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Some Demographics of the Extirpation from the Wild of Eastern Barred Bandicoots (*Perameles gunnii*) in 1988–91, near Hamilton, Victoria, Australia

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Abstract

The threatened, free-ranging mainland population of the eastern barred bandicoot in the Hamilton area of Victoria declined to near extinction in late 1992. Demographic changes associated with the decline were monitored from 1988 to 1992. About 200 different animals were captured in 1988, 49 in 1989, 16 in 1990, 3 in 1991 and 3 in 1992; capture rates (number of bandicoots captured per trap-night) displayed a similar pattern: 0·5 in 1988, 0·1 in 1989, 0·05 in 1990, 0·05 in 1991 and 0·02 in 1992. Observed declines lay within the 5% confidence intervals predicted by a demographic model for a population subjected to a removal rate of 14 animals per three months (the number removed for captive breeding by managers). Removal of bandicoots to stock a captive population hastened the demise of the wild population by about seven years; however, even in the absence of removals of animals, extinction was impending within 5–10 years. Sex ratios were male-biased in all years except 1988; the bias may have resulted from stochastic events. Average litter sizes did not differ between the 1988 population and subsequent populations, except for the 1991 population, in which a predominance of non-reproductive females contributed to a strong decline in average litter size. These demographic trends illustrate how the synergy between stochastic and deterministic forces can rapidly drive a small population to extinction.

Introduction

The global extinction rate is increasing (World Conservation Monitoring Center 1992). Some of these extinctions are occurring in Australia, which has had more mammal extinctions in the last 200 years than the rest of the world combined (Biological Diversity Advisory Committee 1992). Despite the growing extinction problem, little opportunity exists to study ongoing extinction processes in detail as they happen. The last free-ranging mainland population of eastern barred bandicoots (*Perameles gunnii*) near Hamilton, Victoria, has been under study since 1972, intensively so since 1988, and over this period, despite management efforts, numbers declined to near extinction by late 1991. A related subspecies resides in Tasmania and its status is unclear. Many aspects of the conservation effort directed at the Victorian population were described by Clark and Seebeck (1990). Fortunately, before the near-total loss of the wild population, a relatively large sample of bandicoots was taken into captive breeding for eventual restoration back to the wild in secure locations. This paper describes the demographics of the last wild mainland population of eastern barred bandicoots in the Hamilton area as it declined to near extinction and of a semi-wild captive population established immediately north of Hamilton in the fenced, predator-exclosed Hamilton County Parklands.

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Methods

Study Area

The eastern barred bandicoot was historically distributed throughout the Western District plains of Victoria and into South Australia (Seebeck 1979; Brown 1989), but in recent years it has been limited to environs of the City of Hamilton. This region and the Hamilton environment have been described by Minta *et al.* (1990). In recent years, wild bandicoots were trapped in or near Hamilton in the areas of Chatsworth and Digby roads and in the semi-wild population established at the Hamilton Community Parklands in 1989.

Population History

Historically, the species occupied about 23000 km^2 (Clark and Seebeck 1990). In recent studies (1989–90), the species occurred at about 1 animal ha^{-1} (Minta *et al.* 1990), but the range of densities that occurred in pre-European western Victoria is unknown. Concern for its survival was first noted in 1937, and the history of major events in bandicoot conservation since then are given by Backhouse (1992). The first investigation of the species status was conducted in 1960. Between 1967 and 1975 continued concern for the bandicoot's future was repeatedly expressed. A study of the species' distribution and status was made and a few bandicoots were taken into captivity in 1972 (Seebeck 1979). By this time the mainland form had declined to a single population near Hamilton. Various field studies were carried out between 1980 and 1989 (Brown 1989; Minta *et al.* 1990; Dufty 1991). The history of the species' decline and probable causes of this decline, including a host of deterministic (e.g. habitat loss) and stochastic (e.g. droughts) factors are described by Seebeck *et al.* (1990).

Field Studies

Between 1988 and 1991, a series of grids and lines was used to live-trap bandicoots. Animals were examined, marked and released or taken into captivity upon trapping. Detailed records were kept of each capture. Number and placement of traps used in 1988 were described by Minta *et al.* (1990). Methods used in 1989, 1990 and 1991 were standardised and described by Clark and Goldstraw (1991). Data on bandicoot capture rates and sex ratios were derived from studies conducted at the Chatsworth Road and Digby Road areas, and data on litter sizes from Chatsworth Road and Digby Road and the Hamilton Community Parklands study areas.

Population Modelling

We compared patterns of decline observed in the wild population with patterns of decline predicted by a stochastic population-growth model. The model used means and variances of biological parameters, such as survival and fecundity, to project population trends over time. The variation specified for model parameters caused each population trajectory to be unique despite having the same initial conditions. By repeatedly simulating population trends ($n = 5000$ projections), we were able to estimate changes in average population size over time as well as the probability that the population might fall to or exceed a particular threshold. The model recognised three age-classes of bandicoots: newborns (0–3 months old), juveniles (3–6 months old), and adults (>6 months old) and was based on a post-breeding census of the population (see Lacy and Clark 1990; Burgman *et al.* 1993). Environment-related variation was modelled in two ways. First, survival rates were permitted to vary randomly during each 3-month interval according to a normal distribution with mean and coefficient of variation determined from field studies and truncated at 0 and 1. Variation in survival rates was considered to be perfectly and positively correlated among each age-class. Second, litter sizes of reproducing females were permitted to vary according to a normal distribution of mean and variance determined from field studies and truncated at zero. Demographic stochasticity was modelled by drawing a random number of individuals in any interval from a binomial distribution of n (number of individuals alive in the previous interval) and P (their probability of surviving during that interval). Similarly, a random number of male offspring was determined from a binomial distribution of n (number of offspring produced) and P (sex ratio of newborns). Finally, females reproduced only if at least one adult male was alive. The simulation model was written in Turbo Pascal 5.0 (Borland International, Scotts Valley, California), with numerical algorithms taken from Press *et al.* (1990).

Two management scenarios were simulated with the model: (1) removal of individuals from the wild population at a rate of 14 individuals (if available in the population) per three months (i.e. the average rate that equals the removal of 114 individuals from the population over two years to stock the captive breeding population) and (2) no removal of bandicoots for stocking a captive population. A comparison of these two

Table 1. Demographic parameters used in population simulations of eastern barred bandicoots

Data were derived from studies conducted in 1989 and 1990 of the free-ranging Hamilton population (Minta *et al.* 1990; Lacy and Clark 1990; Dufty 1991)

Initial population size: 200
Age and sex distribution
32 male and 32 female juveniles (3 months old)
68 male and 68 female adults (≥6 months old)
Survival
S_0: 50% survival between 0 and 3 months of age (CV[A] = 15%)
S_1: 56% survival between 3 and 6 months of age (CV = 15%)
S_2: 75% survival of adults per three months (≥6 months of age; CV = 15%)
Age at first reproduction: six months
Mean litter size
F_2: 2·20 ± 0·95 (1 s.d.; CV = 41%)
Interval between litters: three months

[A]Coefficient of variation.

simulations provides insight into how much the removals accelerated extinction of the wild population. Model parameters were specified with data derived from field studies of the Hamilton population during 1988–89 (see Lacy and Clark 1990; Minta *et al.* 1990; Dufty 1991) and are presented in Table 1. We performed a sensitivity analysis to determine which population parameters contributed most to population growth rates. We increased each population parameter by 10%, while holding the other parameters constant, to evaluate the relative contribution of each parameter to the average net reproductive rate (R_0) of the population.

We examined changes in sex ratios and average litter sizes of eastern barred bandicoots during 1988–91 and asked whether these changes could be due to chance events alone. We first determined whether sex ratios observed in the wild population each year differed from parity. We did this by comparing the observed sex ratios each year with those from 1000 samples of an equal number of bandicoots drawn at random from a population with an unbiased sex ratio. Calculating the 5% minima and 5% maxima of the random samples and comparing the observed sex ratio with these values permitted us to accept or reject the hypothesis that sex ratios were at parity. Because stochastic events are cumulative in nature, we repeated the randomisation process using the preceding year's population to derive the random sample. This permitted us to ask whether the observed sex ratio might be expected from a random sampling of the preceding years' population (which may have already possessed a biased sex ratio). Changes in fecundity (mean litter sizes) were examined in a similar manner, using the distribution of litter sizes in the 1988 population to derive the random samples. We also repeated the randomisation procedure using the preceding year's distribution of litter sizes to derive the random sample for comparisons of mean litter size between successive years.

Results

Observed and Predicted Changes in abundance of Eastern Barred Bandicoots between 1988 and 1991

The wild population of eastern barred bandicoots declined precipitously between 1988 and 1991. Although true population numbers remain unknown, about 200 different animals were captured in 1988, 49 in 1989, 16 in 1990, 3 in 1991 and 3 in 1992. Capture rates (number of bandicoots captured per trapnight) displayed a similar pattern: 0·456 in 1988, 0·101 in 1989, 0·054 in 1990 and 0·052 in 1991. Although the area trapped and trapping methodology remained the same over the study period, large portions of the sampled area became vacant of bandicoots in the later years; this largely accounted for the rapid decline in capture rates. Sex ratios were strongly male-biased during this period: 1·88 : 1·00 ~~males~~ (males : female) in 1989, 2·20 : 1·00 in 1990, all males in 1991 and 2·00 : 1·00 in 1992.

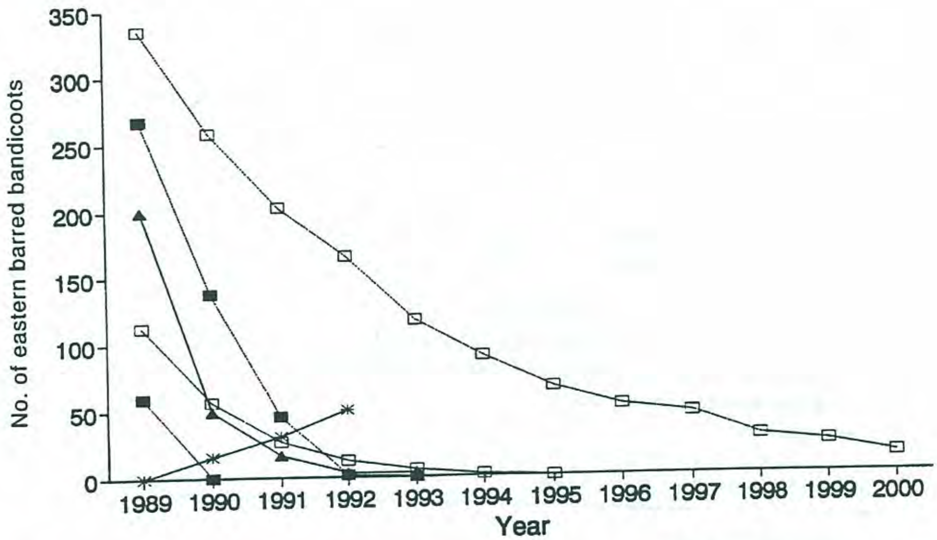

Fig. 1. Simulated and observed population trends in the wild population of eastern barred bandicoots in and near Hamilton, Victoria, Australia, during the period 1988–2000. -□-, the 5% minima and 5% maxima of 5000 population simulations under the scenario of no removals of bandicoots to a captive colony; -■-, the 5% minima and 5% maxima of 5000 simulations in which 14 bandicoots were removed per every three months. The observed trend in numbers of bandicoots captured during 1988–91 is also indicated (-▲-), as is the size of the captive colony during this period (-✳-).

Table 2. Sensitivity analysis of the relative contribution of various population parameters to growth rate (R_0) of the wild population of eastern barred bandicoots in Hamilton, Victoria

Each parameter was increased by 10% while the other parameters were held constant to evaluate the relative contribution of each parameter to the population growth rate. See Table 1 for symbol definitions

Parameter varied	S_0	S_1	S_2	F_2	R_0	Change in R_0 (%)
None	0·50	0·56	0·75	1·10	0·62	0
S_0	0·55	0·56	0·75	1·10	0·68	10
S_1	0·50	0·62	0·75	1·10	0·68	11
S_2	0·50	0·56	0·82	1·10	0·88	43
F_2	0·50	0·56	0·75	1·29	0·72	17
S_2, F_2	0·50	0·56	0·82	1·29	1·03	67

Observed declines in the Hamilton population of eastern barred bandicoots lay within the 5% minima and maxima predicted by our model for a population subjected to a removal rate of 14 animals (seven adult males and seven adult females) per three months (Fig. 1). The observed decline mirrored an increase in the size of the captive population (Fig. 1). Simulations that examined the fate of the wild population had it not been subjected to removals for the captive colony also indicated a strongly declining population (R_o = 0·62) (Fig. 1). Simulations revealed a chance of greater than 5% of population extinction by 1994, and a chance of greater than 95% of falling below 50 by 2000. Also, removals hastened the time to extinction by about seven

Table 3. Sex ratios of eastern barred bandicoots in the 1989, 1990 and 1991 populations in comparison with sex ratios expected from a random sampling of a population with equal proportions of males and females

Year	*n*	Males (%)	Percentile[A] 5%	Percentile[A] 50%	Percentile[A] 95%
1988[B]	88	59	40	50	60
1989[B]	52	65	38	50	62
1990[C]	36	67	36	50	64
1991[C]	37	78	35	50	62

[A]Of 1000 populations of *n* individuals selected at random from a population comprised of 50% males.
[B]Chatsworth Rd and Digby Rd areas in and near Hamilton, Victoria.
[C]Chatsworth Rd, Digby Rd and Hamilton Community Parklands in and near Hamilton, Victoria.

Table 4. Sex ratios of eastern barred bandicoots in the 1989, 1990 and 1991 populations in comparison with sex ratios expected from a random sampling of surviving individuals from the preceding year's population

Year	*n*	Males (%)	Percentile[A] 5%	Percentile[A] 50%	Percentile[A] 95%
1988[B]	88	59	–	–	–
1989[B]	52	65	48	60	69
1990[C]	36	67	53	64	78
1991[C]	37	78	54	68	81

[A]Of 1000 populations of *n* individuals selected at random from the previous year's population.
[B]Chatsworth Rd and Digby Rd areas in and near Hamilton, Victoria.
[C]Chatsworth Rd, Digby Rd and Hamilton Community Parklands in and near Hamilton, Victoria.

years: median time to extinction was 10 years without removals, whereas median time to extinction was three years with removals. A sensitivity analysis indicated that trends in the bandicoot population were influenced substantially more by adult survival than by other population parameters. Increasing adult survival in the wild population by just 10% increased the population growth rate by 43%, whereas a comparable increase in early juvenile survival (0–3 months; pouch life-phase), late juvenile survival (3–6 months; emergent and dispersing life-phase) and mean litter size resulted in increases in population growth rates of only 10–17% (Table 2). The sensitivity analysis also indicated that a 10% increase in both adult survival and fecundity was the minimum required for the wild population to have attained stability (i.e. $R_o \geq 1$) (Table 2).

Changes in Sex Ratios and Litter Size

Sex ratios were male-biased in all years except 1988 when data from the wild and semi-wild Hamilton population were combined (Table 3). Our analysis indicated, however, that sex ratios observed each year reflected a random sampling of surviving individuals from the previous year's population (Table 4), that is, sex ratios may have become skewed toward males owing to stochastic events alone. Mean annual litter size did not differ, on average, between 1988 and

Table 5. Litter size in eastern barred bandicoots in the 1989, 1990 and 1991 populations compared with that expected from a random sampling of litter sizes observed in the previous year's population

Year	*n*	Litter size					Mean	Percentile[A]		
		0	1	2	3	4		5%	50%	95%
1988[B]	32	5	5	13	8	1	1·84	–	–	–
1989[B]	15	1	1	6	7	0	2·26	1·33	1·80	2·27
1990[C]	10	0	1	4	4	1	2·50	1·80	2·30	2·70
1991[C]	8	5	2	0	1	0	0·62	2·00	2·50	3·00

[A]Of 1000 sets of *n* litters selected at random from the litter size distribution in the preceding year's population.
[B]Chatsworth Rd and Digby Rd areas in and near Hamilton, Victoria.
[C]Chatsworth Rd, Digby Rd and Hamilton Community Parklands in and near Hamilton, Victoria.

Table 6. Litter size in eastern barred bandicoots in the 1989, 1990 and 1991 populations compared with that expected from a random sampling of litter sizes observed in the 1988 population

Note that the mean litter size in the 1991 population was significantly smaller ($P < 0{\cdot}01$) than that expected by chance alone

Year	*n*	Mean	Percentile[A]		
			5%	50%	95%
1989[B]	15	2·26	1·33	1·80	2·27
1990[C]	10	2·50	1·30	1·80	2·40
1991[C]	8	0·62	1·13	1·87	2·50

[A]Of 1000 sets of *n* litters selected at random from the 1988 population with the following distribution of litter sizes: litters of 0 ($n = 5$), 1 ($n = 5$), 2 ($n = 13$), 3 ($n = 8$), 4 ($n = 1$).
[B]Chatsworth Rd and Digby Rd areas in and near Hamilton, Victoria.
[C]Chatsworth Rd, Digby Rd and Hamilton Community Parklands in and near Hamilton, Victoria.

1989 or between 1989 and 1990, but declined between 1990 and 1991 (Table 5). Similarly, average litter sizes did not differ between the 1988 population and subsequent populations, except for the 1991 population, which had a smaller average litter size than the 1988 population (Table 6). A predominance of non-reproductive females in the 1991 population contributed to the decline in fecundity that year (Table 5).

Discussion

Removal of bandicoots during 1988–91 for stocking a captive population clearly hastened the demise of the remaining population of wild eastern barred bandicoots in the Hamilton area. However, even in the absence of removals of animals into captivity, several population viability analyses (e.g. Lacy and Clark 1990; this paper) predicted impending extinction of the wild population (i.e. within 5–25 years). The trend observed during field studies of the wild population of eastern barred bandicoots and that estimated by a computer model exhibited concordance (Fig. 1). This result emphasises the usefulness of population-viability analysis (PVA) as a tool for evaluating management alternatives for the eastern barred bandicoots and other species reduced to a few small populations (see Lindenmayer *et al.* 1993).

Several demographic traits of the last wild population of eastern barred bandicoots illustrate how the synergy between stochastic and deterministic forces can rapidly drive a small population to extinction. For example, bandicoot sex ratios were male-biased during the last three years that the population was monitored, a pattern that may have resulted from stochastic changes in sex ratios that by chance to favour males. Sex ratios in all years, except 1990, were close to the maximum expected by chance, however, suggesting that deterministic factors, such as exclusion of females by males from high-quality habitats, also may have contributed to a male-biased population. Whatever the ultimate cause of the skewed sex ratio, the demise of the wild population was hastened by the differential disappearance of females. Additionally, an 'Allee' effect may have been operating in the population owing to abnormally low densities of bandicoots, which might have interfered with social stimulation of reproductive behavior or simply prevented potential mates from finding one another (Allee *et al.* 1949).

We speculate that small population size could also have permitted genetic drift and inbreeding to play a pervasive role in genetically structuring the bandicoot population. The total wild population of bandicoots was comprised of than 50 individuals during the final years of monitoring and was subdivided among three isolated areas. Additionally, reproductive output varied considerably among females and sex ratios were strongly male-biased. Together, these factors may have substantially reduced the effective genetic size of the bandicoot population (see Lande and Barrowclough 1987; Robinson *et al.* 1990), thereby permitting drift and inbreeding to operate at high levels. Prolonged drift and inbreeding tend to reduce the average fitness of individuals and may have affected the bandicoots during the relatively short period that wild populations of bandicoots were monitored (1988–91), owing to the short generation time characteristic of this species (*c.* 1 year: Lacy and Clark 1990). Reduced fitness often is manifested in reduced fecundity (Falconer 1981; Ralls and Ballou 1983), which might partly account for the reduction in litter size observed in the bandicoots during the final year of monitoring (Tables 5, 6).

In addition to these largely stochastic processes, several deterministic forces have been implicated in the collapse of the remnant, wild population of eastern barred bandicoots in the Hamilton area. Collisions with motor vehicles as bandicoots attempted to cross roads were a major mortality factor, accounting for more than half (57%) of all recorded deaths (Lenghaus *et al.* 1990). Road trauma differentially affected adult males, perhaps owing to the more extensive seasonal movements of adult males than of female or juvenile bandicoots (Minta *et al.* 1990). Our population-sensitivity analysis implicates road trauma as an important factor in regulating the wild population, given the relative importance of adult survival to population growth coupled with the high susceptibility of adults to road-associated mortality.

Predation by domestic cats, dogs and introduced foxes also represents an important mortality factor, particularly for juveniles. In addition to acting as predators, cats serve as an important source of *Toxoplasmosis gondii*, which occurs as a potentially fatal, generalised infection in many bandicoots (>10%: Lenghaus *et al.* 1990). Several other disorders, notably debilitating infestations of ectoparasites, have been identified as potentially important secondary causes of mortality. Pesticide contamination has had a potentially large but unknown effect on bandicoot survival and vigour, given the tendency of soil invertebrates to concentrate pesticide residues and the dependence of bandicoots on these organisms for food (Lenghaus *et al.* 1990). Accidental deaths also occur occasionally during live-trapping of animals for the population-monitoring programme (Lenghaus *et al.* 1990) and at other times.

The possibility of extinction of the eastern barred bandicoot on the mainland was foreseen for several years prior to its near extirpation. Despite management efforts, severe declines in the wild population could not be prevented. Demographic changes described here need to be compared with healthy as well as declining wild populations of other bandicoots and mid-sized marsupials to ascertain whether any consistent patterns are evident. From such studies, we might better understand how small populations behave in deteriorating environments.

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References

Allee, W. C., Emerson, A. E., Park, O., Park, T., and Schmidt, K. P. (1949). 'Principles of Animal Ecology.' (Saunders: Philadelphia.)

Backhouse, G. N. (1992). Recovery plan for the eastern barred bandicoot *Perameles gunnii*. Department of Conservation and Environment and Zoological Board of Victoria, Melbourne.

Biological Diversity Advisory Committee (1992). A national strategy for the conservation of Australia's biological diversity. Nature Conservation Branch, Department of Arts, Sport, and the Environment and Territories, Canberra.

Brown, P. R. (1989). Management plan for the conservation of the eastern barred bandicoot, *Perameles gunnii*, in Victoria. Arthur Rylah Institute Technical Report Series, No. 63.

Burgman, M. A., Ferson, S., and Akcakaya, H. R. (1993). 'Risk Assessment in Conservation Biology.' (Chapman and Hall: London.)

Clark, T. W., and Goldstraw, P. W. (1991). Report on field monitoring of the Hamilton population of the eastern barred bandicoot. Report to the Department of Conservation and Environment, Victoria.

Clark, T. W., and Seebeck, J. H. (1990). 'Management and Conservation of Small Populations.' (Chicago Zoological Society: Chicago.)

Dufty, A. C. (1991). Some population characteristics of *Perameles gunnii* in Victoria. *Wildlife Research* **18**, 355–66.

Falconer, D. S. (1981). 'Introduction to Quantitative Genetics.' (Longman: New York.)

Lacy, R. C., and Clark, T. W. (1990). Population viability assessment of the eastern barred bandicoot in Victoria. In 'Management and Conservation of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 131–46. (Chicago Zoological Society: Chicago.)

Lande, R., and Barrowclough, G. F. (1987). Effective population size, genetic variation, and their use in population management. In 'Viable Populations for Conservation'. (Ed. M. E. Soulé.) pp. 87–124. (Cambridge University Press: Cambridge.)

Lenghaus, C., Obendorf, D. L., and Wright, F. H. (1990). Veterinary aspects of *Perameles gunnii* biology with special reference to species conservation. In 'Management and Conservation of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 89–108. (Chicago Zoological Society: Chicago.)

Lindenmayer, D. B., Clark, T. W., Lacy, R. C., and Thomas, V. C. (1993). Wildlife conservation policy and population viability assessment: a review with reference to Australia. *Environmental Management* **17**, 745–58.

Minta, S. C., Clark, T. W., and Goldstraw, P. (1990). Population estimates and characteristics of the eastern barred bandicoot in Victoria, with recommendations for population monitoring. In 'Management and Conservation of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 47-76. (Chicago Zoological Society: Chicago.)

Press, W. H., Flannery, B. P., Teukolsky, S. A., and Vetterling, W. T. (1990). 'Numerical Recipes in Pascal. (Cambridge University Press: New York.)

Ralls, K., and Ballou, J. (1983). Extinction: lessons from zoos. In 'Genetics and Conservation'. (Eds C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and L. Thomas.) pp. 164–84. (Benjamin/Cummings: Menlo Park, California.)

Robinson, N. A., Sherwin, W. B., Murray, N. D., and Graves, J. A. M. (1990). Applications of conservation genetics to the eastern barred bandicoot. In 'Management and Conservation of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 109–30. (Chicago Zoological Society: Chicago.)

Seebeck, J. H. (1979). Status of the barred bandicoot, *Perameles gunnii*, in Victoria: with a note on husbandry of a captive colony. *Wildlife Research* **6**, 255–64.

Seebeck, J. H., Bennett, A. F., and Dufty, A. C. (1990). Status, distribution and biogeography of the eastern barred bandicoot, *Perameles gunnii* in Victoria. In 'Conservation and Management of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 21–32. (Chicago Zoological Society: Brookfield, Illinois.)

World Conservation Monitoring Center (1992). 'Global Biodiversity: Status of the Earth's Living Resources.) (Chapman & Hall: London.)

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