegetation quality and their interaction were the dominant predictors. The interaction between site area and vegetation condition suggests that there are more species in larger sites not in response to area *per se*, but because there is more suitable habitat within them. Small sites (< 10 ha) with degraded vegetation had the fewest species and this was due predominantly to declining habitat quality. The results suggest that declining area has little impact on sites with pristine vegetation, but there was some confounding between area and vegetation quality as there were few sites < 10 ha that also had high quality vegetation and all sites < 5 ha were degraded (HQV ≤ 0.2, Appendix 1). This reinforces the principle that the key to survival of any species is the maintenance of a minimum area of suitable habitat (Atmar and Patterson 1993, Lamont *et al.* 1993).

Changes in habitat quality caused by urbanization may benefit some butterfly species (Connor *et al.* 2002, Shapiro 2002) and in some urban areas most species that remain are those that have adapted to introduced host plants (New and Sands 2002b, Shapiro 2002). In this study there was only one such native species, and declining vegetation condition caused by disturbance disfavoured many more taxa than it benefited. Although some of the butterflies in this study use weeds and were more prevalent in small or disturbed sites, these were predominantly introduced or ‘urban-adapter’ species. Overall, this conforms with previous studies that have demonstrated the negative impacts of habitat degradation on butterfly species richness in urban areas with relatively few species favoured (Nelson and Nelson 2001, New and Sands 2002a, Brown and Freitas 2004, Hogsden and Hutchinson 2004, McKinney 2008).

The non-resident species showed no species-area effect and some were more prevalent in smaller sites. Because these taxa are adapted to plants within the matrix, they may well avoid all but the edge of fragments. Transects within small sites inevitably sample more areas close to edges and these species may be recorded more frequently as a result. This supports treating the resident and non-resident species separately because they had different responses to fragmentation.

Typically, it is the requirements of the immature stages that define habitat quality for insects in temperate areas (Thomas *et al.* 2001). For the four species where it could be assessed, host plant density was an important factor both for site occupancy and abundance. The importance of host plant density has often been demonstrated

(Wahlberg *et al.* 2002, Dennis 2004, Dennis and Hardy 2004, Krauss *et al.* 2004, Grundel and Pavlovic 2007) and it is likely that better predictive models for many of the species in this study could be obtained if the density of their respective host plants were determined.

For two main reasons, the models for some species should be viewed cautiously. First, a potential shortcoming in species incidence modelling is that many species are imperfectly detected, leading to negative bias in estimates of their site occupancy (MacKenzie *et al.* 2003). Detectabilities (the probability that the species will be detected at a site, given that it is present) for the species analysed in this study have been quantified (Williams in press). They are typically lowest and hence most problematic for the least abundant species and those occurring at few sites, notably *Anisynta sphenosema* (0.12), *Danaus chrysippus* (0.28), *D. plexippus* (0.28), *Junonia villida* (0.53), and *Synemon gratiosa* (0.62). A greater number of surveys and a larger sample of occupied sites would be needed to construct habitat models that incorporate parameters to estimate the seasonal variation in site occupancy and detectability for these species. For the remaining species detectability was high (> 0.86). Second, a common source of error in habitat models is the absence of important covariates (Barry and Elith 2006). Host plant density was only measured for some species but was consistently the best predictor of presence. Similarly, other important covariates may better explain site occupancy and abundance for individual species – factors such as host plant quality or the presence and abundance of ant mutualists may be needed to explain the distributional patterns of some taxa. These additional covariates need to be assessed before a full understanding of each species' patterns of occupancy and abundance can be achieved.

There are several implications for conservation of butterflies within this region. Maintenance or restoration of high quality vegetation will be essential to conserve these remnant populations and to maintain local and regional species richness. Larger remnants harboured more species, including more of the regionally rare taxa, so maintaining or improving vegetation condition is especially important for these sites. Although many species still occur in small (< 10 ha) habitat remnants it is likely that stochastic events will take a proportionally greater toll on smaller fragments (New and Sands 2002b, Ewers and Didham 2006). Similarly, this study found that such sites are more prone to species losses following disturbance and consequent decreases in vegetation quality. Small patches also have a greater proportion of edge to interior, making them generally more exposed to exogenous disturbances and more difficult to maintain (Samways 2007). Several of the fragments in this study were seperated by cleared areas such as roads but even such relatively narrow features may be significant barriers to dispersal, especially if the contrast between the fragment and the matrix is high (Ewers and Didham 2006). Although establishing and maintaining connectivity between these fragments may increase the total effective population size within each subfragment, and provide greater resilience for the combined population, maintaining and improving vegetation quality is of greater importance.

The ongoing SLOSS (Single Large or Several Small) debate, which contrasts alternative strategies for maximising species diversity within reserve networks, parallels the habitat resource/metapopulation paradigms of species persistence in fragments. The results of this study support the preservation of a few large, rather than many small remnants. Large reserves are generally considered to be superior to small reserves for the persistence of area- and extinction-prone species, despite some studies that show greater species numbers in small, widespread reserves (Gibb and Hochuli 2002, Tscharntke *et al.* 2002, Ewers and Didham 2006). This study found that the impact of disturbance was proportionally much greater in small remnants. However, the responses shown by butterflies and day-flying moths need to be considered together with the distribution patterns of other fauna in these remnants.

If improvement or restoration of habitat can be achieved within the degraded sites, deliberate translocations of selected taxa may be possible to re-establish locally extinct populations. The individual models for each species, summarized in this paper, will assist in determining those species at greatest risk of local extinction and in identifying the sites where they are notably absent. However, there are also species-specific factors that need to be considered to conserve particular taxa (Garden *et al.* 2006). Host plant density was a crucial factor, and a better understanding of this relationship will help to guide future conservation. Further studies that examine the interaction between site area and vegetation quality in small (< 10 ha) fragments would clarify the roles of these factors on species presence and persistence. The responses of fauna to habitat fragmentation may take many years or decades to manifest (Garden *et al.* 2006, Kadlec *et al.* 2008), and there is no evidence that the fauna in these fragments is at equilibrium. Species presence within a fragment may not equate to long-term viability. Currently, there are no species known to be locally extinct within the region but the extent of vegetation clearing (82% removed) suggests that there is potentially an unresolved extinction debt. Periodic monitoring of these sites, and comparison of any changes in fauna with management practices and disturbance (fencing, weed control and changes in vegetation condition) or stochastic events (fires), offer an opportunity to identify causes of species loss or recruitment.

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Appendix 1.

Attributes of 46 urban habitat fragments sampled for butterflies and day-flying moths, south-west Western Australia. Site number (Site), number of surveys (n), transect length (L, m), site area (A, ha), distance from the urban centre (D, km), distances to the nearest and nearest larger remnants (N, NL, km), average vegetation condition (AVC) and fraction of high quality vegetation (HQV), density of *Eucalyptus*, *Casuarina* and *Allocasuarina* spp. trees (T, number of stems > 10 cm dbh per 100 m of transect), density (number per 100 m of transect) of three host plants, *Daviesia divaricata* (Dd), *Jacksonia sternbergiana* (Js), and *Patersonia occidentalis* (Po), and number of resident (S_{res}), non-resident (S_{nres}) and total (S_{tot}) species.

Site	n	L	A	D	N	NL	AVC	HQV	T	Dd	Js	Po	S_{res}	S_{nres}	S_{tot}
1	8	3098	288	26.9	0.17	0.49	5.2	0.75	0.6	0.0	0.0	5.3	10	2	12
2	8	2699	92	27.4	0.02	0.17	5.2	0.75	2.8	0.1	12.9	3.0	10	3	13
3	8	2115	312	20.1	0.03	0.21	7.0	0.75	0.0	0.0	10.9	0.8	5	3	8
4	8	1861	77	19.7	0.03	0.03	5.2	0.80	1.6	0.0	0.1	4.1	7	1	8
5	8	2640	32	33.1	0.49	0.49	6.8	0.90	4.0	0.0	15.8	0.9	10	3	13
6	8	2320	27	14.9	0.03	0.03	1.6	0.00	6.2	3.1	0.0	0.9	4	3	7
7	7	5095	362	7.4	1.47	16.3	4.4	0.60	7.6	0.5	0.0	0.0	10	5	15
8	8	2380	117	31.5	0.49	0.75	7.6	0.90	6.1	0.0	0.8	5.9	9	3	12
9	8	1424	11	7.8	1.20	1.20	5.0	0.75	6.0	1.6	13.6	25.4	7	3	10
10	8	1613	41	20.8	0.13	0.13	4.4	0.60	1.2	0.0	0.0	1.3	6	2	8
11	8	1301	79	22.2	0.02	0.25	4.4	0.60	0.1	0.0	0.0	8.1	8	2	10
12	8	1070	8.5	13.7	0.62	0.62	5.4	0.85	1.6	5.9	6.9	16.0	11	4	15
13	8	1480	26	25.2	0.46	0.46	4.8	0.70	3.5	0.0	4.3	2.3	6	4	10
14	8	1687	72	19.3	0.13	0.69	6.0	0.75	0.8	0.0	0.0	1.8	5	2	7
15	8	769	13	14.0	2.24	2.24	4.4	0.00	13.7	6.8	10.0	0.0	5	3	8
16	8	1748	98	18.3	0.03	0.36	5.0	0.60	2.8	0.0	0.1	0.7	5	1	6
17	8	957	4.2	9.4	0.28	1.47	5.0	0.75	10.4	0.0	11.2	0.0	3	4	7
18	8	346	0.7	6.5	1.65	1.65	3.0	0.00	0.0	0.0	0.0	0.9	2	2	4
19	8	1035	9.1	4.6	1.65	4.91	5.0	0.75	7.6	4.4	2.4	35.8	0	3	3
20	8	4810	321	1.3	1.62	3.96	4.4	0.15	16.8	3.6	8.9	0.0	6	4	10
21	8	4044	124	11.5	1.50	1.50	5.0	0.75	5.3	7.6	32.3	75.3	13	5	18
22	8	1732	16	14.6	0.92	0.92	6.8	0.90	4.3	3.6	0.8	4.6	6	3	9
23	8	1655	4.3	17.4	0.02	0.02	2.8	0.20	2.4	0.0	3.6	0.1	3	4	7

Appendix 1. Continued.

Site	n	L	A	D	N	NL	AVC	HQV	T	Dd	Js	Po	S_{res}	S_{nres}	S_{tot}
24	8	2281	33	13.5	0.92	1.30	4.5	0.00	9.5	2.4	0.6	3.4	11	5	16
25	8	695	242	29.9	0.49	4.18	7.6	0.90	0.6	0.0	0.7	8.6	7	3	10
26	8	2658	12	8.3	0.01	0.01	4.4	0.60	4.3	0.0	1.1	0.0	7	3	10
27	8	1403	36	21.0	0.69	0.69	6.6	0.80	5.1	0.0	0.0	4.8	7	1	8
28	7	900	3.3	8.4	0.97	0.97	1.8	0.00	2.0	0.0	0.0	0.0	0	1	1
29	8	3962	201	28.8	0.08	0.08	5.2	0.80	3.3	0.0	1.8	3.0	11	5	16
30	9	1450	20	5.5	0.15	0.15	4.0	0.50	7.3	0.1	0.0	0.6	3	2	5
31	8	1184	15	16.7	0.85	0.85	3.2	0.00	17.9	5.5	2.1	0.0	6	3	9
32	8	2296	104	21.6	0.25	0.25	6.0	0.80	1.2	0.0	0.0	1.7	9	3	12
33	8	849	3.3	7.1	1.77	1.77	2.5	0.00	5.4	1.9	0.0	1.5	0	4	4
34	6	3194	94	13.5	0.78	3.28	3.0	0.00	4.5	0.4	15.9	0.0	8	4	12
35	8	2190	58	19.5	0.01	2.61	4.3	0.30	7.9	0.3	4.0	0.0	8	4	12
36	8	2052	308	20.6	0.01	0.03	4.3	0.30	5.3	0.0	2.4	0.0	5	4	9
37	7	2336	33	11.5	0.02	0.02	5.0	0.75	0.0	0.0	0.0	0.0	4	2	6
38	7	1210	20	12.6	0.14	0.22	5.0	0.75	26.7	0.0	13.5	0.0	7	6	13
39	7	1641	45	12.0	0.02	1.78	5.0	0.75	2.6	0.0	0.0	0.0	5	5	10
40	7	1379	12	12.5	0.03	0.03	5.0	0.75	2.7	0.0	0.0	0.0	4	2	6
41	8	257	1.5	9.9	0.28	0.28	5.0	0.00	13.6	7.4	6.6	0.0	0	2	2
42	8	1363	13	13.3	0.01	0.02	5.4	0.85	6.1	7.3	0.0	11.7	11	2	13
43	8	3221	34	12.6	0.02	3.82	5.4	0.85	3.3	3.8	0.3	15.2	11	3	14
44	8	1242	12	12.6	0.01	0.02	5.4	0.85	4.3	4.8	0.0	1.6	7	2	9
45	8	2144	35	8.7	1.47	4.56	3.1	0.00	10.7	5.2	0.5	0.2	5	4	9
46	8	2164	23	17.9	0.02	0.14	2.8	0.20	5.5	0.3	16.3	0.0	6	3	9

Appendix 2.

Counts of butterfly and day-flying moth species in 46 urban habitat fragments, south-west Western Australia.

SITE NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Resident butterflies																																														
Trapezites sciron												19									9	1		3																		1	2	1		
Trapezites argenteoornatus							7																														19		7	5						
Anisynta sphenosema	3	4			2					4										18							2					5			6											1
Hesperilla donnysa																										1			1					4												
Hesperilla chrysotricha			1																																											
Motasingha trimaculata									1		1										6			2	1									1									1			
Croitana croites																																					3		2	1						
Mesodina cyanophracta	1		2	1	1			2	4		1	9	1								41	3		6	1																	1	5			
Taractrocera papyria	2	1		7	2	2	14			2	2	2	6		2	3				3	7					14	1		9	1	1	1		4	2			2				1	3	1		1
Geitoneura klugii	63	22		20	53	10	180	34	25	3	82	12	8	17	27	21				192	104		1	32	19	25	19		100	11	20	8		21	44	16		5	3	1		40	36	2	11	2
Geitoneura minyas	60	1			42	49	435	4		1	1				55	7				145			11	17		31			97		19	16		187	531	35										63
Heteronympha merope	22			2	2	1	30	11		1	2				1	3				8	4						1		12			2		1	8			2				2	3	2		
Hypochrysops halyaetus									10			8									41			14																		7	11	13		
Ogyris amaryllis																	4									12																				
Candalides acastus		5	16	1			2						2	1																		3					1			3						
Nacaduba biocellata		1			1		8			1		2						3			9	2		1	1	1	1		2			4						1				2				1
Theclinesthes miskini		1					3																																1							
Theclinesthes serpentata							2																																							
Neolucia agricola	1	3			5			7	10		1	3				1				9	231	6		3	5		1		7		2			9	1	10		2				2	6		1	
Zizina labradus	1		1	4			4	3				8	2	2	2		1				4		4						3			44			1	2	33	1	1						1	2
Resident day-flying moths																																														
Synemon sp. (Perth)					2			13	2			7		1							66	5		37	12				1		11			3				9				5	11	13	8	
Synemon gratiosa												1									1			3						1												1	12			
Pollanisus cupreus	38	15	1	1	52			35	3			10	16	14			1	1			24	33		6	5	2	1		1		1				4	1						7	16	2	1	
Hecatesia thyridion																																1														
Periscepta polysticta	3	2						2			2																		2																	

Appendix 2. Continued

SITE NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Non-resident butterflies																																														
Delias aganippe							3										1																						1							
Pieris rapae	2	12	2		3	8	16	2	16	2	4	20	6	3	10		25	3	7	7	20	26	14	20	1	18		24	3	1	11	8	21	32	7	1	152	42	17	35	7	10	19	13	12	33
Junonia villida			2									4							5		1			1														2	1							
Vanessa kershawi	54	8	22	22	29	8	19	18	24	6	32	31	10	13	2	10	4	3	3	192	181	28	2	26	16	20	4		27	17	4	15	4	13	12	13	2	4	2	2	1	14	31	19	12	9
Vanessa itea							1														3												1													
Danaus chrysippus																								1		2			1					1				1	1							
Danaus plexippus						2							1							1			1		1				2			1			1	3		1							1	
Lampides boeticus		10			1		2	1	2			7	2		1		1			1	20	1	1	4					3		1		1	14	1	7		5					1		4	2

Appendix 3.

Akaike weights (*w*) for the best-fitting models of species incidence, multi-model averaged parameter estimates, and estimates of the relative importance (w_+) of each predictor variable. The most important variables, which also corresponded with those in the best fitting models, are bolded. Variables as in appendix 1. A, D, N and NL were log transformed; density of trees and host plants were square root transformed.

	Parameter estimates													w_+										
	w	Intercept	A	D	N	NL	AVC	HQV	T	Dd	Js	Dd+Js	Po	A	D	N	NL	AVC	HQV	T	Dd	Js	Dd+Js	Po
Trapezites sciron	0.87	-3.393	-0.002	-0.002	0.000	0.000	0.012	**2.423**	0.001					0.02	0.01	0.01	0.01	0.03	**0.87**	0.01				
Anisynta sphenosema	0.38	-2.673	**0.179**	0.134	-0.004	0.003	0.016	0.031	-0.003					**0.38**	0.14	0.06	0.06	0.08	0.06	0.06				
Motasingha trimaculata	0.54	-1.865	0.030	0.008	0.015	**0.295**	0.006	0.008	-0.011					0.09	0.04	0.07	**0.54**	0.04	0.05	0.05				
Mesodina cyanophracta	0.88	-9.773	0.003	**2.337**	0.000	0.000	0.050	0.186	-0.005				**0.997**	0.01	**0.88**	0.00	0.00	0.06	0.06	0.01				**0.98**
Taractrocera papyria	0.13	-0.907	**0.146**	0.069	-0.023	-0.013	-0.039	0.090	**0.084**					**0.51**	0.17	0.18	0.15	0.20	0.14	**0.29**				
Geitoneura klugii	0.64	-2.270	**0.546**	0.099	-0.005	-0.002	-0.020	-0.005	0.448					**0.90**	0.12	0.04	0.04	0.08	0.03	0.69				
Geitoneura minyas	0.71	-1.049	**0.701**	0.152	-0.001	-0.001	**-0.464**	-0.413	0.010					**0.91**	0.09	0.01	0.01	**0.75**	0.16	0.03				
Heteronympha merope	0.27	-2.402	**0.434**	0.027	0.001	0.001	-0.002	0.070	**0.105**					**0.90**	0.11	0.09	0.09	0.10	0.14	**0.30**				
Hypochrysops halyaetus	0.95	-3.851	0.000	0.000	0.000	0.000	0.000	0.040	0.000	**1.373**	0.000	0.014		0.00	0.00	0.00	0.00	0.00	0.02	0.00	**0.95**	0.00	0.02	
Candalides acastus	0.60	-1.205	0.058	0.035	-0.006	-0.008	0.022	0.216	**-0.536**					0.12	0.04	0.03	0.03	0.06	0.07	**0.60**				
Nacaduba biocellata	0.19	-1.847	-0.001	0.098	0.040	-0.002	0.057	**1.014**	0.007					0.12	0.18	0.21	0.12	0.22	**0.65**	0.12				
Neolucia agricola	0.18	-2.523	**0.331**	0.119	0.005	0.023	0.043	0.022	0.091	**0.114**	0.023	0.068		**0.72**	0.13	0.05	0.10	0.13	0.05	0.21	0.21	0.10	**0.23**	
Zizina labradus	0.16	-1.894	**0.203**	0.222	-0.009	-0.003	0.003	0.075	-0.001					**0.58**	0.34	0.14	0.13	0.13	0.15	0.12				
Synemon sp. (Perth)	0.20	-2.909	0.000	0.118	0.067	0.027	**0.275**	0.416	**0.162**					0.08	0.17	0.25	0.14	**0.53**	0.26	**0.34**				
Synemon gratiosa	0.27	-2.049	-0.008	-0.051	0.002	0.004	0.009	**0.300**	0.013					0.08	0.11	0.08	0.08	0.08	**0.27**	0.08				
Pollanisus cupreus	0.23	-3.208	-0.002	0.247	0.002	0.003	**0.478**	0.175	-0.002					0.10	0.32	0.10	0.10	**0.81**	0.19	0.10				
Pieris rapae																								
Junonia villida	0.30	-2.139	0.005	-0.031	0.016	0.035	0.032	**0.420**	0.016					0.06	0.08	0.09	0.13	0.11	**0.30**	0.07				
Vanessa kershawi																								
Danaus chrysippus	0.24	-2.219	0.016	0.000	-0.012	-0.006	-0.013	-0.040	0.105					0.10	0.08	0.10	0.09	0.09	0.09	0.21				
Danaus plexippus	0.24	-2.413	**0.318**	0.038	-0.012	-0.009	-0.052	-0.523	0.130					**0.62**	0.10	0.10	0.09	0.16	0.38	0.26				
Lampides boeticus	0.38	-1.398	0.006	0.005	0.034	0.084	-0.035	-0.022	**0.222**		**0.629**			0.04	0.03	0.13	0.26	0.11	0.03	**0.42**		**0.96**		
Rare resident species	0.14	-4.249	**0.196**	-0.003	-0.067	-0.006	-0.034	0.923	-0.686					**0.51**	0.08	0.29	0.10	0.14	0.43	0.20				

Appendix 4.

Akaike weights (*w*) for the best models of species abundance, multi-model averaged parameter estimates, and estimates of the relative importance (w_+) for each predictor variable. The most important variables, which also corresponded with those in the best fitting models, are bolded. Variables as in appendix 1. A, D, N and NL were log transformed; density of trees and host plants were square root transformed.

			Parameter estimates											w_+										
	w	Intercept	A	D	N	NL	AVC	HQV	T	Dd	Js	Dd+Js	Po	A	D	N	NL	AVC	HQV	T	Dd	Js	Dd+Js	Po
Trapezites sciron	1.00	2.444	0.000	0.000	0.000	0.000	0.000	0.000	**-0.936**					0.00	0.00	0.00	0.00	0.00	0.00	**1.00**				
Anisynta sphenosema	1.00	0.502	0.000	**-0.098**	0.000	0.000	0.000	0.000	0.000					0.00	**1.00**	0.00	0.00	0.00	0.00	0.00				
Motasingha trimaculata	0.59	-0.015	0.013	0.000	0.000	0.000	**0.014**	0.000	0.000					0.39	0.00	0.01	0.00	**0.59**	0.00	0.00				
Mesodina cyanophracta	0.85	-0.045	0.000	0.000	**0.051**	0.000	0.000	-0.002	0.000				**0.138**	0.01	0.01	**0.85**	0.01	0.01	0.01	0.01				**1.00**
Taractrocera papyria	0.39	0.207	-0.001	-0.001	0.001	-0.002	-0.001	0.008	-0.001					0.12	0.11	0.12	0.16	0.12	0.13	0.11				
Geitoneura klugii	0.14	0.844	**0.354**	-0.092	0.036	0.124	0.025	-0.010	0.001					**0.69**	0.21	0.23	0.46	0.16	0.13	0.13				
Geitoneura minyas	1.00	2.101	0.000	0.000	**-2.940**	**3.929**	0.000	0.000	0.000					0.00	0.00	**1.00**	**1.00**	0.00	0.00	0.00				
Heteronympha merope	0.49	-0.326	**0.129**	0.007	-0.001	0.001	0.003	0.015	0.002					**1.00**	0.12	0.06	0.05	0.10	0.12	0.06				
Hypochrysops halyaetus	0.83	0.595	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	**0.089**		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	**0.83**	
Candalides acastus	1.00	-1.157	0.000	0.000	0.000	0.000	**0.257**	0.000	0.000					0.00	0.00	0.00	0.00	**1.00**	0.00	0.00				
Nacaduba biocellata	0.83	1.187	-0.019	**-0.259**	0.001	0.011	0.000	0.000	**-0.102**					0.17	**0.83**	0.01	0.16	0.00	0.00	**0.83**				
Neolucia agricola	0.45	-1.400	**0.197**	0.008	0.002	0.001	0.007	0.039	-0.061	0.002	0.085	**0.474**		**0.47**	0.03	0.03	0.02	0.04	0.05	0.17	0.00	0.17	**0.83**	
Zizina labradus	0.34	0.776	-0.016	-0.028	0.005	-0.020	0.004	0.033	**-0.152**					0.15	0.10	0.08	0.19	0.06	0.09	**0.72**				
Synemon sp. (Perth)	0.51	0.743	0.011	-0.005	0.008	0.004	0.007	-0.037	0.008					0.10	0.06	0.10	0.08	0.08	0.09	0.09				
Synemon gratiosa	0.69	0.169	0.000	0.000	-0.004	**0.030**	0.001	0.000	0.000					0.00	0.00	0.12	**0.69**	0.01	0.00	0.00				
Pollanisus cupreus	0.30	-0.891	-0.026	**0.291**	**0.118**	0.006	0.144	**0.475**	-0.001					0.15	**0.51**	**0.79**	0.08	**0.50**	0.49	0.04				
Pieris rapae	0.30	2.958	**-0.437**	-0.064	-0.009	-0.034	-0.003	0.072	-0.002					**0.91**	0.18	0.16	0.23	0.14	0.16	0.14				
Junonia villida	1.00	0.693	**-0.129**	0.000	0.000	0.000	0.000	0.000	0.000					**1.00**	0.00	0.00	0.00	0.00	0.00	0.00				
Vanessa kershawi	0.09	1.534	**0.181**	**-0.497**	0.060	0.009	0.083	0.224	-0.029					**0.66**	**0.69**	0.37	0.16	0.34	0.28	0.18				
Danaus chrysippus	1.00	0.170	**-0.026**	0.000	0.000	0.000	0.000	0.000	0.000					**1.00**	0.00	0.00	0.00	0.00	0.00	0.00				
Danaus plexippus	0.86	0.026	0.000	**0.024**	0.000	0.000	0.000	0.000	0.000					0.00	**0.86**	0.02	0.01	0.01	0.01	0.01				
Lampides boeticus	0.27	0.078	0.001	0.001	0.000	0.000	-0.002	-0.001	-0.002		**0.072**			0.06	0.06	0.06	0.06	0.08	0.06	0.08		**0.98**		
Rare resident species	0.79	0.142	0.000	**-0.045**	-0.007	-0.001	0.000	0.000	-0.001					0.01	**1.00**	0.79	0.15	0.00	0.01	0.04				

Chapter 6 – General Discussion

The aim of this research was to review and adapt existing methods to assess and model biodiversity of butterflies and day-flying moths in south-west Western Australia, and to determine those factors affecting their presence, abundance and species richness in urban habitat fragments. The specific objectives were to:

- Assess the effectiveness of transect-based sampling to quantify the species richness of habitat fragments;
- Examine patterns of species richness in habitat fragments and quantify the detectability of each species recorded;
- Review and rationalize the methods used to fit species–area–habitat models; and
- Determine those factors affecting incidence, abundance and species richness of butterflies in urban habitat fragments and determine priorities for their conservation.

6.1 Overview of main findings

6.1.1 Survey regimes to measure butterfly diversity

The main results of chapter 2, in which I examined methodology with which to sample butterflies within the Swan Coastal Plain bioregion, were as follows:

- Although used widely to inventory butterfly diversity in habitat remnants, the effectiveness of the strip transect method has rarely been examined;
- A sampling fraction of at least 1.3% was adequate for these sites, a result comparable with the two previous studies that have examined this factor in relation to completeness of species lists;
- Sampling frequency was of critical importance and once an adequate sampling fraction is determined, resources are better allocated to more frequent rather than more intensive sampling;

- A survey regime of variable-length transects sampled on six occasions in spring detected more than 85% of the resident fauna; and
- Sampling should be restricted to 1030–1430 hr and temperatures above 19 °C, but wind speeds and cloud cover had little effect on species counts.

The accuracy and completeness of species lists compiled using the strip transect method has been assessed only rarely, and given the increased concern about the possible bias that ‘false negatives’ may introduce it is important to ensure that survey intensity is sufficient. A regime of six spring transects conducted at two-weekly intervals detected > 85% of the resident species present, consistent with the few previous studies that have examined survey completeness. The shortfall in observed species comprise those species that are difficult to detect, which are typically those of low abundance. These results highlight the importance of examining sampling adequacy in compiling site species lists. However, while an estimate of the proportion of the total fauna detected using a standard sampling regime can be determined, for species-level studies estimates for each individual taxon are also needed and these were determined in chapter 3.

Although most species were recorded with a high level of detectability, the adult stage of many species of butterflies and day-flying moths in Australia may be easily overlooked because they are cryptic or difficult to detect, even though they may be relatively common in the habitat. For example, some species fly high above ground level (e.g. *Ogyris, Arhopala*), or are only active outside of the standard sampling times, such as in the late afternoon (e.g. *Hecatesia* spp.) or early morning (e.g. many agaristines). Others may only congregate in particular areas, such as where the males establish leks (e.g. *Acrodipsas* spp.), while others are difficult to identify in flight (e.g. many Hesperiidae). For these reasons, some workers have abandoned the conventional standard pollard census approach and rely on qualitative, ‘incidental’ surveys, such as searching for the larval host plants and early stages to detect presence of species. Similarly, an alternative approach to inventory butterflies is to repeatedly census point sites, especially prominent hilltops (e.g. Newland 2006). However, lack of a standardised, quantitative approach precludes accurate estimation of detectability, density or abundance, and precludes objective comparisons between studies.

Therefore, qualitative and site- or species-specific sampling methods should be used only as adjuncts to standardised sampling regimes.

6.1.2 Patterns of species richness

The main results of chapter 3, in which I examined the distribution of butterflies at 46 urban bushland remnants in the Swan Coastal Plain bioregion, were as follows:

- A total of 17 075 individuals of 35 butterfly and 5 day-flying moth species were recorded. Individual site species richness varied between one and 27 species;
- Two main groups of taxa were identified: (i) species that rely on native vegetation for breeding and are predominantly or entirely restricted to remnant bushland (resident species or urban avoiders, 27 species); and (ii) species that disperse readily through the urban matrix and breed primarily on introduced plants, but which also visit remnant bushland and sometimes breed there (non-resident species or urban adapters, 13 species);
- Detectability varied widely both between species and seasonally, but for most taxa was consistent across the three years of the study. Peak detectability was strongly related to observed abundance, something that has rarely been demonstrated quantitatively;
- Only one listed endangered species was recorded, the graceful sun-moth (*Synemon gratiosa*), which was observed in low numbers at six sites. Several species were encountered less frequently, although these have populations outside the region;
- During the autumn flight period, when few species were present and abundances were low, detecting species was more problematic. Although only two species occurred within this period, one of these was the endangered *Synemon gratiosa* and four surveys in March are needed to obtain accurate estimates of its presence within remnants;
- Few of the surveyed remnants were considered to have an intact butterfly fauna; it was inferred that the majority had lost some or all of their original resident species. The reliance of many species on specific host plants, and the

ability of some to adapt to introduced weeds, are important factors in their presence within remnants;

- These habitat fragments are effectively 'islands' for butterflies and day-flying moths and the few remaining species-rich bushlands are therefore of regional importance for conservation of this group;
- Because many species had short flight periods and large temporal variation in abundance and detectability, timing of surveys is of critical importance in determining site occupancy. This reinforces the need to carefully plan survey times and frequency to achieve accurate estimates of site occupancy. These data enable the number of surveys needed to detect each species to a given level of accuracy to be determined (Table 6.1).

The butterfly species in this region were allocated to existing categories based on their ecological characteristics – resident species that depend on remnant patches of habitat and non-resident species that have adapted to matrix and edge habitats. The resident species were resource-sensitive, being less prevalent in small or degraded fragments. Such species are sometimes called area-sensitive but I found that they are in fact more sensitive to resource quality, not quantity.

Non-resident species showed no relationship to area and were more abundant in smaller remnants. I hypothesize that this is a result of them favouring the edge and near-edge habitats that are more prevalent in smaller fragments. These species were thus insensitive to the resources in remnant habitat.

Table 6.1. The number of individuals observed during standardised transect sampling between 2002 – 2005, their estimated detectability in a standard survey regime, and the number of targeted surveys required to detect with high (>95%) probability, each species of butterfly and day-flying moth at 46 urban bushland remnants in the Perth metropolitan region. The overall detectability indicates the probability of detecting each species at a given site using the proposed standard survey regime for the region of six spring and two autumn samples. The estimated number of surveys is that required to detect each species with high (>95%) probability using targeted surveys during their peak flying period. [The number of targeted surveys required (*n*) for each species was calculated from the inequality $0.95 < [1 - (1 - p)^n]$, where *p* is the maximum detectability, i.e that during during the peak flying period].

	Number observed	Overall detectability	Peak detectability	Peak flight period	Number of surveys
Resident butterfly species					
Trapezites sciron	49	0.73	0.52	1–15 Oct	5
Trapezites argenteoornatus	38	1.00	1.00	16–31 Oct	1
Anisynta sphenosema	45	0.12	0.12	15 Mar–7 Apr	> 10
Hesperilla donnysa	6	0.08	0.01	15 Mar–7 Apr	> 10
Hesperilla chrysotricha	1	0.08	0.01	-	> 10
Motasingha trimaculata	28	0.78	0.46	1–15 Nov	5
Motasingha dirphia	-	-	0.00	-	> 10
Croitana croites – year 1	1	0.54	0.12	-	> 10
Croitana croites – year 2	5	1.00	1.00	16–31 Oct	1
Mesodina cyanophracta	170	0.96	0.79	16–30 Nov	2
Taractrocera papyria	99	0.89	0.46	16–30 Sep	5
Geitoneura klugii	1481	1.00	0.92	16–30 Nov	2
Geitoneura minyas	1807	1.00	1.00	16–31 Oct	1
Heteronympha merope	129	0.74	0.43	16–30 Nov	6
Hypochrysops halyaetus	325	1.00	1.00	1–15 Nov	1
Ogyris amaryllis	16	0.78	0.22	15 Mar–7 Apr	> 10
Ogyris idmo	1	0.00	0.00	-	> 10
Candalides acastus	34	0.90	0.25	16 Sep–7 Apr	> 10
Nacaduba biocellata	49	0.67	0.13	16 Sep–7 Apr	> 10
Theclinesthes miskini	7	0.22	0.03	16 Sep–7 Apr	> 10
Theclinesthes serpentata	2	0.91	0.26	-	>10
Neolucia agricola – year 1	138	1.00	1.00	1–15 Oct	1
Neolucia agricola – year 2	284	0.96	0.57	1–16 Dec	4
Neolucia agricola – year 3	42	0.89	0.62	1–15 Oct	4
Zizina labradus[1]	130	0.81	0.37	1–15 Nov	7
Resident day-flying moths					
Synemon sp. (Perth) – year 1	185	1.00	1.00	1–15 Nov	1
Synemon sp. (Perth) – year 2	164	0.98	0.82	1–15 Nov	2
Synemon sp. (Perth) – year 3	29	0.72	0.57	16–31 Oct	4
Synemon gratiosa	33	0.62	0.57	27 Feb–14 Mar	4
Pollanisus cuprea	298	0.91	0.76	16–30 Sep	3
Hecatesia thyridion	1	0.00	0.00	-	> 10
Periscepta polysticta[2]	11	0.82	0.66	1–15 Oct	3
Non-resident butterflies					
Cephrenes augiades	-	-	0.00	-	> 10
Cephrenes trichopepla	-	-	0.00	-	> 10
Papilio demoleus	-	-	0.00	-	> 10
Catopsilia pomona	-	-	0.00	-	> 10
Belenois java	-	-	0.00	-	> 10
Delias aganippe	5	0.80	0.18	16 Sep–7 Apr	> 10
Pieris rapae – year 1	150	1.00	1.00	1–15 Oct	1
Pieris rapae – year 2	470	1.00	0.97	16–31 Oct	1
Pieris rapae – year 3	111	0.98	0.64	16–30 Nov	3
Junonia villida	17	0.53	0.09	16 Sep–7 Apr	> 10
Vanessa kershawi	1031	1.00	0.79	1–15 Nov	2
Vanessa itea	6	0.08	0.01	16 Sep–7 Apr	> 10
Danaus chrysippus[3]	8	0.28	0.21	15 Mar–7 Apr	> 10
Danaus plexippus	15	0.28	0.04	16 Sep–7 Apr	> 10
Lampides boeticus – year 1	141	1.00	1.00	1–31 Oct	1
Lampides boeticus – year 2	63	0.86	0.50	1–16 Dec	5
Lampides boeticus – year 3	28	0.70	0.44	16–31 Oct	6

[1]: Now *Zizina otis* (Yago et al. 2008).

[2]: Now *Periscepta butleri* (M.F. Braby pers. comm.).

[3]: Now *Danaus petilia* (Lushai et al. 2005).

By excluding non-resident species, any relationship between species richness and site connectivity should be more easily detected. Species existing as metapopulations are expected to demonstrate patterns of site occupancy largely determined by the degree of separation between suitable habitat, but I found no such species. This may be because these habitat fragments, which have been isolated relatively recently, are not yet at equilibrium. Some sites may retain relictual populations that, in time, will not persist – after which, metapopulation effects may begin to appear.

6.1.3 Modelling species–area–habitat effects

The main results of chapter 4, in which I reviewed 16 functions proposed as models of the species–area relation, were as follows:

- Many of the functions are special cases of others, some are identical, and two arose as a result of transcription errors. The 16 functions reduce to a set of nine general functions;
- Previous studies that have compared alternative functions suffered from three shortcomings: (i) too much emphasis was placed on maximising goodness-of-fit between species number (S) and area, ignoring the effects of other factors; (ii) most made implicit or untested assumptions about the distribution of S; and (iii) some repeated the mispractice of using R^2 to compare models with different numbers of parameters or differing error distributions;
- An empirical comparison showed that including covariates in addition to area resulted in a different best-fitting function, so that ignoring the effects of these covariates can result in an incorrect choice of the best-fitting function. Conversely, the choice of function may also affect which covariates are found to be important;
- The generalized linear model provides a framework with which to fit alternative species–area functions and the information-theoretic approach a suitable method with which to compare their fit; and

- Determining the appropriate statistical model with which to relate species number to area and other covariates requires careful consideration of many issues, not just the functional relationship between species number and area.

An appropriate methodology for fitting species–area models should include the following steps: (i) choose a suitable link function based on good theory, including consideration of whether a model with an asymptote is appropriate; (ii) select a distributional model for S; (iii) include appropriate covariates (predictors) in the model fitting process; (iv) fit the model paying due care to tests of assumptions; and (v) consider interactions between the covariates (Hosmer & Lemeshow, 2002; Vittinghoff *et al.*, 2005; Barry & Elith, 2006). Few studies have addressed all of these issues, especially the study of interactions between covariates. The Poisson and binomial distributions are under-utilized in applied ecology but provide better models of variation in count data (Richards, 2008). Insight into ecological processes, appropriate methodology, and careful consideration of assumptions are needed to progress the study of species–area relationships.

6.1.4 Habitat preferences

The main results of chapter 5, in which I examined the effects of area and habitat on species presence, abundance and richness in urban habitat fragments, were as follows:

- Site area and vegetation condition were the dominant determinants of species presence: large sites with more high quality (undisturbed) vegetation favoured 16 of 20 native species whereas only one benefited from disturbance. A further nine species were not sufficiently widespread or abundant to enable individual analysis, but were collectively more prevalent at larger sites;
- Host plant density was an important predictor of both site occupancy and abundance for all of the species for which it was assessed;
- Higher shade tree densities had positive impacts on occupancy for some species, but lower densities were associated with greater abundance of others;
- Increased site connectivity did not favour any species;

- Site species richness reflected the collective responses of the individual species: increasing with area and declining with vegetation disturbance. The effects of area and vegetation quality were not simply additive: disturbance had a far greater impact on small remnants;
- The dominance of resource quality and quantity on the patterns of site occupancy is consistent with habitat resources, not metapopulation effects, determining current distribution patterns;
- The interaction between area and vegetation condition is inconsistent with the area *per se* hypothesis: in the absence of disturbance there was no evidence of a species–area effect. However, few sites < 10 ha were undisturbed; and
- Restoration or maintenance of high vegetation quality will be essential to maintain regional species diversity and to prevent local extinctions of butterflies and day-flying moths, especially in small remnants.

These results have important implications for the conservation of butterflies and day-flying moths in this region. Maintenance of vegetation quality is of paramount importance and is vital in smaller remnants. Large remnants, being less susceptible to local extinctions, will be essential for the persistence of many species.

6.2 Synthesis

Anthropogenic fragmentation of habitat is a major threat to global biodiversity. The loss of species from habitat remnants can only be estimated if baseline data is available, and the impact can only be ameliorated if the effects of fragmentation are understood. This study is the first comprehensive, quantitative assessment of the distribution and ecology of butterflies and day-flying moths in Australian urban habitat fragments. The impact of urban and rural development on Australian butterflies has not been examined previously in such detail (Kitching and Dunn 1999) although recent studies have begun to address this (Neyland 2001, Beaumont and Hughes 2002, New and Sands 2002, Braby and Douglas 2004, Douglas 2004, Braby and Edwards 2006, Collier et al. 2006, Eastwood et al. 2008). Urbanization and related impacts have been identified as threatening 40 taxa (Sands and New 2002), although this assessment was based primarily on qualitative studies and anecdotal information. The only other regional conservation study, in a fragmented agricultural landscape in eastern Australia, found a depauperate fauna with few narrow range endemic or threatened taxa that may have already been depleted by local extinctions (Braby and Edwards 2006). This study found a similar situation, with many of the smaller and degraded remnants exhibiting local extinctions.

As well as habitat modification, several other factors expose small populations to greater extinction risk: the Allee effect (decline in individual fitness at low population size or density); the small population paradigm (greater susceptibility of small populations to extinction through stochastic events); trophic cascades (changes in abundance across trophic levels within a food web because of reciprocal predator–prey effects); co-extinction (loss of mutualistic species); and synergistic effects (positive, interactive feedback between effects that are greater than their combined impacts) (Brook *et al.* 2008). In this study the detailed examination of species presence identified site area and decline in vegetation condition as the pre-eminent factors affecting species presence in urban habitat fragments. Larger sites and those that were less disturbed supported more resident species and these effects were synergistic, with disturbance having a greater impact in smaller fragments.

Urban habitat fragments are often studied within a framework derived from the equilibrium theory of island biogeography (ETIB), although the usefulness of this approach continues to be questioned (Saunders *et al.* 1991, Whittaker and Fernández-Palacios 2007). Two major problems exist in extending the ETIB to habitat fragments. Firstly, the sea that surrounds true islands is both uniform and inhospitable for terrestrial species. This is not true of matrix between habitat fragments, which is heterogenous and highly variable in the resources it provides. For many species, both invasive and native, the matrix and associated edges have become habitat. Secondly, a basic assumption of the ETIB is that a state of equilibrium has been attained. However, in comparison with islands habitat fragments are of relatively recent origin and there are insufficient long-term studies to determine if an equilibrial state has been reached.

The persistence of populations in fragmented landscapes is essential for their conservation, but it is important to distinguish presence from persistence. In the short term fragmentation may not reduce species numbers within the landscape, but many of the resulting remnant populations may be inviable in the long term. Because responses to habitat fragmentation may take many years or decades to manifest (Garden *et al.* 2006, Kadlec *et al.* 2008), the presence of a species within a fragment may not equate to long-term viability. Following habitat fragmentation the landscape may carry an extinction debt that takes many years to be repaid (Tilman *et al.* 2002). This study provides baseline data against which future species gains and losses may be determined .

Exemplary studies of lizards, birds, mammals and butterflies on islands have demonstrated the importance of interactions for explaining distribution patterns (Schoener and Adler 1991, Burbidge and Manly 2002, Russell *et al.* 2004, Kallimanis *et al.* 2008). However, interactions have rarely been examined or modelled explicitely. For example, a highly-cited study of butterfly community structure in habitat fragments (Steffan-Dewenter and Tscharntke 2000) (105 citations; Google Scholar accessed 3 December 2008) showed that the slope of the species–area relationship of butterflies increased for groups of species with increasing food plant specialization, but separate models for each group were fitted rather than a single quantitative model that incorporated an area–group interaction. Similarly, the interactive effects of area and habitat diversity were incorporated into the ‘choros’ model of species–area–habitat relations (Triantis *et al.* 2003), but exclusion of both main effects made assessment of the importance of the interaction impossible and led to criticism of the model (Whittaker and Fernández-Palacios 2007). This study is thus one of few to demonstrate and quantify the importance of interactions in explaining patterns of species richness.

Ecological systems have regularities or patterns in the abundance and number of species that reflect underlying ecological rules or processes (Whittaker and Fernández-Palacios 2007). The study of these systems, macroecology, requires sophisticated statistical analysis to identify and separate the causative processes. The equilibrium theory of island biogeography (ETIB), a core macroecological model, postulates that species number is the equilibrium state of species richness that results from the opposing forces of immigration and extinction in isolates. The species–area relationship is central to this model, but the other factors (isolation, elevation, habitat quality, etc.) and their interactions are important modifiers of the relationship that must also be accounted for.

The species–area relationship is a fundamental paradigm in ecology. However, in studies that seek to determine those factors that affect species presence within isolates, area is both an important predictor and a nuisance parameter that may obscure the effect of other factors. The reverse is also true – other factors may mask the relationship between species and area. In many classic species–area studies the focus has been too narrow, examining only the relationship between area and species richness while ignoring important covariates. Attempts to identify biodiversity 'hotspots' have shown that the choice of species–area function is of critical importance because different functions produce conflicting results (Veech, 2000; Ulrich & Buszko, 2005; Fattorini, 2006a, b). Despite almost a century of curve fitting no theoretically or empirically best model of the species–area relationship has been found. Although numerous functions have been proposed there is little theoretical support for many of alternatives.

This study has provided a framework to compare species–area functions, but consideration of several factors is needed to choose an appropriate link function. My advice to those constructing a species–area–habitat model is to start with a power link function and Poisson distribution, unless they are convinced that an alternative model is more theoretically appropriate.

6.3 Management Implications

This research has several implications for the maintenance and management of species richness and diversity within the Swan Coastal Plain portion of the Perth Metropolitan Region. Although not all species known from the region were detected, these findings enable general recommendations to be made about the majority of species.

6.3.1 Regional species diversity

Restoration or maintenance of high vegetation quality is essential to maintain regional species diversity and to prevent local extinctions of butterflies and day-flying moths, especially in small remnants. All of the least widespread native species were those restricted to native host plants and so are dependent on remnant vegetation. Many of the smaller sites and those with degraded vegetation had small faunas and few regionally rare taxa. As the richest site, and the largest containing many of the least common species, Koondoola bushland is the most important site for conservation within this region. Other sites are of regional significance for particular taxa, such as Warwick bushland for *Synemon gratiosa* and Trigg bushland for *Croitana croites*.

6.3.2 Fire

Stochastic events in the history of each site, particularly past fires, may well explain the decline in both species richness and vegetation condition within small sites. Following fire, α diversity of invertebrates declines initially but increases as species recolonize progressively from unburnt areas (Van Heurck and Abbott 2003). In small fragments broadscale (i.e. intense) fires may affect the entire fragment and eliminate butterfly populations. For species unable to cross the matrix and recolonize from other sites these local extinction events reduce overall species richness. Fires also facilitate weed invasion and are of particular concern where a positive feedback occurs between increased non-native grasses and increased fire frequency (Hobbs 2003). Appropriate management of fire regimes will thus be essential to maintain habitat quality for butterflies and day-flying moths.

6.3.3 Conservation of **Synemon gratiosa**

The graceful sun-moth *Synemon gratiosa* is the only listed endangered species occurring in this region. It is a narrow-range endemic restricted to the Swan Coastal Plain between Mandurah and Neerabup, and is listed under both Western Australian and Federal legislation {Threatened Species Scientific Committee, 2008 #2227}. It was recorded at six sites (Errina Rd, Koondoola, Marangaroo, Warwick north, Warwick south-east and Shenton bushlands) and also occurs (but was not detected) at Landsdale bushland (P. Robertson, pers. comm.), and at Whiteman Park (Anonymous 1997). With the exception of Shenton bushland (site 30) these sites are within a relatively small area of the northern suburbs and are within 5 km of each other (see Fig. 1: sites 12, 21, 22, 24, 42 and 43. Whiteman Park is 1.5 km to the north-east of site 21). Most individuals (26 of 36) were observed at Warwick bushland and few (1–5) at the others. High quality vegetation was identified as the favouring site occupancy, although this species is difficult to detect and additional sites and more detailed studies are needed to better understand its life history and ecology. However, maintenance of vegetation condition by reducing disturbance, such as restricting access to the sites where it occurs (e.g. through fencing), is essential. During these surveys oviposition on *Lomandra hermaphrodita* was observed (pers. obs.), which is consistent with the host plant preferences of other members of the *Synemon jcaria* species group (*S. jcaria*, *S. laeta* and *S. gratiosa*). Surveys to determine the density of this plant should be carried out to determine if this is an important factor affecting site occupancy, and whether sites suitable for re-introductions occur within the region. A species recovery team should be formed for this taxon and the information contained in this study should be collated with other information and referred to this team.

Key threatening processes for this species are urban development, public access and track maintenance, inappropriate fire regimes, and localised extinction. Based on these processes, priority actions for the region should be: protect those areas of native vegetation that contain populations at present and those which may support populations in the future; develop and implement a suitable fire management strategy; investigate formal conservation arrangements for existing populations and options for establishing additional populations; and raise awareness of the species within the local community. Appropriate priority actions for local populations of this species are: minimisation of disturbance associated with the use and maintenance of fire breaks and other tracks, particularly during the late February – early April period when males are likely to have established territories; monitoring known sites to identify any changes in threats and numbers; and fencing of known sites to restrict or prevent public access.

6.4 Future research

The interaction between site area and habitat quality (Fig. 3, chapter 5) is a major finding of this study, and an effect that has not been previously identified. However, few small sites are undisturbed, and an investigation of this effect within small sites – those less than 10 ha – would be useful to confirm the effect. More than 250 habitat remnants within the Perth metropolitan region are available for study, and careful selection of sites across a range of areas and levels of disturbance would enable an independent test of the relative importance of area and habitat condition, and determine if a minimum threshold area exists for particular taxa or total species richness. Density of food plants was found to be important for those species for which it could be measured. The importance of food plant density and any threshold levels needed to sustain populations of those species of local or regional conservation concern could also be determined as part of such a study.

Several resident species were not observed, encountered only rarely (< 10 times), or had low overall detectability: *Hesperilla donnysa*, *H. chrysotricha*, *Ogyris idmo*, *Jalmenus inous*, *Candalides cyprotus*, *C. heathi*, *Theclinesthes miskini*, *T. hesperia* and *Hecatesia thyridion*. More extensive surveys are needed to determine the distribution of these taxa within the region.

Proximity of remnants was not important for any of the species in this study but several were not recorded or detected at sufficient sites to enable analysis. A fundamental question that can only be addressed by long-term monitoring is whether species presence indicates likely persistence.

In contrast to species–area models only the logistic and EVF link functions have been used to model species incidence, and the species–incidence and species–area models should be reconciled. A model that unifies these two approaches by combining individual area–habitat incidence functions into a species–area–habitat model is needed.

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Appendix – Statement of Contribution, Chapter 4

M. R. Williams

Drafted the original paper, conducted all data analysis, wrote the final paper and acted as corresponding author.

Signed Date

B. B. Lamont

Reviewed the draft paper, checked Appendix S1 and assisted with writing the final paper.

Signed Date

J. D. Henstridge

Reviewed the draft paper and provided general comments.

Signed Date

15 January 2009