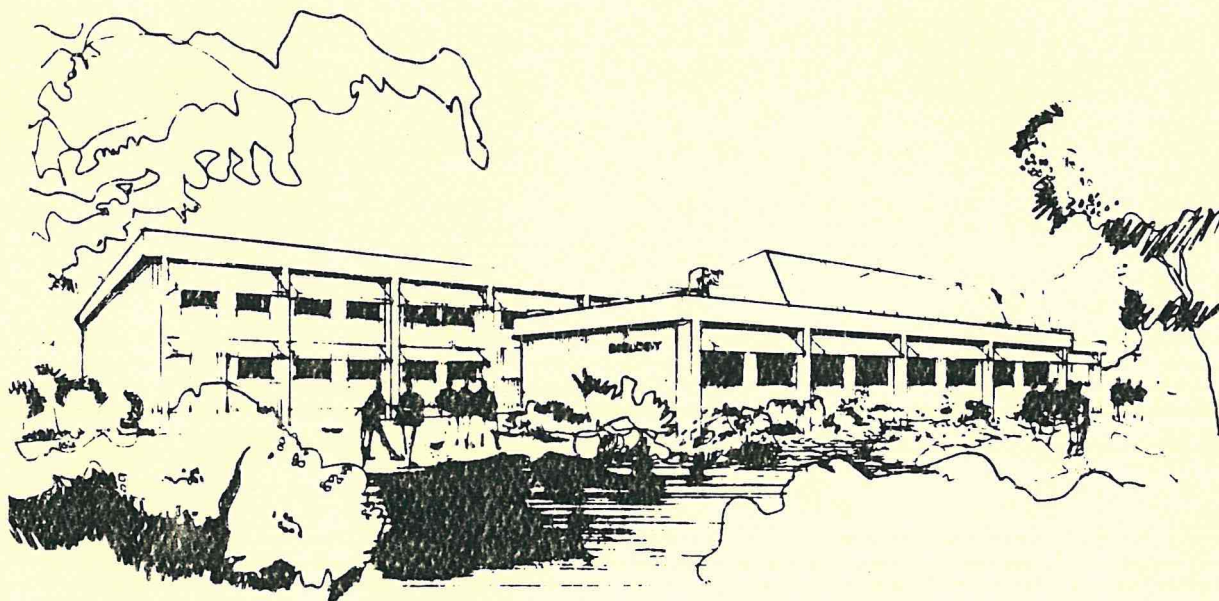


School of Environmental Biology

Conservation requirements of roadside populations of the
gazetted rare species, *Banksia goodii*

Report to Endangered Species Unit,
Australian National Parks and Wildlife Service,
and Roadside Conservation Committee,
Department of Conservation and Land Management

by Dr. Byron B. Lamont and Dr. Edward T. F. Witkowski



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POPULATION FRAGMENTATION MAY REDUCE FERTILITY TO ZERO IN *BANKSIA GOODII*

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ABSTRACT

The size of most populations of *Banksia goodii* has been severely reduced through landclearing. The relationship between the size of 15 populations and reproductive output (fertile plants, fertile cones, seeds) was assessed and compared against four basic models - proportional, threshold, maximum and minimum effects. Using total cone production as the most appropriate index of population size, there was a linear relationship with total seed production down to a threshold below which cones no longer produced any seeds. This corresponded to about 70 cones or 7 plants. Using total canopy cover as the index of population size, there was a power function relation (slope >1 , maximum effect), although a threshold of about 200 m² or 20 plants was still evident. Both relationships indicate fertility is pollinator-limited at the population level in this species, especially as there was no difference in the physical or chemical attributes of the sites. We predict extinction of the small road verge populations is inevitable in the long-term.

INTRODUCTION

Communities and populations of plants are increasingly subjected to size reduction and fragmentation through human action. These remnants have high conservation value when they become the major repositories for the species. This is the case for *Banksia goodii* where nine of the known populations occur on road verges, four on farms and only two on a nature reserve (Taylor and Hopper 1989). We were interested in whether relative seed set was reduced disproportionately in the smallest population remnants, so limiting their role in conserving this gazetted rare species, or whether it was maintained on a proportional basis.

The possible outcomes of population decimation are a) reproductive output (in this case fertile plants, fertile cones, seeds) is reduced in proportion to reduction in population size (null hypothesis), b) there is a threshold in population size below which reproductive output is zero, above which it is proportional to population size, c) there is a disproportionate (curvilinear) reduction in reproductive output dependent on initial and final population size, larger initial populations showing greatest effect, and d) as in c) except larger initial populations show least effect (Fig.1). The 'proportional' hypothesis assumes pollinators are limiting seed set and visits are always on a proportional basis to rewards, or pollinators are not limiting but resources are, such that sufficient nutrients are only available for a fixed proportion of flowers to set fruit. The 'threshold' hypothesis assumes the position of the threshold is controlled by pollinators which fail to visit at all once the rewards fall below a critical minimum. If the regression slopes picks up from the threshold, reproductive output continues to be pollinator-limited, while if it is followed by a sudden jump in output it is then nutrient-limited (Fig. 1b). The 'maximum effect' hypothesis is pollinator-limited as they make disproportionately fewer visits and spend less time on individual plants with initial population reduction - pollinators may cease to be residential for example. The 'minimum effect' hypothesis is also

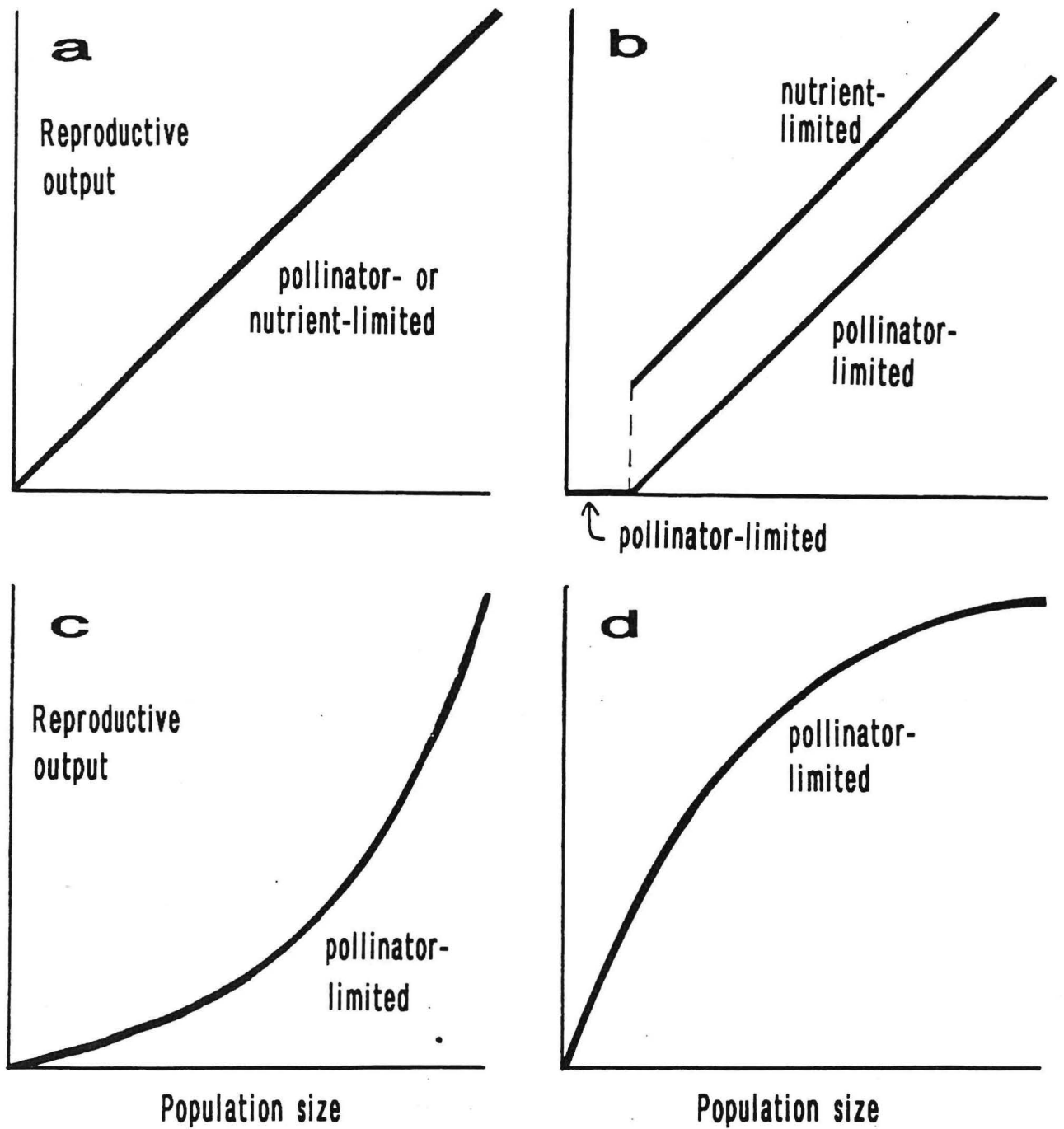


FIG. 1. Models of the possible relationships between population size and reproductive output (eg. number of fertile cones, fruits, seeds) when pollinators and/or resources are limiting. See Introduction for details.

pollinator-limited as they make disproportionately more visits to remaining plants - they may remain residential for example. Hybrids of these models are possible, while refinements involving breeding systems and granivore activity could be incorporated.

For plants, population size should include size of individuals as well as their total number. This is especially relevant to *B. goodii* as it is a long-lived clonal species and definition of an individual is subject to error. For our purposes, we are more concerned with what proportion of the reproductive units produced by the population is converted to fruits and seeds. A more useful index then is the number of inflorescences or flowers, which should combine the effects of plant size and number. While there may be a strong correlation between fruit set per plant and pollinator activity in a given season (eg. Mehroff 1983), and between reproductive effort and pollinator activity (eg. Paton 1982), the role of plant population size rarely enters the equation. There have been a few studies on patterns of pollinator visits to plants varying in size and density (eg. Klinklamer *et al.* 1989), but they have rarely been followed up for their impact on seed set (eg. Schemske 1980). Among banksias, pollinator visits and cone fertility may be linearly-related to reproductive effort, i.e. cone production per plant (Vaughton 1991). There have been no studies on any effect of population size on reproductive output, although seed set is rare or zero in the absence of pollinators (Lamont and Collins 1985, Whelan and Goldingay 1986, Ramsey and Vaughton 1991). Reproductive output in *Banksia* has two basic components: number of flower heads (cones) which produce fruits (follicles), and number of follicles per fertile cone (Copland and Whelan 1989). There are always two seeds per follicle although a variable number may abort, decay or be eaten by granivores (eg. Lamont and Barker 1988).

In this study, all known populations of *B. goodii* were examined for their population and reproductive attributes. The results were then compared with the four models

presented above. Because of the relative abundance of road verge remnants and widespread actual or expected occurrence of similar population fragmentations in other species, most attention was given to comparing these with the larger populations. Since nutrient supply can have a major impact on fruit set in banksias (Stock *et al.* 1989, Wallace and O'Dowd 1989) and closeness of all populations to farms, particular care was taken to gauge if the sites were environmentally-matched. The pattern of fruit set was used aposteriori to impute the importance of pollinator behaviour. While *B. goodii* has been identified on bird and mammal pollinators in the nature reserve (B. Collins and J. Burge, pers. comm.), its sprawling prostrate canopy with flower heads borne on the ground made direct observations impossible. By comparing the accumulated reproductive output versus reproductive effort over at least five years, the problems of interpretation inherent in short-term studies (Calvo and Horvitz 1990) were avoided.

MATERIALS AND METHODS

All populations recorded by the Albany Branch of the Department of Conservation and Land Management were assessed in September-October 1991. The 15 populations were centered on 34°45'S, 117°40'E in an area 37 km E-W and 13 km N-S. At each location the number of plants (clumps with branches (rhizomes) appearing to arise from a common point) were counted. For all plants in the population, or a random sample of 25 if the number exceeded this, plant size was determined by measuring the maximum diameter (D_1) and that at right angles (D_2) and proportion of canopy cover (C) estimated to the nearest 10% by eye. Weighted plant size was given by $0.785 D_1 D_2 C$. Since all plant canopies consisted of upward-inclined leaves of around 250 mm tall from ground level, it was not necessary to include height as a dimension of size.

Preliminary observations indicated that in slow-growing plants the current season's leaves appeared thinner. Six representative leaves per plant were measured for length (L) and width (W) and converted to area ($0.785 L W$). The total sterile (no follicles) and fertile cones were counted. Cones which had decayed (after about 15 years, Lamont *et al.* 1991) were ignored. Only one population contained plants (about 4%) < 6 years old (following disturbance) while the others had not been disturbed for at least 20 years (local records). Since most plants recover from fire and seedling recruitment is rare and restricted to post-fire conditions (unpublished), almost all plants were older than the time since last fire. Overstorey shading (by trees) was determined with a forest densiometer in two positions over each plant. Understorey shading (by shrubs) was estimated by eye to the nearest 10% cover. The depth to rock (laterite) was obtained by digging. Litter thickness beneath the canopy was determined by ruler to the nearest 10 mm. Soils beneath the canopy were sampled to a depth of 150 mm, bulked per site and analysed by CSBP and Farmers Ltd., Perth. They were air-dried and sieved for the gravel, sand, silt and clay fractions and weighed. Organic C was determined by chromic acid digestion and colorimetry, P was extracted with 1 M NaHCO₃ and assayed by molybdenum blue colorimetry, cations (except NH₄) were extracted with 1 N NH₄Cl at pH7 and assayed by atomic absorption spectroscopy, pH was determined on a 1:5 dilution with distilled water and NO₃ assayed on the extract with a specific ion electrode, NH₄ was extracted with 1 N KCl and quantified by indophenol blue calorimetry.

To show the overall relationship between the populations, they were ordinated by canonical correspondence analysis (Ter Braak 1986) using the following demographic attributes: number of plants, plant size, leaf size, distance between nearest plants, total cones per plant and fertile cones per plant. Indices of reproductive output were plotted against indices of population size/reproductive effort. They were submitted to regression analyses - linear, power, exponential and logarithmic - and the curve with the highest coefficient of determination (r^2) selected

for plotting. The results were very sensitive to the value given to replace zero reproductive output values to meet the power function requirements. Values were therefore varied from 0.01 to 0.4 to give the best fit curve at high population sizes. Results for the road verge populations were compared with the non-road populations by t-tests, preceded by transformations to normalize the data as necessary.

RESULTS

Canonical correspondence analysis showed there that was no correlation between the six demographic variables measured per population. For a 2D ordination which accounted for 69% of variation in the data (Fig. 2), the 15 populations were readily separated into two major groups (road and non-road) and a minor group (one on a farm and two road verges). The first two groups appeared to be separated by fewer plants with less total and fertile cones per plant in the road verge populations, while the third group tended to have a few, larger plants with more cones than the rest.

There was a linear relationship (Fig. 3a) between total number of plants per population and number of fertile plants i.e. bearing fertile cones ($\underline{Y} = -1.74 + 0.54 \underline{X}$, $r^2 = 0.80$, $\underline{P} < 0.001$ on 13 *df*). The large recently-disturbed farm population had more fertile plants than predicted by this relationship while the large nature reserve population had fewer. There was a mean threshold of 5 plants below which no plants were fertile. When population size was gauged as the sum of the canopy size of all plants, there was also a linear fit with number of fertile plants ($\underline{Y} = -4.84 + 0.06 \underline{X}$, $r^2 = 0.84$, $\underline{P} < 0.001$ on 13 *df*) with the same deviations as before. The critical population size was 80 m² representing about 8 plants of average canopy size 10 m².

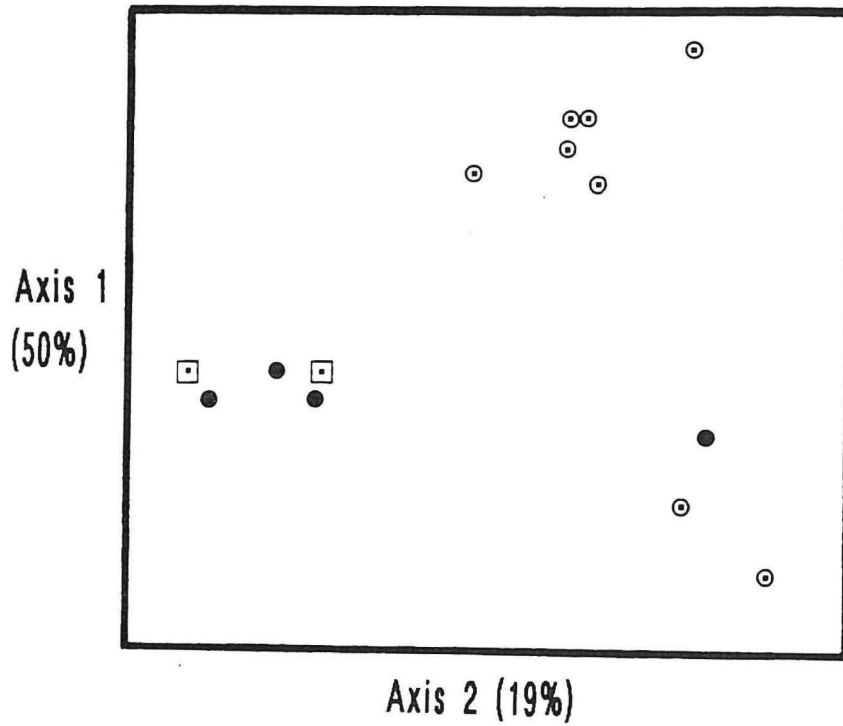


FIG. 2. Two-dimensional ordination for canonical correspondence analysis of *B. goodii* populations based on six demographic attributes. The first two axes accounted for 69% of variation in the data. ○ road verge population, ● farm population, ◻ nature reserve population.

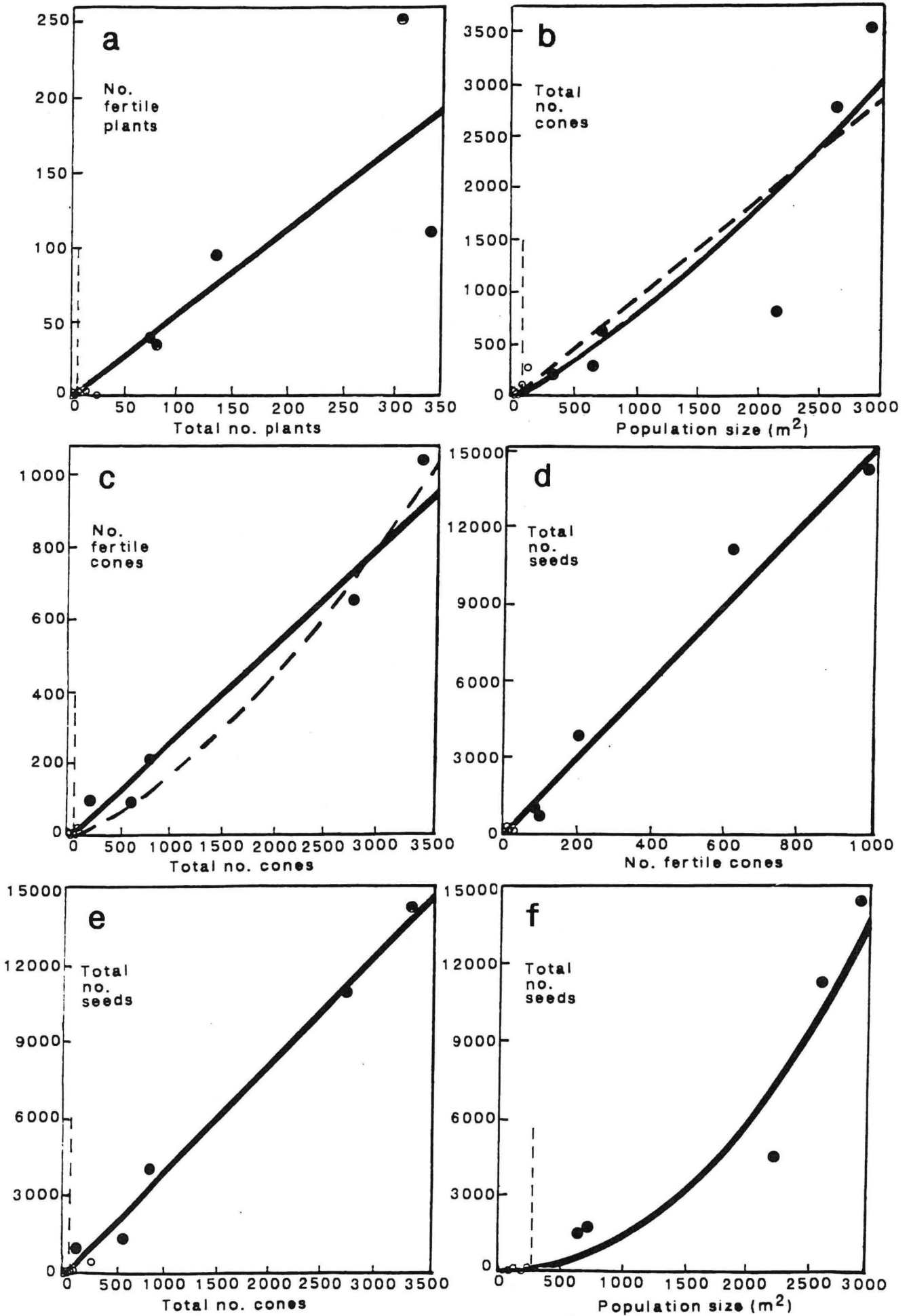


FIG. 3. Relationship between population and reproductive attributes for 15 populations of *Banksia goodii*. Broken vertical lines indicate threshold values on the X-axis for the best-fit line. ○ road verge population, ● non-road population. Other broken lines are alternative fits to the data - see Results for equations.

The best power function relationship (Fig. 3b) between population size (canopy cover) and total number of cones was almost linear ($\underline{Y} = 0.11\underline{X}^{1.27}$, $r^2 = 0.90$, $\underline{P} < 0.001$ on 13 *df*). The linear fit ($\underline{Y} = -69.0 + 0.94\underline{X}$, $r^2 = 0.86$, $\underline{P} < 0.001$ on 13 *df*) produced a threshold of 75 m². The nature reserve population was the sole reason for the slightly better curvilinear fit - there was less than half the number of cones than expected on the basis of population size. The number of fertile cones versus population size also described a power function ($\underline{Y} = 0.00033\underline{X}^{1.80}$, $r^2 = 0.77$, $\underline{P} < 0.001$ on 13 *df*). There was a linear fit (Fig. 3c) between total and fertile cones ($\underline{Y} = -19.24 + 0.27\underline{X}$, $r^2 = 0.96$, $\underline{P} < 0.001$ on 11 *df*) with a threshold of 70 cones. By setting 0 fertile cones to 0.025, a power function also fitted the data well ($\underline{Y} = 0.0044\underline{X}^{1.51}$, $r^2 = 0.79$, $\underline{P} < 0.001$ on 11 *df*) mainly through the influence of the large undisturbed farm population with less than expected fertile cones.

Total number of seeds was linearly-related to number of fertile cones (Fig. 3d) and passed through the origin ($\underline{Y} = 13.36\underline{X}^{1.01}$, $r^2 = 0.99$, $\underline{P} < 0.001$ on 8 *df*). Thus there were means of 7.3 follicles and 14.6 seeds per fertile cone independent of population size. There were fewer seeds per cone than expected in the large, recently disturbed population. Total number of seeds was linearly-related (Fig. 3e) to total number of cones ($\underline{Y} = -301.6 + 4.30\underline{X}$, $r^2 = 0.99$, $\underline{P} < 0.001$ on 11 *df*). The threshold was 70 cones. There were no clear departures from this pattern. by setting 0 seeds to 0.01, the power function between total canopy cover and number of seeds was $\underline{Y} = 0.00023\underline{X}^{2.23}$, $r^2 = 0.73$, $\underline{P} < 0.001$ on 13 *df* (Fig. 3f). Even without the reduced seed set in the large nature reserve population the rest of the data still described a curvilinear relationship. There was almost a threshold - populations ≤ 200 m² had < 4 seeds per plant on average.

Separating the road verge populations showed that they had less than 5% the number of plants in the rest on average, a tendency for them to be slightly smaller (but NS), a similar distance between plants and identical leaf sizes (Table 1). The

Table 1. Number and size of plants, interplant distances, leaf area and reproductive traits for 9 road verge and 6 non-road populations of *Banksia goodii*. Results are mean \pm S.D. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

	ROAD VERGE POPULATIONS	NON-ROAD POPULATIONS	SIG.
Total plants	7.8 \pm 6.7	163.3 \pm 141.8	***
Plant size (m ²)	8.6 \pm 7.2	14.2 \pm 10.3	NS
Nearest neighbour distance (m)	4.9 \pm 3.6	3.4 \pm 1.5	NS
Nearest population distance (km)	2.0 \pm 3.0	2.8 \pm 3.4	NS
Leaf area (x1000 mm ²)	10.2 \pm 2.3	10.0 \pm 1.5	NS
Total cones/plant	9.6 \pm 17.0	9.9 \pm 7.0	NS
Plants with fertile cones (% total)	14.9 \pm 19.2	53.5 \pm 17.5	**
Fertile cones/plant	0.35 \pm 0.69	1.88 \pm 1.38	**
Fertile cones (% total)	6.7 \pm 12.2	22.6 \pm 10.5	*
Follicles/total cone	0.47 \pm 0.86	1.65 \pm 0.73	*
Follicles/fertile cone	7.1 \pm 2.8	7.3 \pm 1.5	NS
Seeds produced/plant	3.6 \pm 6.0	29.2 \pm 26.2	***

Table 2. Soil and shade analyses for road verge and non-road populations of *B. goodii*. Results are mean \pm S.D. for 9 and 6 sites respectively. Values are for available nutrients in mg kg⁻¹. T-tests produced no significant site differences for all attributes.

ATTRIBUTE	ROAD VERGE SITES	NON-ROAD SITES
P (mg kg ⁻¹)	3.4 \pm 3.5	1.9 \pm 0.7
NO ₃	3.3 \pm 2.8	1.9 \pm 0.4
NH ₄	9.6 \pm 6.5	10.0 \pm 7.0
K	37 \pm 19	44 \pm 42
Ca	468 \pm 321	459 \pm 184
Mg	117 \pm 77	97 \pm 37
Na	33 \pm 19	31 \pm 13
Fe	208 \pm 165	133 \pm 98
C (%)	2.1 \pm 0.6	2.3 \pm 0.7
pH	5.6 \pm 0.5	5.6 \pm 0.5
Gravel (%)	6.9 \pm 9.2	1.7 \pm 1.2
Sand (%)	92.9 \pm 18.3	92.6 \pm 36.3
Silt (%)	6.4 \pm 2.3	6.6 \pm 2.6
Clay (%)	0.7 \pm 0.3	0.8 \pm 0.5
Soil depth (mm)	45 \pm 35	55 \pm 27
Litter depth (mm)	22 \pm 28	19 \pm 15
Overstorey (%)	47 \pm 22	41 \pm 20
Understorey (%)	27 \pm 23	29 \pm 13

total cones per plant were both close to 10 on average but there was a four times greater proportion of fertile plants in the non-road populations. There were on average 5.4 times more fertile cones per plant in the non-road populations with a 3.4 times greater proportion of cones bearing follicles as well. Fertile cones in both groups possessed about 7 follicles each. The net effect was 8.1 times more seeds produced per plant by the non-road populations than the road verge populations. For the 10 chemical and 8 physical attributes measured (Table 2) there was no significant differences between the two groups of sites.

DISCUSSION

Clearing for roads and agriculture has left nine population remnants of *Banksia goodii* containing less than 5% the number of plants as the six populations remaining on partly cleared farmland and a nature reserve. The effects on size of plants and inflorescence (cone) production per plant have been negligible. However, the proportion of cones bearing follicles was much lower in the road verge remnants such that they produced on average only 12% of the seeds per plant as the less fragmented populations. These results enable the proportional and minimum effect models (Fig. 1a, d) to be dismissed as not applicable to this species. Inspection of all the plots (Fig. 3) shows two of the pollinator-limited models (Fig. 1b, c) apply independent of the index of reproductive output chosen (number of fertile plants, fertile cones or seeds). In reproductive ecology we are more interested in the population of flowers or inflorescences than in the population of whole plants (although we would expect a correlation between the two, Fig. 3b). On this basis there is a proportional relationship between total cones produced and seeds set until the population is reduced to about 70 cones (7 plants) when no more fruits or seeds are produced (Fig. 1b, 3e). This threshold can be interpreted as the point at which pollinators are no longer attracted to the

population. It is clearly not due to a fall in soil nutrient availability following clearing as it is just as high as that in the larger populations (Table 2). The advantage of this approach is that it cannot be explained by an unusually 'bad' year - this pattern has built up over at least 5 years and takes into account any annual fluctuations in reproductive effort or pollinator activity (Calvo and Horvitz 1990).

The potential importance of choice of index of population size is indicated by the power function relationship (maximum effect model, Fig. 1c) between (plant size x number) and seed production (Fig. 3f). This can be explained by the amplification of the slightly curvilinear relationships between total plant cover and cone production (Fig. 3b), and between cone production and fertile cones (Fig. 3c). Larger (older) plants have disproportionately more cones (Lamont *et al.* 1991) and pollinator visits. Nevertheless, since seed production is insignificant up to 200 m² (20 plants, including a farm population), this is best interpreted as a threshold followed by a power function relationship with increasing population size. This is consistent with pollinators visiting disproportionately fewer plants, perhaps missing the smaller or more isolated ones (Klinklamer *et al.* 1989), as population size falls until they no longer visit any plants.

The results of this study indicate that it is probably reasonable to speak of a "critical population size" below which long-term local extinction, even of a long-lived, fire-tolerant species such as *B. goodii*, is certain; and above which population size may (Fig. 3f) or may not (Fig. 3e) be important. What are the implications for species and community conservation? *B. goodii* is a minor component of the flora at all locations. Reproductive failure in this species is probably a reflection of the inability of the vegetation remnants to attract pollinators generally. Any attempt to build up the numbers of *B. goodii* beyond the threshold should be accompanied by a similar increase in other nectar-rich species, especially those out of phase with *B. goodii*. In this regard it is interesting to note that the population with by far the

greatest proportion of fertile plants (Fig. 3a) co-occurred with another prostrate species, *B. gardneri*, which finishes flowering as *B. goodii* starts (George 1981). As the results indicate reproductive success in this species is pollinator-limited at the population level, the plants themselves can be used to monitor changes in pollinator activity and any improvement in conservation status.

ACKNOWLEDGEMENTS

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REFERENCES

- Calvo, R.N. and Horvitz, C.C. 1990. Pollinator limitation, cost of reproduction, and fitness in plants: a transition-matrix demographic approach. *The American Naturalist* 136, 499-516.
- Copland, B.J. and Whelan, R.J. 1989. Seasonal variation in flowering intensity and pollination limitation of fruit set in four co-occurring *Banksia* species. *Journal of Ecology* 77, 509-23.
- George, A.S. 1981. The genus *Banksia* L.f. (Proteaceae). *Nuytsia* 3, 239-473.

- Klinklamer, P.G., Jong, T.J. de and Bruyn, G. de 1989. Plant size and pollinator visitation in *Cynoglossum officinale*. *Oikos* 54, 201-204.
- Lamont, B.B. and Barker, M.J. 1988. Seed bank dynamics of a serotinous, fire-sensitive *Banksia* species. *Australian Journal of Botany* 36, 193-203.
- Lamont, B.B. and Collins, B.G. 1985. Flower colour change in *Banksia ilicifolia*: a signal for pollinators. *Australian Journal of Ecology* 15, 129-35.
- Lamont, B.B., Connell, S.W. and Bergl, S. 1991. Population and seed bank dynamics of *Banksia cuneata*: the role of time, fire and moisture. *Botanical Gazette* 152, 114-22.
- Paton, D.C. 1982. The influence of honeyeaters on flowering strategies of Australian plants. *In* Armstrong, J.A., Powell, J.M. and Richards, A.J. (eds.). *Pollination and Evolution*. Royal Botanic Gardens, Sydney. pp. 95-108.
- Ramsey, M. and Vaughton, G. 1991. Self-incompatibility, protandry, pollen production and pollen longevity in *Banksia menziesii*. *Australian Journal of Botany* 39, 497-504.
- Schemske, D.W. 1980. Floral ecology and hummingbird pollination of *Combretum farinosum* in Costa Rica. *Biotropica* 12, 169-181.
- Stock, W.D., Pate, J.S., Kuo, J. and Hansen, A.P. 1989. Resource control of seed set in *Banksia laricina* C. Gardner (Proteaceae). *Functional Ecology* 3, 453-60.

- Taylor, A. and Hopper, S.D. 1989. The *Banksia* atlas. Australian Government Publishing Service, Canberra.
- Ter Braak, C.J. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167-79.
- Vaughton, G. 1991. Proximate and ultimate explanations of low fruit: flower ratios in *Banksia spinulosa* (Proteaceae). Ph.D. Thesis, University of New England, N.S.W.
- Wallace, D.D. and O'Dowd, D.J. 1989. The effect of nutrients and inflorescence damage by insects on fruit set by *Banksia spinulosa*. *Oecologia* 79, 482-8.
- Whelan, R.J. and Goldingay, R.L. 1986. Do pollinators influence seed-set in *Banksia paludosa* Sm. and *Banksia spinulosa* R. Br. *Australian Journal of Botany* 11, 181-6.