Reproductive biology and pollen vectors of the rare and endangered *Banksia verticillata* R. Br.

Consultancy report to the Western Australian Department of Conservation and Land Management

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December 1994
14399-12-94

SUMMARY

Floral biology, reproductive potential and pollen vectors for the rare species *Banksia verticillata* were examined at the Jimmy Newles and Stony Hill sites near Albany, Western Australia during 1993 and 1994. Unlike many other banksias, *B. verticillata* has relatively high levels of reproductive success. Approximately 40% of the inflorescences produced during 1993 developed follicles. Mean fruit set was 9.5% for fertile inflorescences, although significantly fewer follicles were formed than could have been accommodated. Mean viable seed production per plant during 1993 at the Jimmy Newles and Stony Hill sites were 299 and 149, respectively. Of the seed produced, over 80% was considered to be incapable of germination (17.0% damaged by insects; 2.4% diseased/ decayed; 58.1% aborted; 1.7% firm, but non-viable). Total viable seed production per population at the Jimmy Newles and Stony Hill sites during 1993 was estimated to be approximately 23,950 and 15,617, respectively.

New Holland Honeyeaters (*Phylidonyris novaehollandiae*) were the major pollen vectors for *B. verticillata*. White Cheeked Honeyeaters (*Phylidonyris nigra*), Western Spinebills (*Acanthorhyncus superciliosis*) and Honey Bees (*Apis mellifera*) may have effected some pollen transfer, but were much less frequent visitors than *P. novaehollandiae*. All honeyeaters captured carried heterospecific pollen loads, with the presence of "foreign' pollen possibly reducing their effectiveness as pollinators of *B. verticillata*.

Honeyeater movements of up to 15m between inflorescences on different plants were observed, although most consecutive movements occurred between inflorescences on the same plants. Failure to recapture significant numbers of *P. novaehollandiae* at the two sites, and frequent observation of birds moving into and out of these sites, suggest that most honeyeaters were transients rather than residents. Pollen transfer between neighbouring populations, in addition to movement within populations, may therefore be common.

One *Rattus fuscipes* and seven *Mus musculus* were captured over 45 trap nights at the two sites, and found to carry *B. verticillata* pollen. The apparent dearth of these small mammals, and failure to catch any Honey Possums (*Tarsipes rostratus*), suggests that mammals are currently less important than honeyeaters as pollinators of *B. verticillata.*

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INTRODUCTION

Banksias are woody, evergreen members of the Proteaceae, with most species having distributions that are restricted to the sandplains and heathlands of southwestern Australia (Collins and Rebelo 1987; Taylor and Hopper, 1988; Low and Lamont, 1990). Seven of the 58 Western Australian species are currently listed as rare (Wildlife conservation (rare flora) notice, 1993). Banksia inflorescences typically comprise several thousands of tightly-packed hermaphroditic florets, and are a major source of nectar for indigenous animals (Collins and Spice, 1986; Lamont and Van Leeuwen, 1988; Collins *et al.*, 1994). Many are also brightly-coloured and of considerable importance to the tourist and horticultural industries (George, 1987). There are therefore sound conservation and economic reasons why management of banksia-dominated vegetation is necessary (George, 1987; Cowling *et al.*, 1990).

Banksias, like many hermaphroditic angiosperms, have low fruit and seed set (Collins and Rebelo, 1987). This phenomenon may be a consequence of ovule or pre-dispersal seed mortality that results from inadequate or inappropriate pollination (Bierzychudek, 1981), limited nutrient resource availability (Stephenson, 1981; Stock *et al.*, 1989), predation (Wallace and O'Dowd, 1989), genetic constraints (Wiens, 1984), or a combination of these factors.

Effective pollen transfer is required if pollination, fertilisation, seed set, and ultimately seedling recruitment are to occur. Many plant characteristics, such as flowering phenology, floral morphology, and the timing of floral development, affect pollen transfer. The rate and number of florets opening each day, as well as the longevity of inflorescences and the causes of floret opening, are also likely to be important factors (Ramsey, 1988a). Many small mammals, birds and arthropods visit the flowers of banksias, and are therefore potential pollinators (Paton and Ford, 1977; Hopper and Burbidge, 1982). Nevertheless, features such as copious nectar production, large distances between nectaries and stigmas, and the clustering of flowers into large, often conspicuous, inflorescences suggest that vertebrates may be the most important pollen vectors (Ford *et al.*, 1979; Turner, 1982; Collins and Rebelo 1987).

Management of any plant species must be based on a sound understanding of its systematics, distribution and reproductive biology, and is especially important if the species is rare and/or endangered (Hopper and Muir, 1984). The major objectives of the present study were to document the flowering and reproductive success of the rare *Banksia verticillata* R. Brown (1810). Investigations involved two of the approximately 28

populations that occur on granite outcrops at two disjunct locations between Walpole and Two Peoples Bay along the South coast of Western Australia (George, 1987).

METHODS

Study species

Banksia verticillata is a gazetted rare species that occurs in the South west of Western Australia as described above. At least 13 populations occur within conservation reserves (Hopper *et al.,* 1990), on or beside granite outcrops quite close to the ocean, or occasionally in tall shrubland. The mature plant is a shrub, rarely a tree, with a thick branching trunk (Figure 1). Leaves are narrowly elliptic to oblong and arranged in whorls. Inflorescences are terminal, golden yellow throughout and produced between January and April each year (Figure 2). Follicles that develop on infructescences are narrowly elliptic and perianths are persistent (Figure 3; George, 1981).

Figure 1. *Banksia verticillata* shrubs growing on a granite substrate at the Stony Hill site.

B. verticillata is thought to be fire-intolerant and regenerate solely from seed (Taylor and Hopper, 1988). Successful pollination, fertilisation and viable seed bank development are therefore considered essential requirements if long-term survival of the species is to occur (George, 1987). The fact that some stands of *B. verticillata* are infected by *Phytophthora cinnamomi* (Hopper *et al.,* 1990), and exhibit a medium level of suscepti-

bility to the pathogen (McCredie *et al.*, 1985), poses an additional risk to the continued existence of *B. verticillata* (Hopper *et al.*, 1990).

Figure 2. *Banksia verticillata* inflorescence with open florets.

Study sites

Two sites were established within the Torndirrup National Park, near Albany, during June 1993 (Figure 4). The first of these was located on a hilltop near Jimmy Newles Inlet (117° 6' 0"E, 35° 6' 52"S; Figure 5), and the second near the Stony Hill Heritage Trail (117° 6' 44" E 35° 7' 23" S). Both sites had granite substrates, were elevated and often subjected to strong and gusty onshore winds from the adjacent Southern Ocean. Rainfall throughout the year averages in excess of 900 mm, with the heaviest falls typically occurring during winter. Mean air temperatures vary from approximately 7 to 26°C.

Floral biology and tree dimensions

During June 1993, forty plants at each site were tagged and the numbers of inflorescences that had been produced during the 1993 flowering season recorded. Two inflorescences per plant were randomly-selected and their fruiting success calculated during a subsequent visit in 1994. The numbers of infructescences that had been produced during the 1992 flowering season were counted, along with the number of follicles on random samples of two infructescences per plant.

During February 1994, the numbers of inflorescences produced during the most recent flowering season were recorded. The lengths of 40 randomly-selected inflorescences were measured and compared with the numbers of florets present on those inflorescences (Number of florets = -19.859 + 6.721 * inflorescence length; $P < 0.0001$, $R^2 = 0.993$). The regression equation developed was then used in conjunction with measured lengths for 1993 infructescences, assuming that infructescence and inflorescence lengths

Figure 3. *Banksia verticillata* infructescence showing opened and unopened follicles.

were not significantly different, to estimate the numbers of florets present in 1993. The numbers of follicles present on 1993 infructescences were counted, and the percentage fruit set estimated for each original inflorescence.

Ten inflorescences in the late bud stage of development were tagged, and the number of florets opening monitored twice a day for two successive days during the February visit. The length of each of these inflorescences was measured and used as a basis for estimating the total number of florets present. Anthesis rates, as percentages of total florets opening per hour, were then calculated for both day and night.

The location of each study plant was mapped using a compass and 30 m tape measure. A single plant was chosen as a control point and the distance and bearing to neighbouring plants was measured from this point. Plant height and diameter in two directions was measure for all 80 study plants and used to estimate aboveground biovolume (canopy volume) for each plant, assuming that the canopy was hemispheroidal in shape. Regression analysis was then used to search for significant relationships between these parameters and the inflorescence and infructescence production of each plant.

Infructescence and seed bank measurement

B. verticillata infructescences collected from the Jimmy Newles (N = 15) and Stony Hill (N = 65) study sites by W.A. Herbarium staff were examined, and the length, weight and distribution of follicles throughout each infructescence recorded. An additional 55 in-

fructescences from 13 plants were collected from the Stony Hill study site during April 1994 and treated in the same manner. Seeds were extracted from 13 of the additional infructescences and the percentage of firm, aborted, insect-damaged and disease/decayed seed per infructescence recorded. The rate of germination and percentage seed viability for three replicates of 25 firm seed were then determined. Comparison of mean percentage seed viability with the numbers of follicles per infructescence and infructescences per plant provided rough estimates of viable seed production per plant at each site.

Figure 4. *Banksia verticillata* shrubs growing on a granite outcrop at the Jimmy Newles site.

An additional 36 *B. verticillata* infructescences that had been collected from a nearby study site by Leonie Monks, were used to estimate the maximum possible percentage fruit set that could be achieved. The length and mean circumference of each infructescence was measured and used to estimate the surface area available for follicle development, assuming that the infructescence was cylindrical. Lengths and widths of open and closed follicles were measured, and used to determine the mean surface area of these follicles. The maximum number of open and closed follicles that could physically be accommodated on each infructescence was estimated by comparing infructescence and mean follicular surface areas.

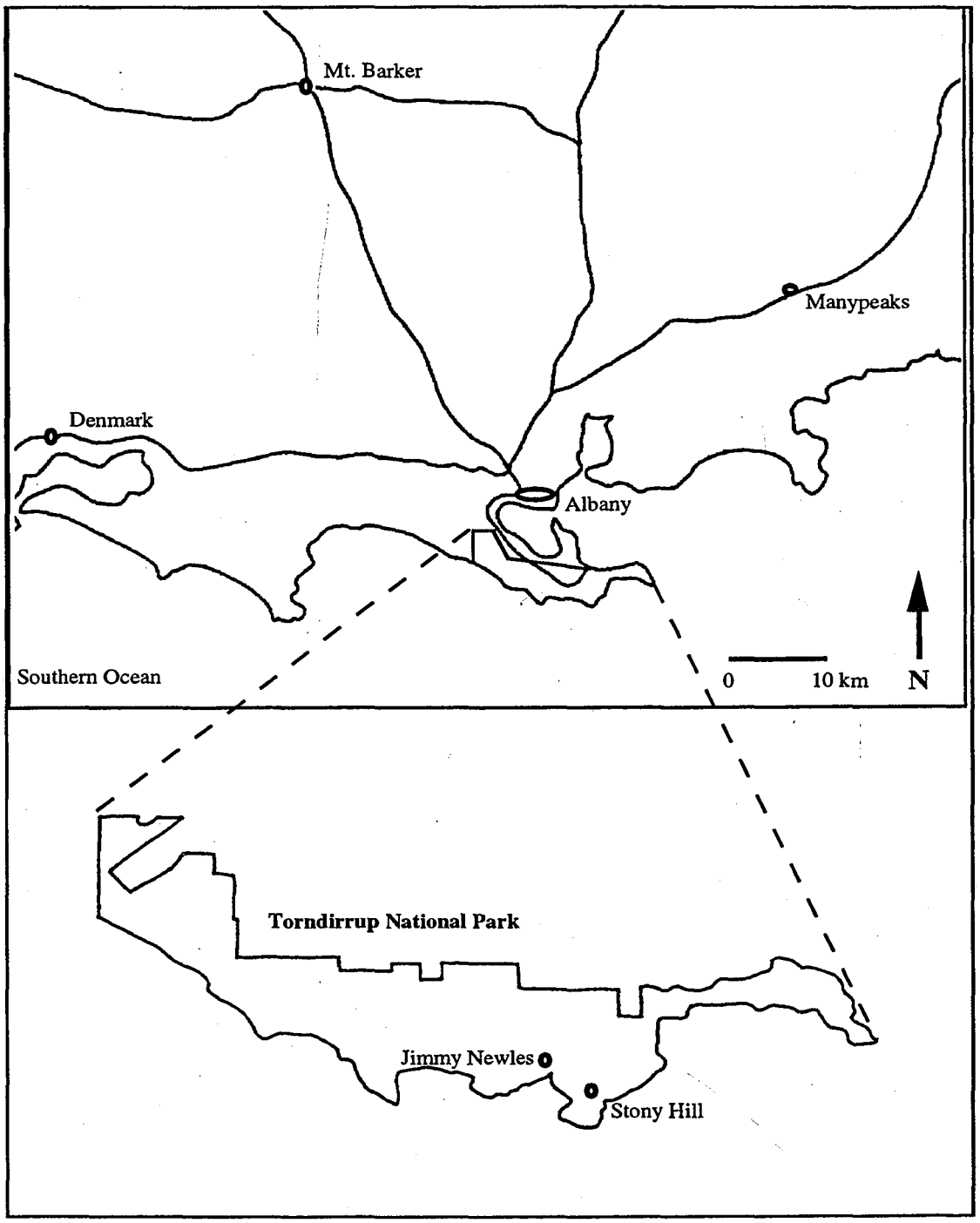

Figure 5. Location of Jimmy Newles and Stony Hill study sites within the Torndirrup National Park.

Pollen vectors

During February 1994, nine Elliott traps were placed next to *B. verticillata* inflorescences. Traps baited with rolled oats, honey and peanut butter were opened for a total of 5 nights at the two sites. Four mist nets were opened at dawn for 3 hours over two mornings at each site. Birds were banded with numbered aluminium bands and their sex, age, weight and moult recorded. Pollen samples were taken from the beak or snout, forehead and ventral body surface of captured animals, and the number and species of

pollen grains scored at 100x magnification (Wooller *et al.*, 1983).

The foraging behaviour of honeyeaters visiting *B. verticillata* plants was observed at both sites from 0730 to 1030 on the 17th of February 1994. Opportunistic observations were also made while conducting other work, and the following information recorded: the location and distance between trees visited; the number of inflorescences visited per tree; position of the bird when feeding and the region of the inflorescence being probed. Opportunistic observations of invertebrate foraging at *B. verticillata* were recorded, as were details of weather conditions.

RESULTS

Floral biology and tree dimensions.

A strong, positive linear relationship between biovolume and inflorescence production existed during the 1992 ($P < 0.0001$, $R^2 = 0.523$), 1993 ($P < 0.0001$, $R^2 = 0.654$), and 1994 ($P < 0.0001$, $R^2 = 0.651$) flowering seasons at the Jimmy Newles and Stony Hill sites (Figure 6). There was also a positive linear relationship between biovolume and infructescence production during the 1992 ($P < 0.0001$, $R^2 = 0.633$), 1993 ($P < 0.0001$, $R^2 = 0.335$), and 1994 ($P < 0.0001$, $R^2 = 0.312$) flowering seasons (Figure 7). A significant positive linear relationship between inflorescence production and percentage fruiting success was evident at the Stony Hill site during 1993 ($P < 0.0032$, $R^2 = 0.223$), although there were no significant relationships between biovolume and fruiting success or mean fruit set, or between inflorescence production and mean fruit set, at either site.

The height, width, canopy area and biovolume of plants at the Jimmy Newles site were significantly greater than for those at Stony Hill ($F_{1,78} = 4.384$, $P = 0.0395$; $F_{1,78} = 8.835$, $P = 0.0039$; $F_{1,78} = 10.453$, $P = 0.0018$; and $F_{1,78} = 9.080$, $P = 0.0035$, respectively; Table 1). During 1992, no significant inter-site differences in inflorescence or infructescence production were evident. Nevertheless, inflorescence (1993: $F_{1,78} = 13.881$, $P = 0.0004$; and 1994: $F_{1,78} = 12.748$, $P = 0.0006$) and infructescence (1993: $F_{1,69} = 6.668$, $P = 0.0119$; and 1994: $F_{1,69} = 5.951$; $P = 0.0173$) production were significantly greater at the Jimmy Newles site during the following two flowering seasons. On average, each plant at the Stony Hill site supported 54 seed-bearing infructescences, and infructescence production was strongly correlated with biovolume ($Y = 3.717+7.361*X$, $P < 0.001$, $R^2 = 0.563$). The number of follicles produced per infructescence, mean inflorescence and infructescence lengths, number of florets per inflorescence and fruiting success did not vary significantly between sites, although the percentage fruit set on

sample inflorescences was significantly greater at the Stony Hill study site during 1993 ($F_{1,75} = 13.181$; $P = 0.0005$).

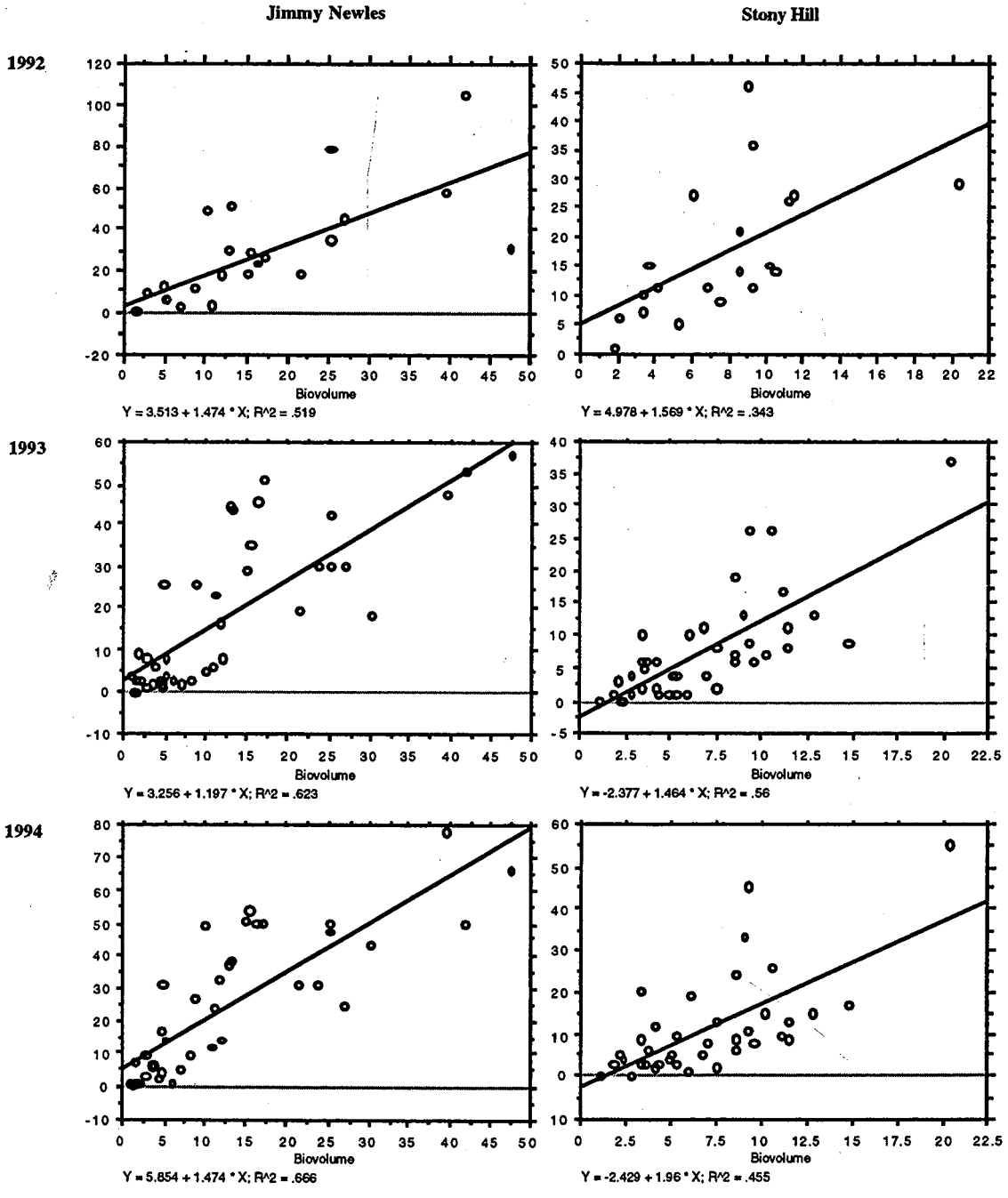

Figure 6. Regression relationships between inflorescence production and biovolume at the Jimmy Newles and Stony Hill study sites during the 1992-1994 flowering seasons. All significant at the $P < 0.01$ level.

Diurnal and nocturnal anthesis rates (percentage of florets opening per hour) at the Stony Hill site were not significantly different, although they varied considerably between inflorescences (Table 2). Overall, the anthesis rate was such as to suggest that approximately 9.5 days were needed for all florets on a given inflorescence to open. Floret opening was loosely basipetalous, although random florets or patches of florets on the

most exposed sides of inflorescences often opened out of sequence.

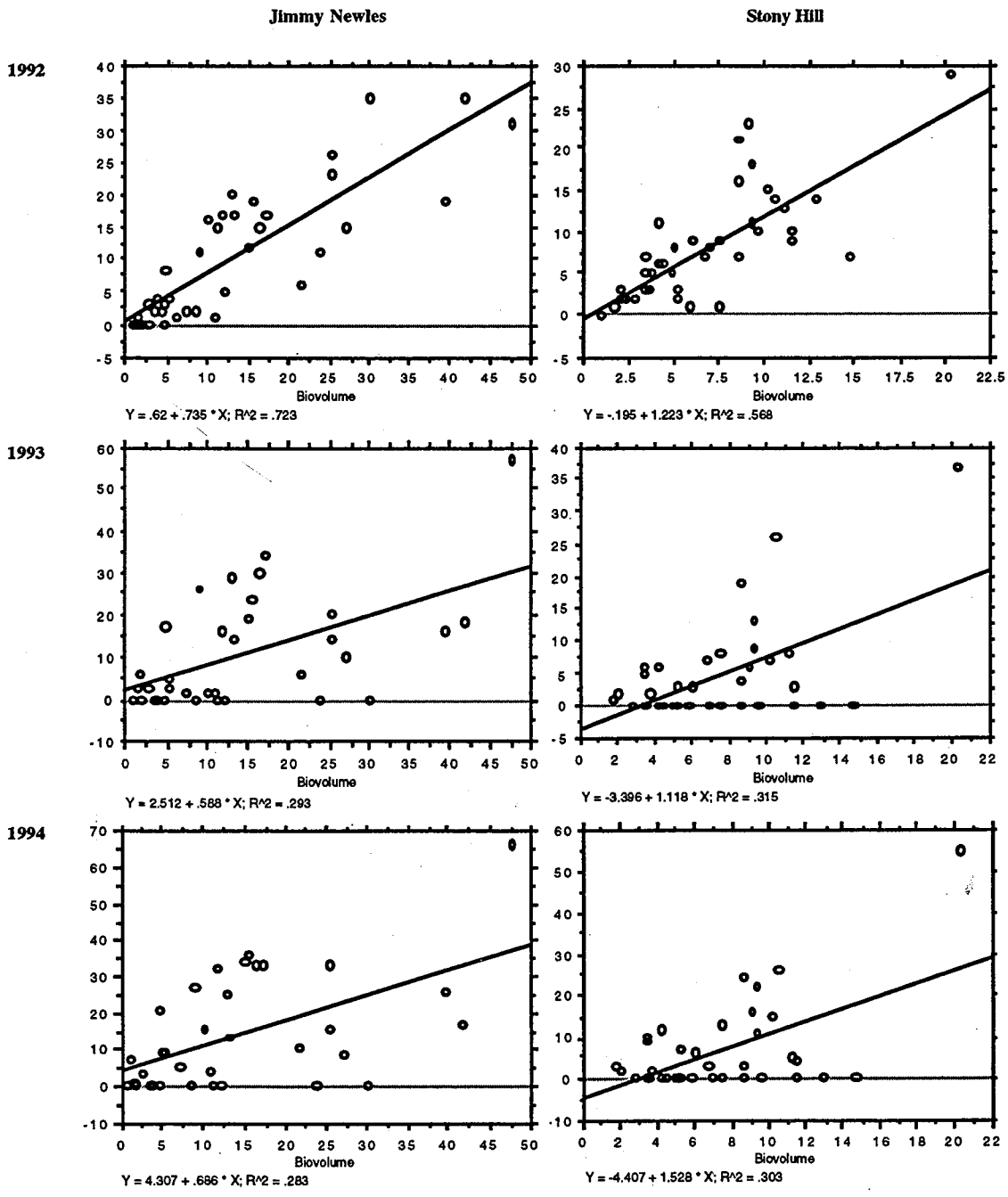

Figure 7. Regression relationships between biovolume and infructescence production at the Jimmy Newles and Stony Hill study sites during the 1992-1994 flowering seasons. All significant at the $P < 0.01$ level.

Infructescence and seed bank measurements.

The weight, length, number of follicles and percentage fruit set were similar for infructescences collected previously from the two study sites and stored at the W.A. Herbarium. Similarly, there were no significant inter-site differences in the weight of seed obtained from these infructescences (Table 3). At both sites, there were significantly more folli-

cles found in the middle third of each infructescence than in either the apical or basal thirds (Jimmy Newles: $F_{2,14} = 23.519$; $P < 0.0001$; Stony Hill: $F_{2,62} = 183.245$; $P < 0.0001$; Figure 8).

Table 1. Inflorescence and infructescence production, fruiting success and biovolume for *B. verticillata* at Jimmy Newles and Stony Hill study sites. Values indicated are means ± standard errors. Sample sizes are given in parentheses. Differences were either not significant (N.S.), or significant at the $P < 0.05$ (*), $P < 0.01$ (**), or $P < 0.001$(***) levels.

Parameter	Jimmy Newles		Stony Hill		Significance
Inflorescences 1992 (est)	27.5 ± 5.3	(24)	17.1 ± 2.6	(20)	N.S.
Inflorescences 1993 (act)	19.4 ± 2.9	(40)	7.7 ± 1.3	(40)	***
Inflorescences 1994 (act)	24.8 ± 3.4	(40)	11.0 ± 1.9	(40)	***
Infructescences 1992 (act)	10.1 ± 1.6	(40)	8.2 ± 1.0	(40)	N.S.
Infructescences 1993 (est)	11.0 ± 2.3	(34)	4.7 ± 1.3	(37)	*
Infructescences 1994 (est)	14.2 ± 2.7	(34)	6.7 ± 1.8	(37)	*
Total infructescences	±	(40)	54.3 ± 2.6	(40)	
Mean follicles /infruct. 1992	89.1 ± 4.1	(81)	95.8 ± 3.3	(80)	N.S.
Mean follicles /infruct. 1993	67.7 ± 6.0	(41)	80.3 ± 5.0	(34)	N.S.
Infructescence length 1993	119.8 ± 4.3	(41)	107.9 ± 3.6	(34)	N.S.
Inflorescence length 1994	107.4 ± 7.1	(20)	123.5 ± 7.9	(20)	N.S.
Florets /inflorescence 1994	685.1 ± 50.6	(20)	826.8 ± 52.3	(20)	N.S.
Fruiting success 1993 (%)	43.1 ± 6.1	(34)	38.7 ± 6.8	(37)	N.S.
Fruit set 1993 (%)	8.4 ± 0.6	(41)	11.4 ± 0.6	(34)	***
Mean plant height (m)	1.9 ± 0.1	(40)	1.7 ± 0.1	(40)	*
Mean plant width (m)	3.3 ± 0.2	(40)	2.7 ± 0.1	(40)	**
Canopy area (m^2)	9.3 ± 1.0	(40)	5.8 ± 0.4	(40)	**
Biovolume (m^3)	12.8 ± 1.9	(40)	6.9 ± 0.6	(40)	**

Table 2. Anthesis rates (% florets opening per hour) for 8 inflorescences at the Stony Hill study site during February 1994.

Parameter	Day	Night	Signif.	Overall
No. florets opening per hr	3.90 ± 1.98	4.39 ± 1.40	N.S.	4.21 ± 1.10
% florets opening per hr	0.38 ± 0.19	0.48 ± 0.16	N.S.	0.44 ± 0.12
% florets opening per 12 hr	4.54 ± 2.23	5.81 ± 1.87	N.S.	5.32 ± 1.39

The mean total surface area of the *B. verticillata* infructescences tested was 13,926.1 mm^2, whereas the surface areas of closed and open follicles averaged 57.3 and 79.2 mm^2, respectively. Spatial constraints would therefore have been expected to limit percentage fruit set to 32.9% if all follicles were closed, and 24.2% if the follicles were to open, both values being considerably greater than the actual mean percentage fruit set of

12.7% (Table 4).

Table 3. Between site comparison of infructescence weight, length, total follicles and % fruit set, and seed weight for *B. verticillata* at Jimmy Newles and Stony Hill study sites. Values are means ± standard errors. Sample size is given in parentheses. Differences were either significant at $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$(***), or not significant (N.S.).

Parameter	Jimmy Newles	Stony Hill	Significance
Infructescence weight (g)	116.57 + 5.66 (15)	117.64 + 2.55 (150)	N.S.
Infructescence length (mm)	127.81 + 4.23 (15)	126.03 + 1.93 (150)	N.S.
Follicles per infructescence	128.67 + 9.87 (15)	127.72 + 2.77 (150)	N.S.
% fruit set	15.34 + 1.02 (15)	15.45 + 0.23 (150)	N.S.
Seed weight (mg)	14.0 + 2.5 (10)	16.0 + 0.3 (144)	N.S.

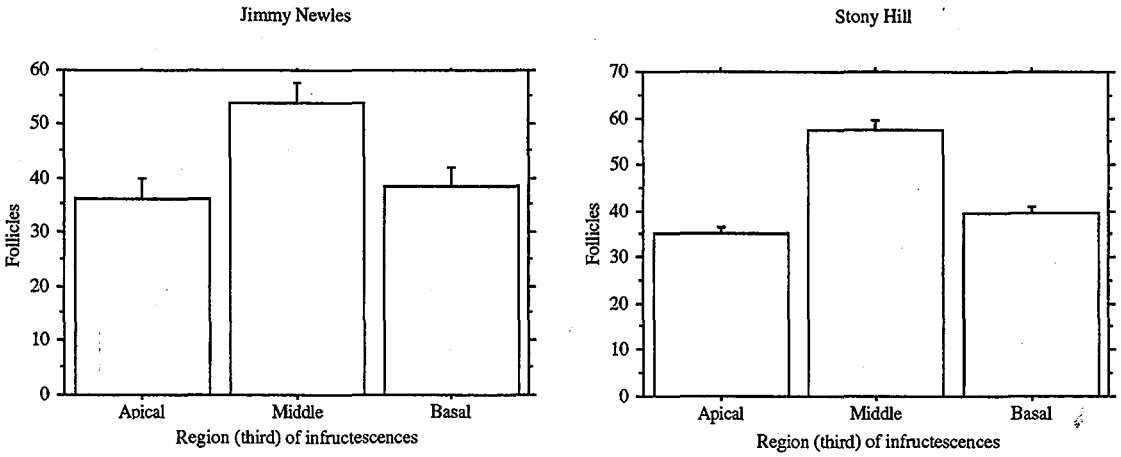

Figure 8. Distribution of follicles along the length of *Banksia verticillata* infructescences collected from the Jimmy Newles and Stony Hill study sites.

An average of 54.3 infructescences per plant were counted at the Stony Hill site during April 1994 (Table 1). Records kept by the Department of Conservation and Land Management (CALM) indicate that there are 105 plants in the Stony Hill population, and thus there would be approximately 5,700 seed-bearing infructescences at this site. CALM records also state that there are approximately 25 plants at the Jimmy Newles site, although our observations suggest that more than 80 plants are present, with approximately 4,340 seed-bearing infructescences.

Approximately 118 follicles per infructescence, each with the capacity to produce two seeds, were detected on material collected at the Stony Hill site by staff of the W.A. Herbarium in April 1994. More than 58% of the potential seed had been aborted, 17% were damaged by insect predation, 2.5% were diseased or decayed, 2% had been re-

leased prior to collection of the infructescences, and 21% were classified as firm (Table 5). The viability of three replicates of firm seed ranged from 88 to 96%, with a mean value of 92%, and was assessed in terms of the extent to which seed germinated on moist vermiculite at 15°C with 12 hours light. This suggests that approximately 19.6% of the total seed produced by the infructescences collected was viable (Table 5).

Table 4. Surface areas of *B. verticillata* infructescences, and associated open and closed follicles, collected from Torndirrup National Park.

Variable	Mean ± s.e.	(Number)
Infructescence surface area (mm2)	13,926.06 ± 792.90	(36)
Follicle surface area (closed) (mm2)	57.30 ± 1.99	(31)
Follicle surface area (open) (mm2)	79.22 ± 2.68	(29)
Actual % fruit set	12.69 ± 0.73	(36)
Maximum possible % fruit set (closed)	32.93 ± 1.30	(31)
Maximum possible % fruit set (open)	24.17 ± 0.91	(29)

Table 5. Fate of *B. verticillata* seed produced by 55 infructescences on 13 plants at the Stony Hill study site during April 1994.

Variable	Mean ± s.e.
No. of follicles	118.15 ± 10.00
% eaten	16.99 ± 2.99
% diseased/decayed	2.43 ± 1.24
% aborted	58.10 ± 2.02
% released	1.20 ± 0.41
% firm:	21.29 ± 3.01
viable	19.58 ± 2.77
non-viable	1.70 ± 0.24

Combining mean infructescence production per plant with the mean number of follicles present on each infructescence and the mean percentage of total seed produced that was viable, it is estimated that a total of 5,949 viable seeds was produced by the forty plants studied at the Stony Hill site during the 1993 season. Assuming that the percentage of viable seed is similar, the corresponding figure for the Jimmy Newles site would have been 11,975. Provided the plants studied are representative of the entire population at each site, and given that there are approximately 80 and 105 plants at the two sites, approximately 23,950 and 15,617 viable seeds would have been produced by the Jimmy Newles and Stony Hills populations during 1993. Most banksias retain the seed pro-

duced in their canopy until a disturbance such as fire causes the mass release of the seed (Cowling and Lamont, 1985a; 1985b; Cowling *et al.*; 1987; Lamont *et al.*, 1991). Since the two study populations had not been burnt for several years, their viable seed stores in 1993 were probably much greater than estimated above.

Pollen vectors

In total, 141 honeyeaters were captured at the two study sites over a four day period. Four nets, two 2.7 x 9 m and two 2.7 x 12 m, were opened between 0700 and 1000 each morning. The majority (135) of captures at both sites were New Holland Honeyeaters (*Phylidonyris novaehollandiae*), with the remainder being 5 Western Spinebills (*Acanthorhyncus superciliosis*) and 1 White Cheeked Honeyeater (*Phylidonyris nigra*) (Table 6). One hundred and one of the birds captured were netted at the Jimmy Newles site, where honeyeaters were noticeably more active.

Table 6. Numbers of honeyeaters captured at the Jimmy Newles and Stony Hill study sites during four 3-hour intervals between the 13th and 16th of February 1994.

Site	Day	New Holland Honeyeaters	Western Spinebills	White cheeked Honeyeaters	Total
Stony Hill	13-Feb	15	1	0	16
	14-Feb	22	2	0	24
Jimmy Newles	15-Feb	63	1	0	64
	16-Feb	35	1	1	37
Total	4	135	5	1	141

Based on their total head-bill lengths, which showed a bimodal distribution with lower and upper peaks separated at approximately 43.0 mm, 72 of the 135 New Holland Honeyeaters caught were identified as males and 58 as females (females smaller, males larger). More females than males were netted on the first day, but males were more abundant on subsequent days (Table 7). The age of New Holland Honeyeaters captured was determined on the basis of their plumage. Forty seven adult birds were captured, along with relatively large numbers of juveniles and immature birds (Table 8).

Seven types of pollen were found in smears taken from the heads and throats of honeyeaters captured at the two sites in February 1994, with pollen from *Adenanthos sericea* and *Banksia verticillata* being most common for all honeyeater species. Smears from all

Western Spinebills contained significant amounts of *A. sericea* pollen (135-1394 pollen grains in five 100x microscope fields of view). Small amounts of *B. verticillata, Eucalyptus preissiana, Myrtaceae* sp. and *Banksia grandis* pollen were also present in some smears. The one White Cheeked honeyeater sample examined contained 665 and 12 pollen grains, respectively, from *A. sericea* and *B. verticillata.*

Table 7. Male and female New Holland Honeyeaters (*Phylidonyris novaehollandiae*) captured at the Jimmy Newles and Stony Hill study site between the 13th-16th February 1994.

Site	Day	Males	Females	Unknown	Total
Stony Hill	13-Feb	6	9	0	15
	14-Feb	13	9	0	22
Jimmy Newles	15-Feb	34	25	4	63
	16-Feb	19	15	1	35
Total	4	72	58	5	135

Table 8. Juvenile, immature and adult New Holland Honeyeaters (*Phylidonyris novaehollandiae*) captured at the Jimmy Newles and Stony Hill study sites between the 13th-16th February 1994.

Site	Day	Juveniles	Juv<Adults	Adult	Unknown	Total
Stony Hill	13-Feb	1	6	8	0	15
	14-Feb	5	6	11	0	22
Jimmy Newles	15-Feb	22	15	22	4	63
	16-Feb	14	15	6	0	35
Total	4	42	42	47	4	135

A. sericea was the most abundant pollen present in smears taken from New Holland Honeyeaters except for those captured on 15th February, when slightly more *B. verticillata* pollen was detected (Figure 9). *B. verticillata* was the second most abundant pollen type over the four days of sampling, followed by *E. preissiana* and *E. calophylla.*

All smears contained significant amounts of *A. sericea* pollen (>10 grains per five fields of view), and 79.2 % of the smears taken from New Holland honeyeaters had significant quantities of *B. verticillata* pollen (Figure 10). Other pollen types were detected much

less frequently (*E. preissiana*, *E. calophylla*, *B. grandis*, *Myrtaceae* sp. and *Dryandra* sp. in 7.2, 4.8, 3.2, 0.8 and 0.8%, respectively, of the smears).

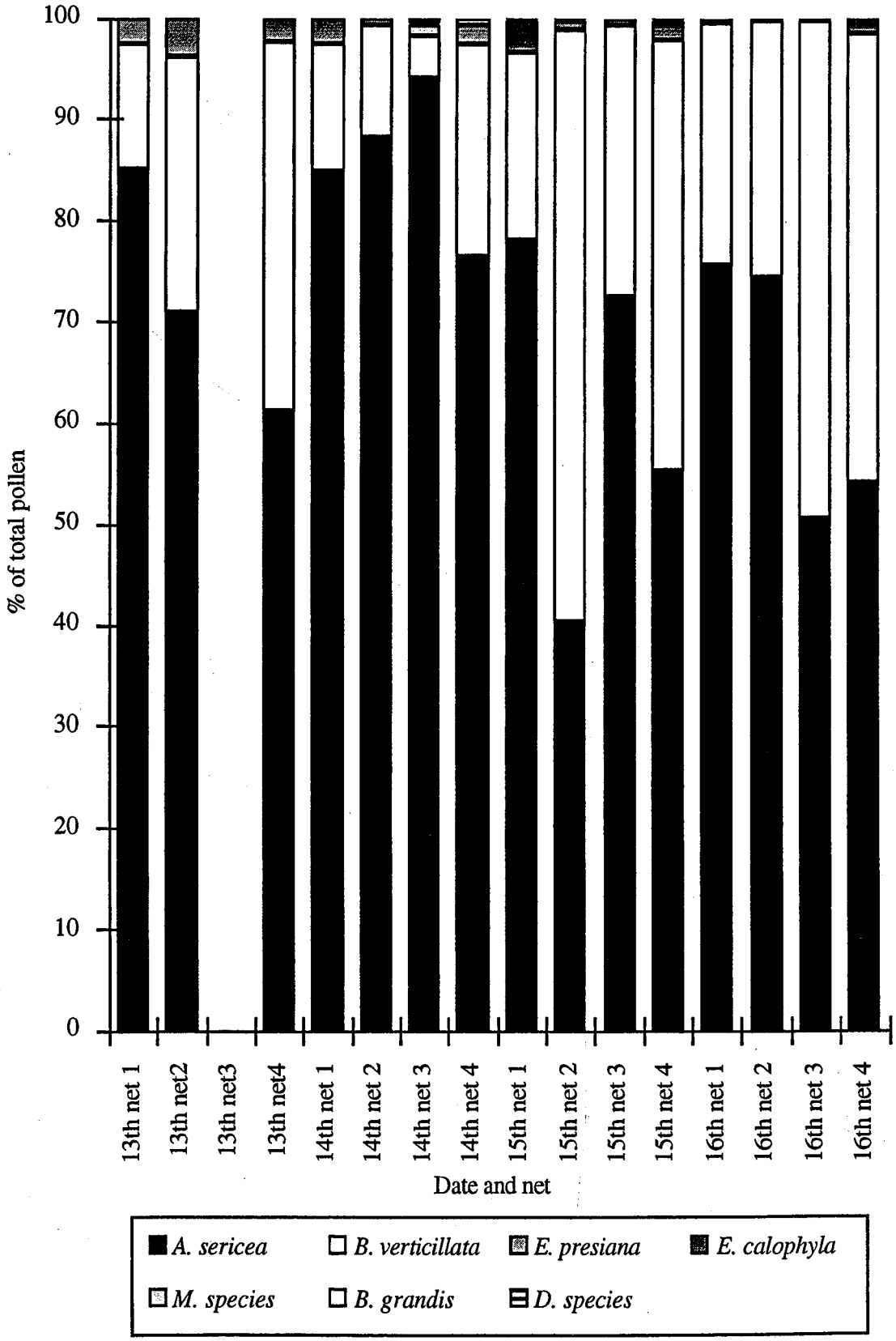

Figure 9. Pollen present in smears taken from New Holland Honeyeaters captured between 13th-16th February 1994.

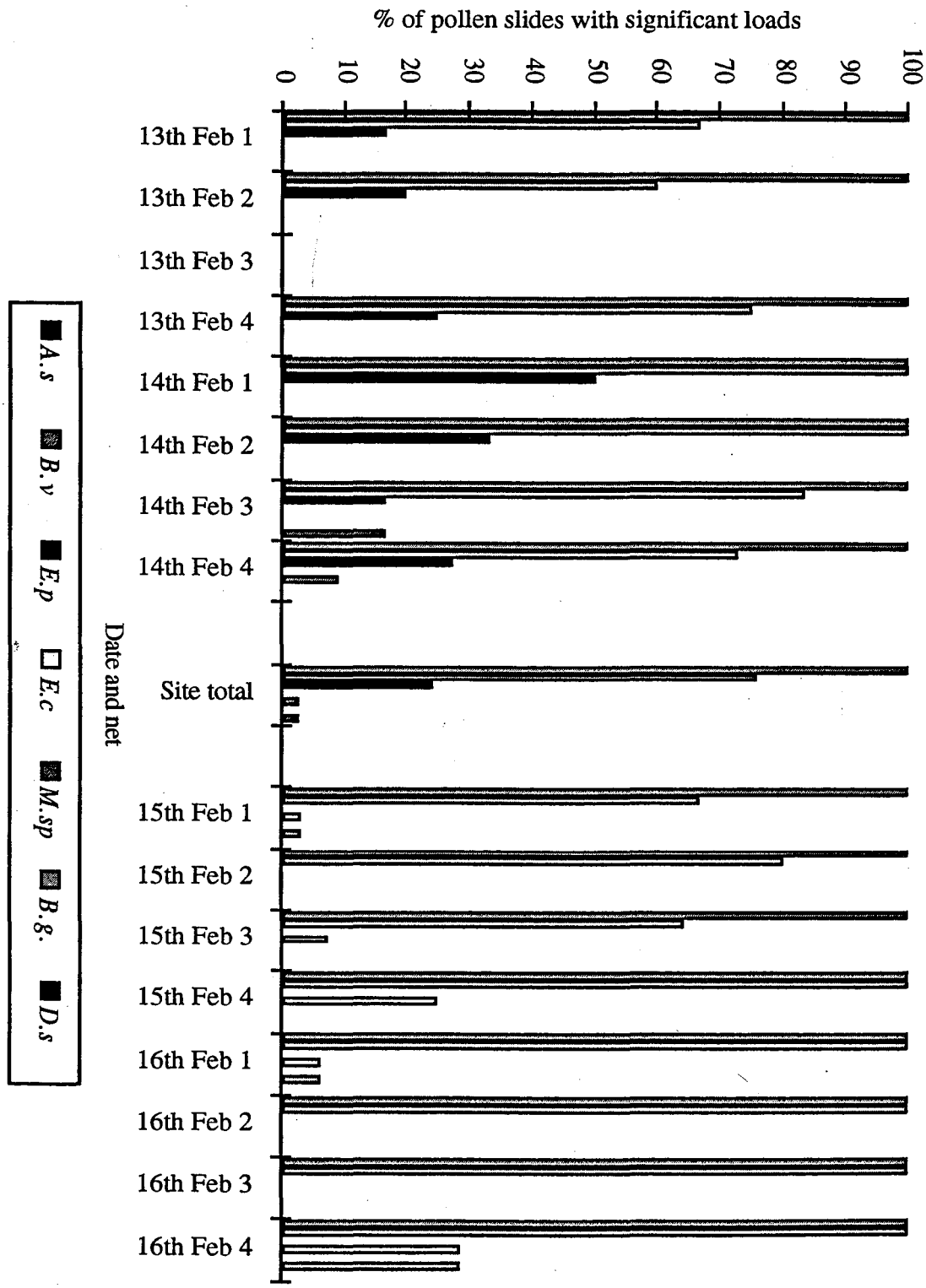

Figure 10. Smears taken from New Holland Honeyeaters that carried significant loads of pollen

One Bush Rat (*Rattus fuscipes*) was captured at the Stony Hill site. Seven Mice (*Mus musculus*) were caught at the Jimmy Newles site over three nights, with one trap capturing an animal every night (Table 9). No Honey Possums (*Tarsipes rostratus*) were captured at either site, although they are common in other areas of the Park (Smith, 1990;

1991).

Table 9. Mammals captured at the Stony Hill and Jimmy Newles study sites between the 13th-17th February 1994.

Site	Day	Trap	Species	Weight (g)
Stony Hill	13-Feb	A	*Rattus fuscipes*	-
	14-Feb	-	-	-
Jimmy Newles	15-Feb	B	*Mus musculus*	15.0
	16-Feb	A	*Mus musculus*	7.5
	16-Feb	B	*Mus musculus*	15.5
	17-Feb	A	*Mus musculus*	6.0
	17-Feb	B	*Mus musculus*	10.5
	17-Feb	C	*Mus musculus*	12.0
	17-Feb	H	*Mus musculus*	14.5

Significant amounts of *B. verticillata* pollen were present in all smears, although larger loads from *A. sericea* were present for six of the eight animals caught. Small amounts of *Banksia grandis* and *Eucalyptus calophylla* pollen were also present (Table 10).

Table 10. Pollen carried on mammals captured at the Jimmy Newles and Stony Hill study sites between 13th-17th February 1994.

Site	Date	Trap	Species	*B. verticillata*	*B. grandis*	*Eucalyptus sp.*	*A. sericea*
Stony Hill	13-Feb	A	*Ratus fiscipes*	19.40 (26)	3.73 (5)	6.72 (9)	70.15 (94)
Jimmy Newles	15-Feb	B	*Mus musculus*	59.64 (99)	3.61 (6)	3.61 (6)	33.13 (55)
Jimmy Newles	16-Feb	A	*Mus musculus*	20.88 (161)	0.26 (2)	0.13 (1)	78.73 (607)
Jimmy Newles	16-Feb	B	*Mus musculus*	10.29 (78)	1.19 (9)	0.40 (3)	88.13 (668)
Jimmy Newles	17-Feb	A	*Mus musculus*	63.29 (319)	1.59 (8)	1.19 (6)	33.93 (171)
Jimmy Newles	17-Feb	B	*Mus musculus*	13.56 (16)	0.00 (0)	8.47 (10)	77.97 (92)
Jimmy Newles	17-Feb	C	*Mus musculus*	35.24 (80)	0.88 (2)	2.20 (5)	61.67 (140)
Jimmy Newles	17-Feb	H	*Mus musculus*	41.43 (29)	1.43 (1)	4.29 (3)	52.86 (37)

Pollinator movements

The activity of honeyeaters was monitored for approximately 200 minutes at each of the study sites. Only New Holland Honeyeaters (*P. novaehollandiae*) were seen foraging at

B. verticillata inflorescences, although Red Wattlebirds (*Anthochaera carunculata*) were present at both sites. Foraging was observed at 57 *B. verticillata* inflorescences that were at various stages of development. Partly-open inflorescences, particularly those with up to 2/3 of their flowers open, were visited more often (Table 11) and for longer periods (Table 12) than either buds or fully-open inflorescences.

Table 11. Frequency of foraging visits by New Holland Honeyeaters (*Phylidonyris novaehollandiae*) to *Banksia verticillata* inflorescences at Jimmy Newles and Stony Hill study sites.

Inflorescence type	Site				Total	
	Jimmy Newles		Stony Hill			
	%	No.	%	No.	%	No.
Bud	14.29	(5)	4.55	(1)	10.53	(6)
Bud-1/3 open	42.86	(15)	22.73	(5)	35.09	(20)
1/3-2/3 open	5.71	(2)	27.27	(6)	14.04	(8)
2/3-fully open	2.86	(1)	9.09	(2)	5.26	(3)
Fully open	20.00	(7)	18.18	(4)	19.30	(11)
Unknown	14.29	(5)	18.18	(4)	15.79	(9)
Total	100	(35)	100	(22)	100	(57)

Table 12. Foraging by New Holland Honeyeaters (*Phylidonyris novaehollandiae*) at *Banksia verticillata* inflorescences at various stages of development. sec = total time spent foraging, Range = range of times spent during individual visits, No. = number of visits observed, Sec/visit = mean duration of individual visits.

Inflorescence type	Site											
	Jimmy Newles				Stony Hill				Both			
	Sec.	Range	No.	Sec/visit	Sec.	Range	No.	Sec/visit	Sec.	Range	No.	Sec/visit
Bud	19	3-5	5	3.8	5	5	1	5.0	24	3-5	6	4.0
Bud-1/3 open	410	5-90	16	25.6	30	5-25	2	15.0	440	5-90	18	24.4
1/3-2/3 open	50	20-30	2	25.0	7	7	1	7.0	57	7-30	3	19.0
2/3-fully open	-	-	0	-	18	18	1	18.0	18	18	1	18.0
Fully open	107	5-30	7	15.3	-	-	0	-	107	5-30	7	15.3
Unknown	30	30	1	30.0	-	-	0	-	30	30	1	30.0

Foraging New Holland Honeyeaters either perched on top of an inflorescence, leaning over the side to probe for nectar, or foraged from the side of the inflorescence while standing on an adjacent stem. Several birds were observed employing both modes of foraging, probing all over inflorescences rather than restricting their foraging to a particular regions. On several occasions, more than one New Holland was observed feeding from the same inflorescence. They were also seen moving between a number of

inflorescences on individual trees, and between inflorescences on adjacent trees. Individual birds were observed moving distances of up to 15 m between plants during foraging bouts (Figures 7 & 8). Nevertheless, the majority of movements between successive inflorescences were within plants or between neighbouring plants.

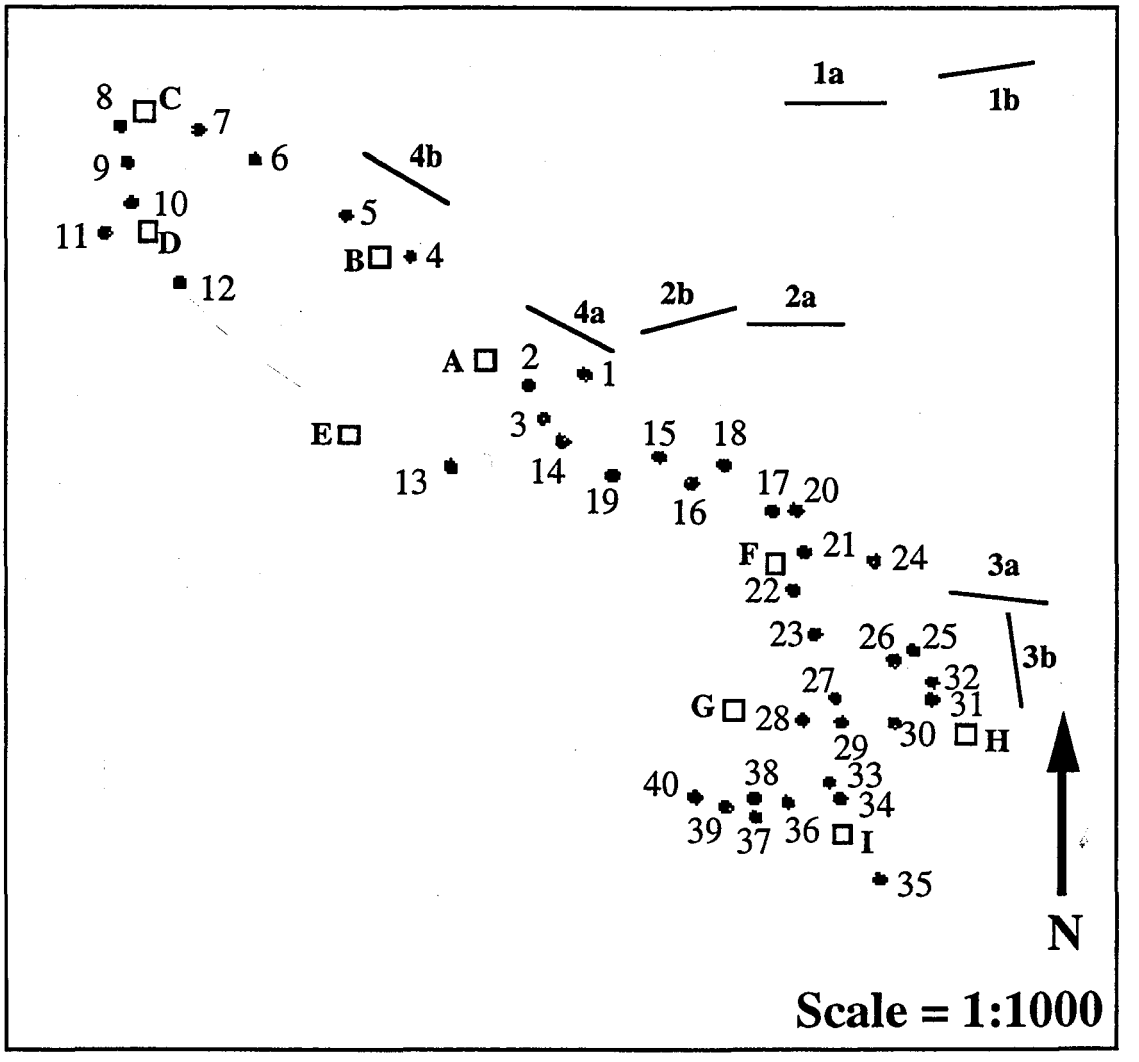

Figure 7. Location of *B. verticillata* plants (• 1-40), mist nets (____ 1a-4b) and mammal traps (□ A-I) within the Stony Hill study site.

On numerous occasions, New Holland Honeyeaters were observed perching in *B. verticillata* plants, or flying within or out of each site. They also congregated in stands of mallee (*Eucalyptus preissiana* and *E. calophylla*) at both sites. Failure to recapture banded birds, and the presence in facial smears of large quantities of pollen from a plant species (*A. sericea)* that did not occur at either site, suggests that individual birds were transients rather than residents at the study sites.

Opportunistic invertebrate foraging observations were made when conducting other work

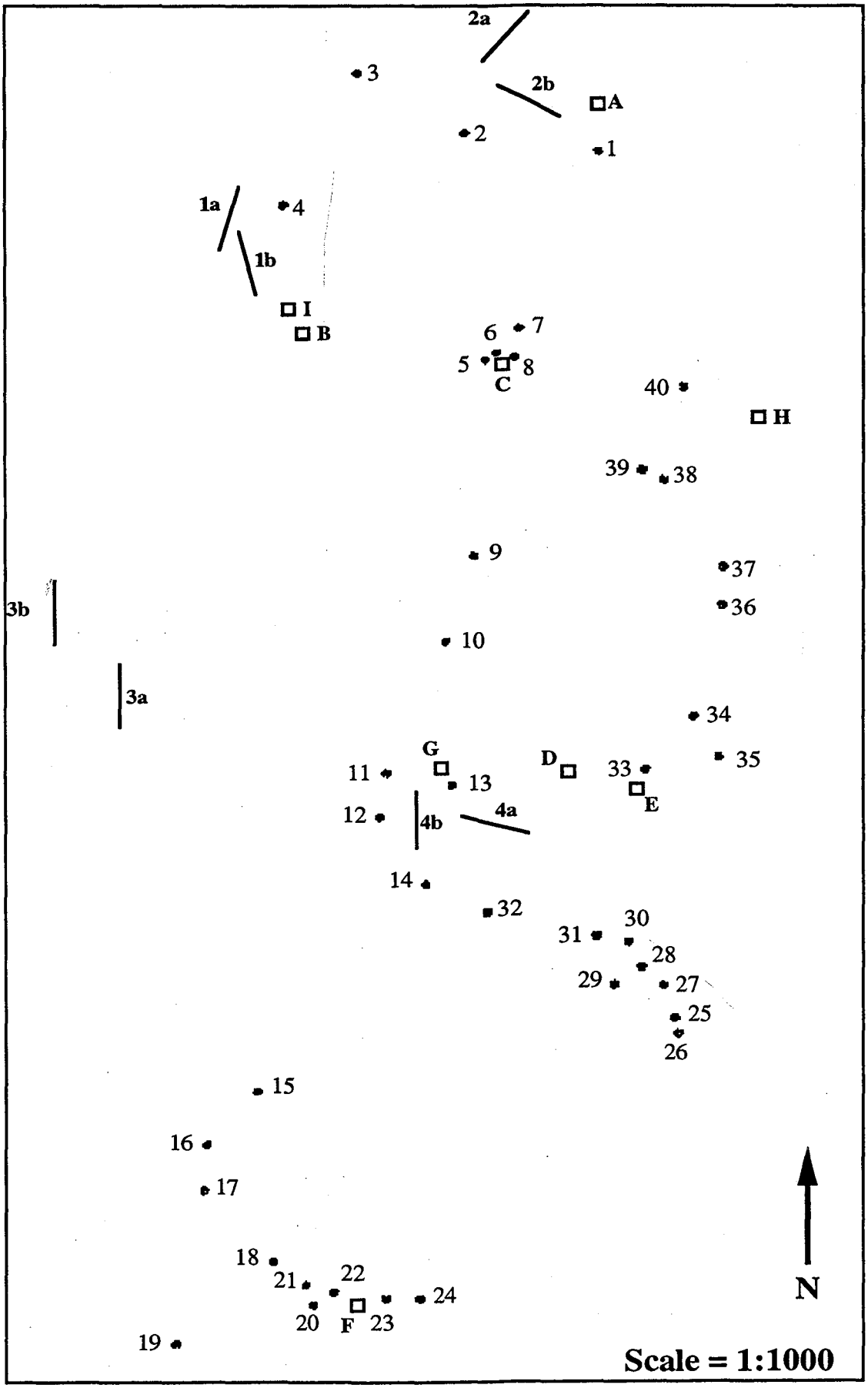

Figure 8. Location of *B. verticillata* plants (• 1-40), mist nets (____ 1a-4b) and mammal traps (□ A-I) within the Jimmy Newles study site.

at both study sites (Table 13).

Table 13. Activity of invertebrates observed visiting *Banksia verticillata* inflorescences at the Jimmy Newles and Stony Hill study sites between 13th-17th February 1994.

Date	Time	Site	Species	Activity
12-Feb	1530	Stony Hill	8 x Apis mellifera	Collecting nectar
			1 x Apis mellifera	Collecting Pollen
			1 x Native bee species	Collecting nectar
			~20 Black ants	Collecting nectar?
	1830	Stony Hill	2 x Apis mellifera	Collecting nectar
			1 x Bull ant	Collecting nectar?
13-Feb	750	Stony Hill	1 x Apis mellifera	Collecting nectar?
			1 x Apis mellifera	Collecting Pollen
			2 x Apis mellifera	Collecting nectar?
			Lots of Black ants	Collecting nectar?
	1550	Stony Hill	33 x Black ants	Collecting nectar?
			1 x Bull ant	Collecting nectar?
14-Feb	810	Stony Hill	1 X Apis mellifera	Collecting nectar
			38 x Black ants	Collecting nectar?
			Lots of Black ants	-
	1500	Stony Hill	2 x Apis mellifera	Collecting nectar?
			1 x Apis mellifera	Collecting nectar?
			~7 Black ants	Collecting nectar?
			1 x Bull ant	Collecting nectar?
17-Feb	810	Stony Hill	2 x Black ants	-
	1100	Jimmy Newles	5 x Black ants	Collecting nectar?
			43 x Black ants	Collecting nectar?
			26 x Black ants	Collecting nectar?
			12 x Black ants	Collecting nectar?
			15 x Black ants	Collecting nectar?
			35 x Black ants	Collecting nectar?

Honeybees (*Apis mellifera*) were observed collecting nectar and pollen at *B. verticillata* inflorescences. Foraging for nectar involved the bees squeezing down between the tight rows of styles, and sometimes contacting the pollen presenters when arriving at, and leaving the inflorescence. Animals tended to move around within the rows of stigmas, and one was seen moving between inflorescences on the same plant that were approximately 80 cm apart. A Native Bee (Anthophoridae, possibly *Amegilla* sp.) and a large

red/black Bull Ant (Formicidae, possibly *Mymecia* sp.) were observed collecting nectar. Numerous medium-sized black ants (possibly the Stick Nest Ant *Iridomyrmex conifer*) were also seen on many inflorescences, particularly those at the very late bud or early opening stages of inflorescence development.

DISCUSSION

B. verticillata plants at the Jimmy Newles and Stony Hill sites flowered between January and April in 1992, 1993 and 1994, averaging 17.1 inflorescences and 9.1 infructescences per plant, respectively, at the two locations. Nevertheless, inflorescence and infructescence production varied considerably between plants, sites and years, as reported for species such as *B. brownii, B. grandis, B. spinulosa, B. paludosa, B. ericifolia,* and *B. serrata* (Abbot, 1985; McFarland, 1985; Copland and Whelan, 1989; Carthew, 1993; Collins *et al.*, 1993).

Seasonal variations in inflorescence production are thought to be caused mainly by changes in factors such as water and nutrient availability, rainfall, sunlight and temperature prior to the onset of flowering (Rathcke and Lacey, 1985). At least some of these factors may also be responsible for differences between plants at particular sites. Positive linear relationships existed between inflorescence production and plant biovolume at the Jimmy Newles and Stony Hill locations during each year of the present study, with plants at the Jimmy Newles site generally larger than those at Stony Hill. A similar linear relationship between tree size and inflorescence production has been demonstrated for other species of *Banksia*, with increased reproductive effort by larger plants thought to be a consequence of superior access to nutrient, water and photosynthetic resources (Collins *et al.*, 1993, 1994; Day, 1993). This explanation is supported by the findings of Lamont *et al.* (1994a), who found that roadside *B. hookeriana* plants were much larger and fecund than plants without access to enhanced water and nutrient resources. Genetic factors may also effect the productivity of individual plants (Carthew, 1993).

Fruiting success can vary considerably between species, with the percentage of inflorescences that developed follicles for 16 species of *Banksia* prior to the present study reported as ranging from 5-97% (Collins and Rebelo, 1987). Lamont *et al.* (1994b) have also demonstrated fruiting success for *B. menziesii* ranging from 33.7- 82.8% at a number of locations during a single year. Fruiting successes for *B. verticillata* at the Jimmy Newles and Stony Hill sites during the 1993 season were 43.1 and 38.7%, respectively. These values are slightly lower than those recorded for the closely-related *B. brownii* during the same and previous years at two other sites near Albany (Collins *et al.*, 1993, 1994; Day, 1993).

Many hermaphroditic members of the family Proteaceae have low levels of fruit set, with values for 15 species of *Banksia* other than *B. verticillata* ranging from 0.1-7.2% (Collins and Rebelo, 1987). Levels of 8.4 and 10.9% recorded for the Jimmy Newles and Stony Hill populations may therefore be considered relatively high, although still well below values that theoretically could be achieved.

Several hypotheses have been proposed to account for low levels of fruit set amongst the Proteaceae. Pollen availability or quality may be a limiting factor (Johnson and Briggs, 1975; Whelan and Goldingay, 1986; Collins and Rebelo, 1987). A deficiency of mineral elements in the soil (Bawa and Webb, 1984; Lamont *et al.*, 1985; Paton and Turner, 1985; Collins and Rebelo, 1987), and/or predation or disease of flowers and fruits (Scott, 1980; Abbott, 1985; Paton and Turner, 1985; Vaughton, 1990) could also be influential. Wallace and O'Dowd (1989) found that fruit set by *B. spinulosa* increased when both nutrients and insecticide were added to plants, thus indicating that fruit set can be influenced by more than one factor .

New Holland Honeyeaters were active at both sites during the present study, and appeared to be the main visitors to *B. verticillata* inflorescences. They carried significant amounts of *B. verticillata* and other pollen, but because of the heterospecific nature of their pollen loads it is not possible to say whether pollen type and quality adversely affected fruit set.

The Proteaceae typically grow on nutrient-deficient soils (Lamont *et al.*, 1985), with low nutrient availability likely to play a crucial role in the regulation of maternal reproductive investment. In general, large seeds with nutrient reserves 8-500 times richer in N, P and K than other plant tissues are produced (Kuo *et al.*, 1982). These nutrient reserves are probably the outcome of selection favouring seedling establishment in low nutrient environments (Fenner, 1986). If seed size and quality are stable characteristics of the Proteaceae, species under nutrient stress would be expected to give priority to seed size rather than the absolute number of seeds (Stock *et al.*, 1989). Since there was little variation in the weight of seeds collected from both *B. verticillata* study sites, competition for nutrients could have been largely responsible for the limited seed set recorded in this study.

Nutrient limitation of seed set in banksias has been clearly demonstrated by Stock *et al.* (1989). When 50% of the pollinated inflorescences on individual plants of *B. laricina* were removed, final fruit set on the remaining inflorescences was not effected, thus suggesting that an endogenous factor such as resources limited seed production. This proposition was further supported by the fact that seed production increased after nutri-

ents were added to the soil.

The soils within the Albany area are reported to be relatively infertile, with the sands surrounding granite outcrops in the Torndirrup Vegetation System described as extremely leached with low pH, salts and low concentrations of plant nutrients (Beard, 1979; McArthur, 1991). A significant positive linear relationship between fruit set and biovolume was found for *B. verticillata* at the Stony Hill site. This evidence supports the suggestion that nutrient availability limited fruit set, as the larger plants would presumably have had access to greater water and nutrient resources via their more extensive root systems. Nevertheless, a similar relationship was not evident at the Jimmy Newles site. Despite the presence of larger plants at Jimmy Newles, fruit set at that location was significantly lower than at Stony Hill. It seems likely, therefore, that, the reproductive success of *B. verticillata* at these two sites is influenced by a combination of several factors.

Inflorescence and follicle damage by predators has been found to influence seed set in species such as *B. ericifolia* (Zammit and Hood, 1986), *B. tricuspis* (Lamont and van Leeuwen, 1988) and *B. spinulosa* var. *neoanglica* (Vaughton, 1990). Infructescences examined during the present study had some seeds that showed signs of insect damage, and numerous weevils were found on *B. verticillata* infructescences collected from a nearby site within the Torndirrup National Park. However, little direct evidence of predation on developing inflorescences was seen at either study site.

Spatial restraints limit the number of follicles that can be fitted on to a *Banksia* infructescence (Lewis and Bell, 1981; Abbott, 1985; Carthew, 1993), so that 100% fruit set is impossible for virtually all species. Infructescence and follicle surface area measurements made during the present study have allowed us to predict that the maximum fruit set which could be achieved by *B. verticillata* is approximately 33% when follicles are closed, and 24% if follicles are open. Maximum levels of fruit set estimated by Lewis and Bell (1981) for four other species of *Banksia* ranged from 1.4-8.9%, although actual fruit set values were significantly less than this. Abbot (1985) has also indicated that the maximum fruit set possible for *B. grandis* is 5.3%. Since actual fruit set is invariably less than theoretical maxima imposed by spatial constraints, other factors must be at least partly responsible for low fruit and seed set.

The production of numerous inflorescences, many of which remain barren, may have several adaptive advantages. For instance, Stephenson (1981) has suggested that they may act as pollinator attractants, thus ensuring that pollinators actually visit individual

plants, or act as pollen donors to increase male fitness for the species. Excess flower and inflorescence production may allow for selective abortion of inferior zygotes. Abbott (1985) and Stock *et al.* (1989) have also suggested that excess production of buds and inflorescences enables plants to adjust follicle and infructescence production in accordance with the availability of nutrients and/or the abundance of effective pollinators. Alternatively, excess inflorescence production may be a means of minimising food availability to potential plant predators (Wallace and O'Dowd, 1988; Ayre and Whelan, 1989).

Since *B. verticillata* regenerates only from seed, it is important that a seed bank capable of generating seedling recruitment that will at least maintain population size and vigour is established (Pate *et al.*, 1990). Mean total viable seed production by *B. verticillata* during 1993 at the Jimmy Newles and Stony Hill sites has been estimated as approximately 23, 920 and 15, 645, respectively. These values suggest that both populations should be able to re-establish themselves after fire, although the capacity for seedlings to become established and survive under natural conditions is not yet known. Studies involving other banksias in the Albany region have shown that these parameters are influenced by various environmental factors. For example, seedling survival for the rare species *B. goodii* was increased when protected from herbivores by wire mesh exclosures (Lamont *et al.*, 1993a). In the case of *B. brownii,* many seeds released after fire or dispersed during transplant trials are removed by granivores before they germinate or are grazed by herbivores (Galea and Lamont, 1993).

Data obtained in this study have shown that significantly more follicles are found within the central third of most infructescences than in the apical or basal thirds. Non-random follicle distribution of this type has also been recorded in *B. spinulosa* var *neoanglica* and *B. brownii* (Vaughton, 1988; 1993; Day, 1993; Collins *et al.*, 1994). This pattern may be a consequence of several factors. For instance, honeyeaters preferentially visit inflorescences which have some but not all flowers open, and tend to restrict their foraging to a section around the "advancing front" of opening flowers (Collins and Spice, 1986; Day, 1993; Collins *et al.,* 1994). Flowers in the middle third of an inflorescence are therefore more likely to be visited and pollinated (McFarland, 1985).

Vaughton (1993) has shown that experimental manipulation of flower distribution in inflorescences of *B. spinulosa* var. *neoanglica* affected fruit set for different portions of the resultant infructescences. Differential resource allocation due to inter-ovary competition may contribute to a reduction in the number of follicles present in the apical portion of inflorescences. Day (1993) and Collins *et al.* (ms) also showed that the foraging patterns of honeyeaters visiting *B. brownii* were likely to contribute to the increased

number of follicles in the middle portions of unshielded infructescences, although a similar pattern was evident among infructescences from which birds had been excluded. A combination of resource limitation in the apical portion, and pollinator limitation in the basal portion of infructescences may therefore contribute to the pattern of follicle distribution seen in both *B. brownii* and *B. verticillata* (Day, 1993; Collins *et al.*, 1994).

The number of flowers opening each day governs the amount of pollen available for dispersal and the number of stigmata that can be pollinated (Ramsey, 1988a). In turn, the time of day at which opening occurs influences the capacity of nocturnal and diurnal animals to act as pollen vectors (Carpenter, 1978; Hopper, 1980; Hopper and Burbidge, 1982; McFarland, 1985; Paton and Turner, 1985; Collins and Spice, 1986; Ramsey, 1988a). Anthesis rates can be increased in some species as a result of animal visitors brushing against previously unopened flowers (McFarland, 1985; Ramsey, 1988a). Day (1993) found that increased rates for *B. brownii* coincided with increased pollen removal, and suggested that floral opening in response to mechanical stimulus was at least partly facilitated by increased water turgor following rainfall. As *B. verticillata* flowers during late summer and early autumn, reduced water availability at these times may be responsible for the generally poor response to mechanical stimulus that is characteristic of flowers for this species.

Flowers present on *B. verticillata* inflorescences examined in this study opened at a mean rate of 10.6 % per 24 hours, with no significant differences evident between rates for day and night. On this basis, we have estimated that approximately 9.5 days are needed if all flowers on the inflorescences are to open, although our observations were made over a 5-day period and the majority of inflorescences examined were in the early stages of opening. McFarland (1985) has shown that the rate at which styles of other banksias straighten increases as the age of flowering inflorescences increases. If this is also true of *B. verticillata*, the normal time required for its inflorescences to open is probably less than the estimate indicated above. This suggestion is supported by the fact that final 98.5% of the florets present on one inflorescence examined during this study opened over a period of five days.

Ramsey (1988a) has classified banksias into two groups, according to the rate at which their florets open and the duration of flowering. The first group has opening rates of 96-360 florets per 24 h and reproductive lifespans of 4-12 days, whereas the second has rates of 12-24 per 24 h and flowering periods of 23-34 days. *B. verticillata* resembles *B. brownii* (Day, 1993; Collins *et al.*, 1994) in that it fits into the first of these two categories. Inflorescences with short flowering periods have less time than those with extended

periods during which pollen can be removed or deposited. It is to be expected, therefore, that plants with such inflorescences would have evolved attributes designed to attract pollinators. Both *B. verticillata* and *B. brownii* flower profusely, although it is not known whether the nectar rewards differ significantly from those offered by banksias with longer flowering periods.

Honeyeaters captured during this study carried heterospecific pollen loads, thus indicating that foraging was not restricted to a single plant species. Nevertheless, pollen smear evidence suggests that the birds exercised a preference for *Adenanthos sericeae* and *B. verticillata*. New Holland Honeyeaters (*Phylidonyris novaehollandiae*), the most common honeyeaters at both sites, were the only ones actually observed visiting *B. verticillata* inflorescences, and were presumably the major pollinators of this species. They preferentially visited *B. verticillata* inflorescences at the bud to partly open stages of development, a phenomenon that has also been documented for *B. prionotes* (Collins and Spice, 1986), *B. menziesii*, (Ramsey, 1988a) and *B. brownii* (Day, 1993; Collins *et al.,* 1994). Nevertheless, birds visiting partly-open inflorescence of *B. verticillata* did not restrict their probing for nectar to the "advancing front" of opening flowers as is the case with the other species mentioned above. *B. verticillata* is essentially basipetalous, but patches of florets sometimes open ahead of the "front", therefore offering nectar rewards that induce birds to forage at these patches.

Most honeyeater foraging movements between inflorescences observed during this study occurred on the same rather than between different plants. Nevertheless, honeyeaters and other nectarivores are known to be capable of transferring pollen analogues such as fluorescent powders between more than 12 successive flowers or inflorescences of plants such as *Ipomopsis aggregata, Dryandra sessilis* and *B. prionotes* (Waser and Price, 1982; 1984; Collins *et al.*, 1984; Grey, 1985; Collins and Spice, 1986). If natural pollen is transferred in a similar manner, *B. verticillata* inflorescences visited during each foraging bout should receive both self and outcross pollen (Collins and Rebelo, 1987).

Movements between inflorescence of up to approximately 15 m were observed, during this study, although other studies have shown that honeyeaters may move 20-30 m between successive plants when foraging (Collins, 1983; Collins and Newland; 1986), and even greater distances when visiting a succession of plants (Collins and Briffa, 1982; Pyke, 1983). Lack of recaptures within and between sites, and the observation of New Holland Honeyeaters moving into and out of the Jimmy Newles and Stony Hill study sites, infers that honeyeaters were quite mobile and not restricted to a site. Pollen smear counts support this view, as many smears contained pollen from species that did not

occur within individual sites but were common in adjacent areas. Bird-mediated *B. verticillata* pollen transfer between neighbouring populations therefore seems likely, although the occurrence of heterospecific pollen on the bodies of pollen vectors may reduce the effectiveness of pollination.

Rattus fuscipes and *Mus musculus* captured during this study carried *B. verticillata* pollen, although neither species appeared to be present in large numbers. *R. fuscipes* has been identified as an effective pollinator of banksias in Eastern Australia (Turner, 1982; Whelan and Goldingay, 1986; Goldingay *et al.*, 1987; Goldingay *et al.*, 1991; Carthew, 1993), but it seems unlikely that the same is true at the sites near Albany. Honey Possums (*Tarsipes rostratus*) were not captured during this study, although the species is a very important pollinator for several other *Banksia* species that occur near the south coast of Western Australia (Day, 1993; Collins *et al.*, 1994).

Opportunistic observations of invertebrates have indicated that honeybees (*Apis mellifera*), native bees, and several species of ant visit *B. verticillata* inflorescences. Nevertheless, most of these animals were observed collecting nectar while making minimal contact with the pollen presenters of *B. verticillata*. Honeybees were the only species observed collecting pollen. Several studies have examined the effectiveness of honeybees as pollinators of banksias (Whelan and Burbidge, 1980; Paton and Turner, 1985; Collins and Spice, 1986; Ramsey, 1988b; Vaughton, 1992). As the distance between successive inflorescences visited by bees tends to be small, their effectiveness as pollinators seems to vary with the level of self-incompatibility and protandry of a species (Paton, 1986; Carthew, 1993). *B. verticillata* flowers during the Summer/ Autumn period, although the cool weather conditions which often occur at coastal sites would reduce honeybee activity.

CONCLUSIONS AND RECOMMENDATIONS

Protection of pollinators

Honeyeaters are the major pollinators of *B. verticillata* at the two study sites, and would seem to be necessary for the maintenance of both populations. Of the honeyeaters present, New Holland Honeyeaters appeared to be most important, carrying high *B. verticillata* pollen loads and making frequent visits to inflorescences of this species. Honeyeaters require a year-round source of nectar if they are to survive in a given area. It is therefore important that the diversity and vitality of ecosystems which incorporate rare species such as *B. verticillata* be maintained. Ecosystem fragmentation commonly reduces pollinator abundance and diversity, and thus pollination and seed output may be reduced

(Rathcke and Jules, 1993). Both *B. verticillata* populations examined in this study were within the 3,800 hectare Torndirrup National Park (Smith, 1990), and at least 13 of the known populations occur within nature reserves (Hopper *et al.*, 1990). Protection afforded in this manner, plus the mobility of most honeyeaters, should ensure the continued survival of pollinators that are needed by *B. verticillata.*

Genetic characteristics of populations

The distribution of genetic variation in rare plant species is a key consideration when developing conservation strategies (Falk, 1992). As an endemic species with a restricted distribution, *B. verticillata* populations would be expected to have low genetic diversity (Hamrick and Godt, 1989). Maintenance of genetic variability is considered essential for the long term survival of a species (Lande and Barrowclough, 1987), and therefore maintenance of populations size is important. For example, small populations of *B. goodii* were found to produce higher proportions of infertile infructescences and less seed than did larger populations. The reduction in viability, or Allee effect, is thought to result from matings between related neighbours that result in poor-quality pollen (Lamont *et al.*, 1993b). The present study has identified the major pollen vectors of *B. verticillata*, but pollination is only the first step in the recruitment of seedlings to maintain plant populations. An understanding of the breeding systems and genetic structures of populations is required if appropriate conservation strategies are to be developed.

Seed banks, seedling recruitment and survival

Examination of infructescence and seed production has indicated that *B. verticillata* plants are successfully producing viable seed that is required to re-establish populations of this seeder-species after fire. However, studies of other banksias have shown that environmental factors such as the presence of granivores and herbivores can reduce the likelihood of seedling germination and survival under natural conditions (Galea and Lamont, 1993; Lamont *et al.*, 1993). A greater understanding of seed dispersal and seedling survival under field conditions would aid the development of management plans for species such as *B. verticillata.* Preliminary investigations are currently being undertaken by the Banksia Research Group, within the School of Environmental Biology at Curtin University

Protection from *Phytophthora cinnamomi*

B. verticillata is rated as having a medium level of susceptibility to the fungal infection *Phytophthora cinnamomi* Rands, with approximately 50% of seedlings killed within

395 days of inoculation. *B. verticillata* was the 27th most susceptible banksia out of 49 species tested by McCredie *et al.* (1985).

A number of *B. verticillata* populations are currently affected by *P. cinnamomi*, either directly or indirectly through the effect of the pathogen on nearby plants. Because proteaceous flora make up a large proportion of the environment in which *B. verticillata* occurs, *P. cinnamomi* infection would lead to loss of species, and alteration of community structure and composition (Wills, 1993). Vegetation changes can effect associated animal groups (pollinators, grazers and soil biota), and has been shown to impact upon honeyeater communities (Recher and Serventy, 1991). Thus it is important that *B. verticillata* populations which are currently free from *P. cinnamomi* infection should be protected. The use of phosphonate to control the disease in areas that are already infected (Komorek *et al.*, 1994), or transplant trials, might also be considered.

ACKNOWLEDGEMENTS

The Australian Nature Conservation Agency, via the Department of Conservation and Land Management, provided financial support for this project. We would like to thank the latter for permission to work with *B. verticillata* populations within the Torndirrup National Park, Anne Cochrane (W.A. Herbarium) for access to *B. verticillata* infructescences, seed and germination results, and Leonie Monks (Curtin University) for access to additional *B. verticillata* infructescences. Shapelle McNee and Denise Day provided valuable field assistance.

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