

# Population Viability Assessment of the Eastern Barred Bandicoot in Victoria

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## Abstract

Small populations are subject to large fluctuations arising from random processes at a variety of levels (genetic, demographic, environmental, and catastrophic), and such variation can place a population at high risk of extinction. We used a computer simulation model to project the likely fate of the remnant population of eastern barred bandicoots (*Perameles gunnii*) in Victoria. With population parameters estimated from available field data, the simulation predicts that the species is almost certain to go extinct in Victoria within 25 years, with a mean extinction time of just 10.6 years. Assuming a greater or lesser frequency of catastrophic floods and droughts alters mean persistence time by only about one year. Increasing the estimated carrying capacity of the habitat has little effect, because the declining population would have no opportunity to exploit a greater carrying capacity. A decrease in available habitat (or a fragmentation of habitat into independent isolates) would accelerate extinction. Even if mortality were decreased to the extent necessary to balance the birth rate, the expected fluctuations around the 'stable' population are sufficient to cause a 19% probability of extinction within 25 years. Greatly reduced mortality, a considerable increase in habitat, and protection from catastrophic events would all be necessary to make the population viable over a moderate time span.

## Introduction

Humans are radically altering the environment: clearing vegetation, replacing diverse, natural ecosystems with agricultural monocultures, eliminating native predators and introducing novel ones, killing native herbivores and placing high

densities of grazing livestock on the lands, and spreading disease vectors globally. As a result, many populations of animals that were once large, widely distributed and diverse are in rapid decline, becoming small, fragmented isolates in remaining natural areas, managed nature preserves, or even zoos. Clearly, the eastern barred bandicoot is one of many species that could soon disappear because novel causes of mortality exceed potential reproductive output. Traditionally, wildlife managers have focussed on mean, age-specific determinations of birth and death rates, using life table analyses to determine, for example, whether a population could sustain culling or harvest, or whether it requires increased protection or even supplementation. Recent population estimates show that the eastern barred bandicoot population around Hamilton, Victoria, is not presently self-sustaining; yet in this paper we focus our analyses on processes that put small populations at risk of extinction whether or not the average birth rate exceeds the average death rate.

## Risks of Being Small

When a population is small and isolated from any and all other conspecifics, chance events such as the occurrence, timing, and extent of disease outbreaks, floods and fires, random fluctuations in the sex ratio, and even the randomness of Mendelian transmission of genes can become more important than whether the population has

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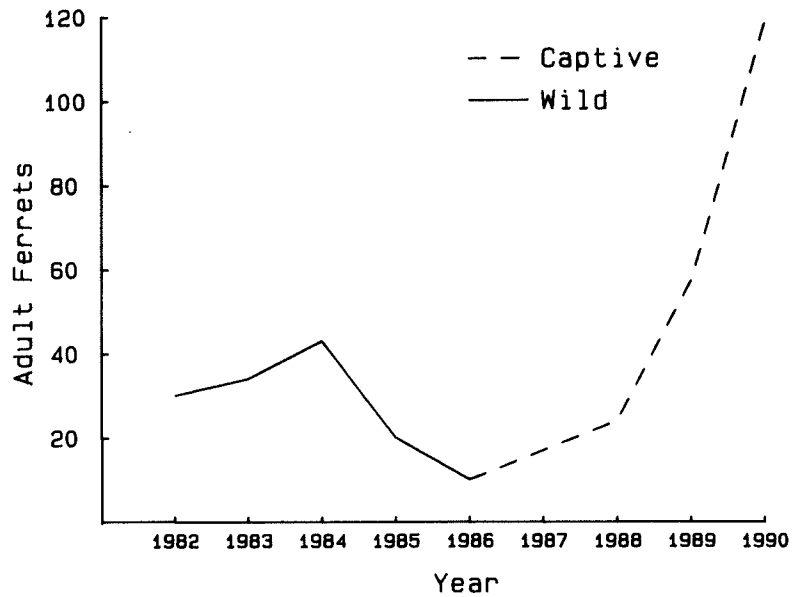


Figure 1.—Numbers of adult black-footed ferrets in the only remaining wild population at Meeteetse, Wyoming, and then in captivity from the time that the Meeteetse population was discovered until 1990. Data from Forrest *et al.* (1988) and B. Miller (personal communication).

sufficient habitat to persist, is well adapted to that habitat and has a mean birth rate that exceeds the mean death rate. Populations neither stay constant in size nor follow perfectly linear decline or growth. When numbers are few, fluctuations of a few tens of animals due to the vagaries of reproduction and mortality can lead to large relative changes in overall population size. Figures 1 and 2 show the fluctuations in two remnant populations, black-footed ferrets (*Mustela nigripes*) and Puerto Rican parrots (*Amazona vittata*), during recent years. Both populations were intensively studied and managed; yet the fluctuation in numbers is striking, even for the very long-lived parrot. The primary danger to a small population is simply that with such fluctuations the population size is likely to hit zero before long. Although the underlying causes of extinction may be predictable factors such as habitat destruction, increased predation, or over-hunting, the final extinction event is more likely to result from 'bad luck' that strikes a population that had been

reduced previously to such low numbers that it has little buffering from the vicissitudes of the physical, biotic and human environments, and little capacity to recover from short-term perturbations.

#### Demographic Stochasticity

Many events in the life of an organism have a random, or stochastic, component, but it is often useful to categorise the stochasticity in the fate of a population into four types (Shaffer 1981). *Demographic* or individual stochasticity is the fluctuation in population size that results from individual reproductive or mortality events being relatively independent outcomes 'sampled' from the mean population parameters. For example, the probability of an individual being killed by a predator may be 25% per year, but somewhat more or less than 25% will be killed in any given year. If predation is random and at a constant probability,  $p$ , we would expect the proportion killed to

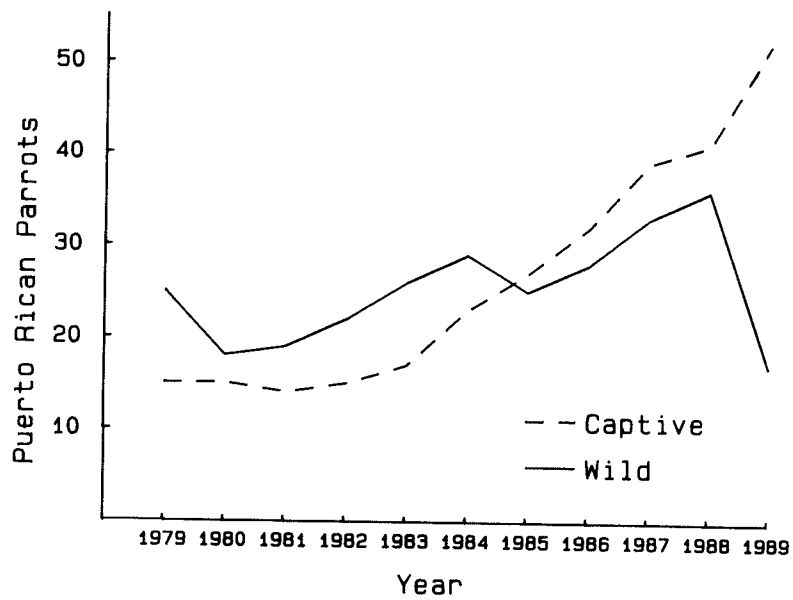


Figure 2.—Numbers of Puerto Rican parrots in the wild and in captivity during the past decade. The wild population was decimated in 1989 by a hurricane. Data from Snyder *et al.* (1987), G. Lee and M. Wilson (personal communication).

follow a binomial distribution, with variance  $p * (1 - p) / N$ . Other causes of mortality and reproduction are similarly probabilistic, for example, the (binomial) probability distribution of finding a mate, and the (multinomial) probability distribution of producing litters of various sizes. Such demographic stochasticity is unimportant if numbers are on the order of 100 or more, but can cause the final extinction of a very small population. By chance, the last five dusky seaside sparrows (*Ammodramus maritimus nigrescens*) were males.

#### *Environmental Stochasticity*

*Environmental stochasticity* is the variation in population birth and death mean rates caused by random fluctuations of the environment. Rainfall, temperature, and local abundance of prey and predators are just a few of many aspects of the environment that can fluctuate more or less randomly, often following normal distributions.

#### *Catastrophic Events*

The third level of stochasticity, *catastrophic events*, are the extreme of environmental variation, but are examined and modelled separately because occasional catastrophes often fall outside the normal range of environmental variation (*e.g.* a hurricane is not just a more extreme storm), because the effects on a population may be much greater than the effects extrapolated from more typical variation (*e.g.* a year-long drought could be much more than four times as damaging as a 3-month drought), and because some catastrophes (*e.g.* fires) are not simply extremes of typical environmental variation. Moreover, rare disasters are often the final insult that drives a small, but otherwise healthy, population extinct. A hurricane decimated one of the two extant populations of whooping cranes (*Grus americana*) in the 1940s. The only remaining wild population of black-footed ferrets was destroyed by an epidemic of sylvatic plague among their prairie dog

prey, followed by an epidemic of canine distemper among the ferrets themselves (Seal *et al.* 1989, Clark 1989). Recently, a hurricane decimated the only wild population of Puerto Rican parrots, apparently killing about half of the birds, and leaving the remainder extremely vulnerable to starvation and predation in a defoliated forest.

#### *Genetic Stochasticity*

A fourth source of stochasticity affecting small populations is random *genetic* change. In sexually reproducing, diploid organisms, progeny are not perfect genetic replicas of their parents, but rather a random draw of one (quite possibly recombined) chromosome of each homologous pair from each parent. As allele frequencies change at random each generation ('genetic drift'), genetic variance is depleted and genetic variants are successively lost from the population. The resulting increased homozygosity (a form of inbreeding) typically reduces fecundity and viability, and the loss of genetic variants reduces the opportunity for natural selection to adapt the population to changing environments (Lacy 1987; Robinson *et al.*, this volume).

#### *Population Viability Analysis*

Unfortunately, each of the diverse risks faced by a small, isolated population is likely to cause further decline (at least temporarily) in the population size, in turn exacerbating each of the other stochastic factors. The population can be pushed by the cumulative impacts of random events ever more rapidly toward extinction (Gilpin and Soulé 1986), a process described as an 'extinction vortex'. The process of modelling and analysing the various deterministic and stochastic forces determining the fate of a population is termed *Population Viability Analysis* (PVA; Soulé 1987). The result of a PVA is an estimate, based on available information, of the probability that a population will persist over time scales of interest. PVA is a very recent approach, but has already been applied to several species (*e.g.* Parker and Smith

1988; Seal *et al.* 1989; Seal and Lacy 1989; Lacy *et al.* 1989).

Why bother with a PVA, rather than (or in addition to) putting efforts into protecting and recovering an endangered population, regardless of whether it has a 1% or 50% or 99% probability of going extinct within a decade? First, many species need protection, but resources for conservation are limited. We need to know whether a species is in a crisis—literally on the verge of extinction. Will the population be likely to recover if left on its own, or will it require aggressive management to pull it away from the extinction vortex? Secondly, we need to identify those factors that are the primary sources of risk for the population. A recent PVA has suggested that Florida panthers (*Felis concolor coryi*, the only remaining subspecies of mountain lion in the eastern United States) are disappearing because 25% are killed by cars annually, because mercury contamination of the Everglades ecosystem has reached lethal levels for top carnivores, and because deer hunting by humans in southern Florida keeps prey sufficiently scarce to prevent successful reproduction by panthers over much of the habitat. A PVA of the Puerto Rican parrot, on the other hand, demonstrated that species recovery was sufficiently steady to minimise the risk of extinction, unless a hurricane were to strike the island and devastate the Luquillo forest that is home to the 40 or so wild and 40 or so captive parrots. The primary recommendation arising from the parrot PVA was that it was urgent that a subpopulation of captive parrots be moved off the island to provide insurance against the possibility of a catastrophic storm. As evidence that PVAs can be valuable predictors of the future, and that ignoring available information can be disastrous, a severe hurricane did strike Puerto Rico just months after the PVA and before any birds were removed from the Luquillo forest. Similarly, the extreme risk to the one wild population of black-footed ferrets of a canine distemper disease outbreak was identified several years before a distemper epidemic largely exterminated the wild population in 1985 (Clark 1989). Fortunately, 12

ferrets were brought into captivity during the course of the epidemic; even then, six of those died from distemper.

PVA can and should also be used to assess the improved probability of survival that would result from each possible management action. For example, a PVA on the ferrets in 1986 suggested that captive breeding was the only strategy that increased the probability of species survival substantially above zero (Harris *et al.* 1989).

Before presenting our PVA of eastern barred bandicoots, we will stress that the models we use are all still crude. We do not assess all risks in the models, nor do we adequately incorporate the feedback among demographic and genetic components. As a result, our projections of extinction probabilities are almost certainly *underestimates*. Fortunately, our expertise with PVAs evolves and improves with each species considered.

### *Simulation Modelling*

Our approach to population viability analysis involves simulation modelling. It is in theory possible to derive equations for the needed probability distribution, but no one has yet proceeded beyond very simplistic analytical treatments. Goodman (1987) has provided equations for estimating the probability of extinction over time from the maximum population size sustainable in the habitat (carrying capacity,  $K$ ), the mean population growth rate ( $r$ ), and the variance in  $r$ . For bandicoots, we know neither  $r$  nor the variance in  $r$  across years. To model the Hamilton bandicoot population, we used a computer program (SIMPOP), written by one of us (Robert C. Lacy) in the C programming language. Many of the algorithms in SIMPOP were taken from a simulation program, SPGPC, written in BASIC by James W. Grier of North Dakota State University (Grier 1980a,b; Grier and Barclay 1988). Grier makes his program freely available to anyone with a use for it, and we similarly will provide the source code and provide compiled versions (for use on

microcomputers using the MS-DOS operating system) of SIMPOP. The open flow of information among biologists concerned with conservation has been essential to the very rapid spread of concepts, tools and data needed by many.

SIMPOP models population processes as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator. (For example, a typical random number generator uses the number of seconds elapsed since the year 1900, divides that by the largest single precision number the computer can store in its memory, and then uses the fractional remainder of that division to generate a random number between zero and one. If a number so determined is greater than the probability of an event, that event is deemed to have occurred in the simulation.) The SIMPOP model simulates the birth and death processes of a population by generating random numbers to determine whether each animal lives or dies, and whether each adult female produces broods of size 0, or 1, or 2, or 3, or ... during each year. Mortality and reproduction probabilities are assumed to be the same for each sex, and fecundity is assumed to be independent of age (after an animal reaches reproductive age). Mortality rates are specified for each pre-reproductive age class and for reproductive-age animals. Each simulation is started with a specified number of males and females of each pre-reproductive age class, and a specified number of males and females of breeding age. The computer program simulates and tracks the fate of each population, and outputs summary statistics on the probability of population extinction over a specified time span and the mean time to extinction of those simulated populations that went extinct. A population carrying capacity is imposed by truncation of each age class if the population size after breeding exceeds the specified carrying capacity. Each year in the simulation, the number of animals surviving, as well as the number reproducing, would be expected to follow binomial distributions with means equal to the specified probabilities. Environmental variation in reproduction, survival and the carrying capacity is incor-

porated into the model by increasing the binomial or Poisson variances in these parameters by an amount specified by the user. These variances are functions of the starting population size, so the effect of doubling the variance in survival, for example, depends on the initial population size (smaller N yields larger binomial variance).

In SIMPOP, catastrophes affecting mortality and breeding are independent. The frequencies and severities of breeding catastrophes and survival catastrophes are specified by the user. A catastrophe is determined to occur if a randomly generated number between 0 and 1 is less than the probability of occurrence (*i.e.* a binomial process is simulated). If a breeding catastrophe occurs, the probability of breeding is multiplied by a severity factor that is drawn from a binomial distribution with mean equal to the severity specified by the user. Similarly, if a survival catastrophe occurs, the probability of surviving each age class is multiplied by a severity factor that is drawn from a binomial distribution with the mean equal to the severity specified by the user. Thus, not all catastrophes are of equal magnitude; rather, they are distributed around a mean specified by the user, with variances set relative to initial population sizes (as for environmental variation). SIMPOP also allows the user to supplement or harvest the population for any number of years in each simulation (see Maguire *et al.* this volume).

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Some of its artificialities are the absence of trends across years (*e.g.* no long-term changes in the environment, and no multi-year environmental perturbations or catastrophes), the independence of environmental variation in birth and death rates, and the lack of density dependence of birth and death rates except when the population exceeds the carrying capacity. The first two of these simplifications are likely to lead to underestimates of extinction rates, while the third may cause underestimation or overestimation of extinction.

### *Population Biology Parameters—Eastern Barred Bandicoot*

Accurate estimates of both means and variances of population parameters are essential to population viability analysis. Extensive field research is therefore a prerequisite to all population modelling and management. Our data were obtained from reports by Brown (1989), Dufty (1988), and Minta *et al.* (this volume), and from work on eastern barred bandicoots in Tasmania by Heinsohn (1966). We are indebted to the many field researchers who contributed to collection of these data, and we hope that the shortcomings of our analyses will encourage further field work so that future analyses can be more accurate and more useful in directing the recovery and management of the species in Victoria.

### *Population Size and Growth Rate*

Based on the number of hectares occupied by bandicoots and the presumed density of bandicoots per hectare, it was estimated that about 1,750 eastern barred bandicoots existed when Moon (1984) surveyed the habitat in 1982-1983, a maximum of 633 in 1985 (Brown 1989), and an estimated 229 (maximum of about 300) in 1988 (Dufty 1988). Although these estimates are based on varied field techniques and areas sampled, it is obvious that the Victorian population of eastern barred bandicoots is in rapid decline. Regression analysis of the above data indicates that the population has declined about 25% per year during the 1980s. This is a slower rate of decline than would be projected from the replacement rate (0.48 female offspring per female) estimated by Robinson *et al.* (this volume).

An optimistic estimate of the present population size (in mid-1989) would be 300 bandicoots; a more conservative estimate would be 150. This remnant population is divided between two relatively discrete areas of habitat, a population centered around the Hamilton Municipal Tip, a few other areas in and near the city of Hamilton, and

a secondary (though perhaps more healthy) population of about 60 animals in the Chatsworth Road area a short distance east of Hamilton. It is not known whether bandicoots move between these two centres with any regularity. To assess the viability of the Victorian eastern barred bandicoot population as a whole, and the viability of sub-populations such as that in the Chatsworth Road area, we have analysed simulations started with 60, 150 and 300 bandicoots.

#### *Population Carrying Capacity*

The steady and rapid rate of decline of eastern barred bandicoots in Victoria suggests that the habitat in Hamilton is unable to support more bandicoots than are presently there. It is entirely possible that the population currently exceeds the sustainable carrying capacity. We simulated populations with carrying capacities of 60, 150, and 300 bandicoots. A greater capacity, if available, would have little effect on the simulation results because the negative growth rate of the population makes it unlikely that the Hamilton population would exceed 300 animals (unless causes of mortality are reduced and the present decline reversed; see Maguire *et al.*, this volume).

#### *Fecundity*

Bandicoots have among the highest reproductive potential of any mammal of their size (Henne-mann 1983), with a 12-day gestation (the shortest known for any mammal), weaning at 60 days of age, first breeding at about 4.5 months of age or less, and interbirth intervals of 70-90 days. Studies by Heinsohn (1966) in Tasmania, Dufty (1988), Brown (1989), and Minta *et al.* (this volume) indicate that most females over 500 g were carrying pouch young or were clearly lactating (suggesting that a litter was in a nest) when trapped. The few adult females not observed to be lactating could be the fraction of the adult females expected to be gestating (12/72) if breeding occurs immediately after each litter is weaned. Thus it appears that eastern barred bandicoots in Victo-

ria breed almost continuously after reaching about 500 g (4.5 months). Data from Brown (1989), Dufty (1988), and Minta *et al.* (this volume) all suggest that the mean litter size (after early non-observed mortality) is about 2.20, distributed as about 17% litters of one, 50% litters of two, 29% litters of three and 4% litters of four.

Although it requires 2 to 3 months for a female to raise a litter to independence, the computer simulation assumes that breeding is instantaneous. To model the bandicoot population, we considered the bandicoot life cycle to consist of events occurring at 3-month intervals. We therefore assumed that bandicoots first breed at 6 months of age (about the mid-point in the first breeding cycle), and that they produce subsequent litters every 3 months until they die. Three months is slightly longer than the mean observed interbirth interval, thus allowing for a small fraction of females not breeding at any given time or delaying a breeding episode briefly.

#### *Mortality*

Unless a large number of marked individuals can be followed over time (by radio-tracking, or by repeated and frequent recaptures), it is very difficult to estimate accurately the age-specific mortality of any natural population. Mortality data on the bandicoots will present a biased view of the causes and frequency of deaths (Lenghaus *et al.* this volume), because most carcasses are never recovered, especially those taken by natural predators. Minta *et al.* did recapture 62 of 106 bandicoots that had been marked 3 to 10 months earlier by Dufty (1988) (and also captured 83 bandicoots not so marked). If Minta *et al.*'s trapping effectively sampled the area used by the bandicoots marked by Dufty, these data would suggest that about 58% of adult eastern barred bandicoots survive 6 months, or about 75% survive each 3-month interval of the simulated population. Given the high mortality rate, it is unlikely that many bandicoots survive long enough to become senescent or even to decline in fertility.

Juvenile mortality is even harder to assess than adult mortality, but is likely to be much greater. The mortality estimates used in our simulations are simply plausible guesses that would result in the observed mean population decline of about 25% per year (given the observed reproductive rate). We assume that mortality from birth to 3 months of age (primarily pre-weaning mortality) would be 50%, that juvenile mortality (3 months to 4.5 months) would be 50% (the period just after independence from the mother being likely to be the time of greatest mortality), and that mortality of young adults entering reproductive condition (4.5 months to 6 months) would be 37% (intermediate between juvenile and adult mortality). (The combined 3 to 6 month mortality would then be 68.75%.) For the purposes of demographic analysis and projection of population growth, it does not matter how pre-reproductive mortality is distributed among infant, juvenile and sub-adult age classes (although effective management of the population may require knowledge of the causes and stages of greatest mortality). Nor will it change demographic trends if litters are initially larger than assumed, but reduced to the observed sizes by undocumented mortality that occurs early in life. The population growth rate will be determined solely by the number of progeny per female that reach reproductive age. Recognizing the uncertainty in these mortality estimates, we also simulated populations with 15% lower mortality at each post-weaning age class, thereby modelling a population with no mean increase or decrease ( $\lambda=1.00$ ) in years without catastrophes.

#### *Sex Ratio*

Because male and female bandicoots probably utilise differently sized home ranges (Dufty 1988; Minta *et al.* this volume) and have different patterns of activity, it is difficult to assess the population sex ratio from trapping data. Brown (1989) reported a ratio of 69 males: 74 females among trapped adults, Dufty (1988) trapped 73 males and 33 females, and Minta *et al.* (this volume) trapped 52 males and 36 females. Although there is perhaps an excess of males in the population (it is more likely that males range more widely and

are therefore more readily trapped), we conservatively assumed in our analyses that there is a 1:1 sex ratio at birth and that mortality affects both sexes equally.

#### *Environmental Variability*

The Australian climate is highly variable. Rainfall, temperature and population dynamics of other species (both floral and faunal) probably affect bandicoot survival. Although eastern barred bandicoots appear to breed year-round in Victoria, it is likely that there is some seasonal and annual variation in reproduction. Unfortunately, no study of the Hamilton population of bandicoots has extended long enough to provide data on annual variation in reproduction and mortality. For the purposes of this preliminary PVA, we have conservatively assumed that breeding is continual (a litter every 3 months beginning at age 6 months) and therefore without seasonal and annual variation, and that variation in the mean mortality rate and carrying capacity of the population is approximately comparable to the variation expected to occur due to the random demographic stochasticity. With 25% mortality of adults per 3 months, the binomial variance in mortality expected if mortality is wholly random among individuals is  $V = pq/N = 0.00125$  for a population of 150. Thus, we assumed an additional environmental variation in mortality of 0.00125, so that the adult mortality rate every 3 months was drawn from a distribution with mean 0.25 and standard deviation 0.035. Similarly, the environmental variation in carrying capacity was assumed to mirror random (Poisson) variation, so that  $K$  varied seasonally around a mean with variance equal to that mean ( $SD = 12.2$ , when mean  $K = 150$ ).

#### *Catastrophes*

Droughts, floods, and fires are all likely to affect bandicoot populations. Seebeck (1979; Seebeck *et al.* this volume) reported anecdotal evidence that the bandicoots declined markedly during droughts in 1916 and 1966-1968, Heinsohn (1966) reported that drought caused an early termination



of the 1961-1962 breeding season in Tasmanian eastern barred bandicoots, and Brown (1989) reported that reproduction ceased during the 1982-1983 drought. Floods and fires could kill bandicoots (often indirectly by forcing them to areas lacking adequate cover to avoid predators), but would be more localised in effect than would droughts. Based on little more than intuition, we estimated that a drought would cause a cessation of breeding for a year but with minimal effect on survival, while a fire or flood would cause an immediate mortality of about 25%, but have little effect on breeding for the year. Historical records indicate that the Hamilton area has had three severe and prolonged droughts this century (1916, 1966-1967, and 1982-1983), four floods (1909, 1946, 1970, and 1983), and one large fire. Thus we estimate the probability of a year-long drought at 3.4% (3/88 years), and the probability of fire or flood at 1.4% per 3-month interval (five occurrences/88 years). Lesser droughts and very local perturbations of the habitat (*e.g.* slashing) undoubtedly cause some mortality and reproductive failures, but could be considered under the category of environmental variation (above) rather than catastrophe. Recognising the considerable uncertainty in these estimates of the severity and frequency of catastrophes, we also examined scenarios with either no catastrophes or double the above frequencies.

#### *Time Scale of Population Projection*

The goals of managing any endangered species should include (minimally) recovery of a self-sustaining population at numbers that make further interventive management unnecessary. A self-sustaining population must be defined in terms of an acceptably low probability of extinction over an acceptably long period of time. (No population is assured of persistence over any time scale, of course, and every population is certain to go extinct eventually.) Shaffer (1981) suggested that a viable population of grizzly bears (*Ursus arctos horribilis*) be defined as one with a 99% probability of persistence for 1,000 years. In the case of the eastern barred bandicoot, a linear projection of the present 25% annual decline

suggests that the Hamilton population will decline to extinction within 20 years. Management must reverse this decline within a few years if the species is to persist in Victoria, and we therefore have confined this preliminary PVA to a 25-year time frame. Once it is believed that population stability has been achieved, it will be important to reassess population viability with the new population parameters in order to determine whether the population is sufficiently robust to survive the various identifiable sources of stochasticity well into the future.

#### *Results*

Table 1 summarises the population biology parameters that represent our best estimate of the current conditions at Hamilton, the 'Basic scenario', as described above. Figure 3 shows the fates of 10 simulated eastern barred bandicoot populations under this basic scenario. The figure clearly shows the rapid decline projected from the past decade, but also shows moderate variation among runs, including some periods of apparent population stability and short-term increases. Figures 4 and 5 show the frequency distribution and cumulative frequency distribution of times to extinction from 10,000 simulations using the basic parameters. In the majority of simulations, the Hamilton bandicoot population was extinct by the year 2000.

Table 2 shows the results generated from 1,000 computer simulations of the Hamilton population of bandicoots, under several plausible scenarios describing the present population dynamics. For the basic scenario, the SIMPOP program projects that the Hamilton bandicoot population is virtually certain to go extinct within 25 years, with a mean time to extinction of just 10.6 years.

Table 2 also shows scenarios in which we altered several of the parameters for which we have few data. If catastrophes such as fires, droughts and floods have little or no impact on the eastern barred bandicoot population, the simulation still projects that the Hamilton population is likely to

*Table 1.*—Population parameters estimated for the current conditions in the Hamilton population of eastern barred bandicoots; basic scenario used for computer simulations. Deterministic calculations of mean population growth rate and generation time also given.

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First age of reproduction: 6 months (approximate mid-point of first breeding cycle)

Litter size distribution:

- 0 % females produce litters of size 0
- 17 % females produce litters of size 1
- 50 % females produce litters of size 2
- 29 % females produce litters of size 3
- 4 % females produce litters of size 4

Mortality:

- 50 % percent mortality between 0 and 3 months of age
- 50 % mortality between 3 and 4.5 months of age
- 37 % mortality between 4.5 and 6 months of age
- 25 % 3-month mortality of adults (> 6 months of age)

Carrying capacity of 150

Environmental stochasticity in mortality and carrying capacity assumed to match demographic variance of the starting population of 150. No environmental variance assumed in reproduction (all adult females assumed to breed every 3 months).

Frequency and severity of catastrophes:

- 0.034 probability of drought, causing total reproductive failure
- 0.056 annual probability of flood or fire, causing 25% mortality

Initial population size:

- 24 male, 24 female juveniles (3 months old)
- 51 male, 51 female adults (age  $\geq$  6 months)

Annual population growth rate:

- in absence of catastrophes,  $\lambda = 0.75$
- including catastrophes,  $\lambda = 0.69$

Generation time = 13.5 months

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go extinct, with a mean time to extinction just a year longer than in the basic scenario. Doubling the frequency of catastrophes decreases the mean time to extinction by about one year. A greater carrying capacity (300 vs. 150) has virtually no impact on the population viability, because the declining population would be unable to expand into additional available habitat. If the carrying capacity is only 60, extinction is accelerated considerably. This scenario (#5 in Table 2) also represents the expected fate of the smaller Chatsworth Road population, if it is demographi-

cally isolated from the rest of the Hamilton-area bandicoots and if the basic population biology parameters used in the modelling describe accurately the Chatsworth Road sub-population.

The mortality rates used in the basic scenario were chosen so that the population declined at an average rate of 25% per year in the absence of catastrophes. It could be argued, however, that, although the Hamilton bandicoot population has been declining at such a rate through the 1980s, the population is now relatively stable. (This is

Table 2.—Results from 1,000 computer simulations of the Victorian population of eastern barred bandicoots. Probability of extinction is given at 5-year intervals, with the mean time to extinction of those simulated populations that became extinct within 25 years.

Scenario <sup>1</sup>	Probability of extinction					Mean no. years to extinction
	5 yr	10 yr	15 yr	20 yr	25 yr	
1. Basic <sup>2</sup>	0.01	0.48	0.91	0.99	1.00	10.6
2. No catastrophes	0.01	0.35	0.81	0.97	0.99	11.9
3. 2X catastrophes	0.04	0.68	0.95	0.99	1.00	9.3
4. K = 300	0.00	0.48	0.90	0.98	1.00	10.8
5. K = 60	0.18	0.81	0.98	1.00	1.00	7.8
6. Zero population growth <sup>3</sup> (ZPG)	0.00	0.01	0.04	0.11	0.19	19.0
7. ZPG + no catastrophes	0.00	0.00	0.01	0.03	0.05	19.3
8. ZPG + 2X catastrophes	0.00	0.03	0.14	0.31	0.47	17.7
9. ZPG + K = 300	0.00	0.00	0.02	0.07	0.13	19.4
10. ZPG + K = 60	0.01	0.15	0.34	0.51	0.63	14.8
11. ZPG + no catastrophes + K = 300	0.00	0.00	0.00	0.01	0.02	20.6

<sup>1</sup>Population parameters as in the basic scenario, with changes as indicated.

<sup>2</sup>Population parameters estimated for current conditions in the Hamilton population, as described in text and Table 1.

<sup>3</sup>Achieved by a 15% reduction in mortality.

perhaps the most optimistic scenario that is at all plausible; it could not be argued logically that the population is experiencing population growth.) Scenario #6 projects that the Hamilton population has a 19% probability of extinction, if the mean growth rate is zero in those years not affected by a catastrophe. Even if the population growth rate approximates zero and no catastrophes occur (scenario #7), there is a modest probability (5%) that the eastern barred bandicoot will go extinct in Victoria within 25 years. Assuming a carrying capacity of 300 and zero population growth, but with catastrophes (scenario #9), improves the prospects for population survival (13% extinction vs. 19%), but not by much. A small eastern barred bandicoot population, such as that at Chatsworth Road, has a high probability of extinction even if mean birth and death rates are equal (scenario #10).

### Discussion

The simulation results presented here do not tell us what will happen to the Hamilton population of eastern barred bandicoots; rather, they project what is most likely to occur given the mean population parameters estimated from field data and the sources of stochasticity identified in the population. The current population may have birth rates higher or death rates lower than estimated, and other parameters may be more favorable than determined from available data. Thus, even in the absence of amelioration of circumstances, the eastern barred bandicoot may have longer to survive than we have projected—if just because of luck (*e.g.* 21 of 10,000 simulations of the basic scenario survived the 25 years; the Hamilton population could be lucky as well). It is perhaps more likely, however, that we have ne-

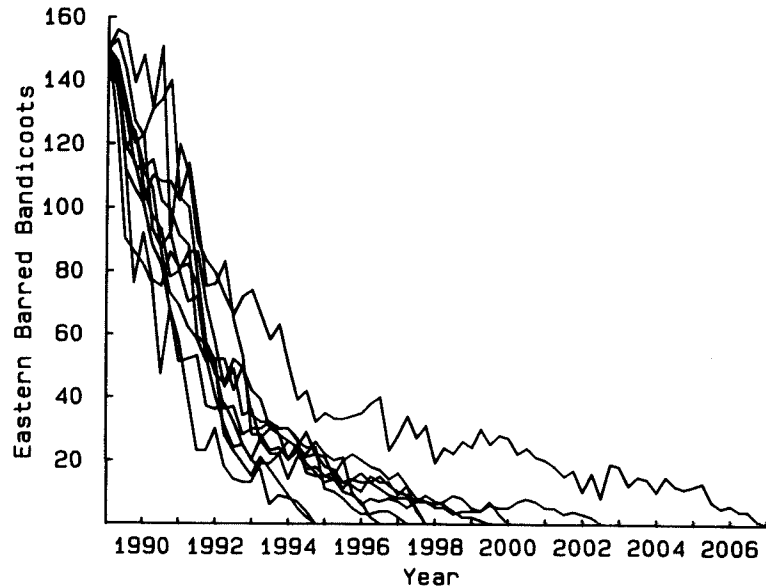


Figure 3.—Fates of ten simulated populations of the eastern barred bandicoots, with population biology parameters as described in the text and Table 1 (basic scenario).

glected some sources of population instability (e.g. inbreeding effects) in our models, and that the Hamilton population is more at risk than indicated in Table 2 and Figures 4 and 5.

Based on our current best estimate of the population biology of the species, the size of the present population, and the habitat available, we project that the eastern barred bandicoot will be extinct in Victoria in about a decade, and almost certainly within two decades, unless actions are taken to reverse the decline. Alternative, plausible estimates of the current population size, growth rate, and frequency of catastrophe often project greater probability of survival, but in none of the cases examined do we project that the eastern barred bandicoots are secure from extinction in the next few decades.

These results, in accord with PVAs of other species mentioned previously, demonstrate that random fluctuations in population size, caused by easily identifiable sources of stochasticity, make populations as small as the bandicoots in Victoria sufficiently unstable so as to be inviable over modest time scales. Even in the absence of further habitat decay, increased predation, or other causes of population decline, apparently healthy populations of small size have limited expected duration. In widely distributed species, local populations often do go extinct, but are readily recolonised from adjacent populations. A single or a few remnant populations isolated from any possible source of supplementation and recolonisation will not survive indefinitely and perhaps not even for long. Thus, it is not sufficient to protect a remnant population, such as the Hamilton eastern barred

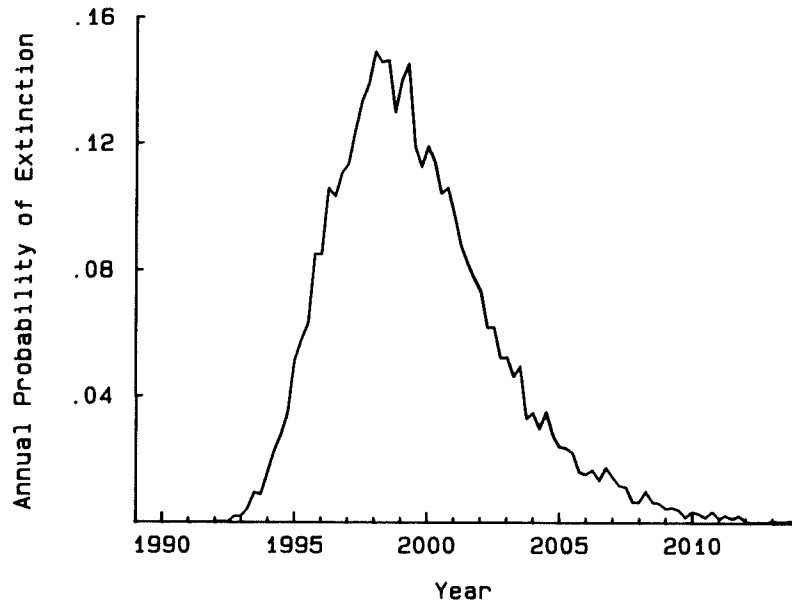


Figure 4.—Frequency distribution of times to extinction of the Hamilton population of the eastern barred bandicoot from 10,000 computer simulations, using population parameters as described in the text and Table 1 (basic scenario).

bandicoots, from those causes of decline that eliminated other populations of the species; aggressive action must be taken quickly to increase the numbers of the population and to establish or re-establish additional populations. The goal of recovery must be to pull a population out of the extinction vortex, by returning it to numbers, range and diversity such that normal population dynamics (including temporary local extinctions) do not lead to irreversible regional or global extinction of a taxon.

Population viability assessment is a tool, not a conclusion. It allows quantification of the compound impact of a number of forces impinging upon a population, often when intuition and subjective synthesis are incapable of perceiving the magnitude of extinction risks. By understanding the risks faced by a population, we can determine

the urgency of action to change those parameters. Perhaps some of the parameters utilised in the modelling of eastern barred bandicoots in Victoria are wrong—certainly many are based on few data. One consequence of a PVA is that critical aspects of the biology of a species can be identified, indicating where further field work may substantially increase our ability to predict the fate of a population and where management actions to change population dynamics might be especially effective. From Table 2, it can be seen that the bandicoot carrying capacity of the Hamilton area is of little relevance if high mortality continues to cause population decline. Maguire *et al.* (this volume) explore further the efficacy of possible management actions in reducing the probability of extinction of the eastern barred bandicoot in Victoria.

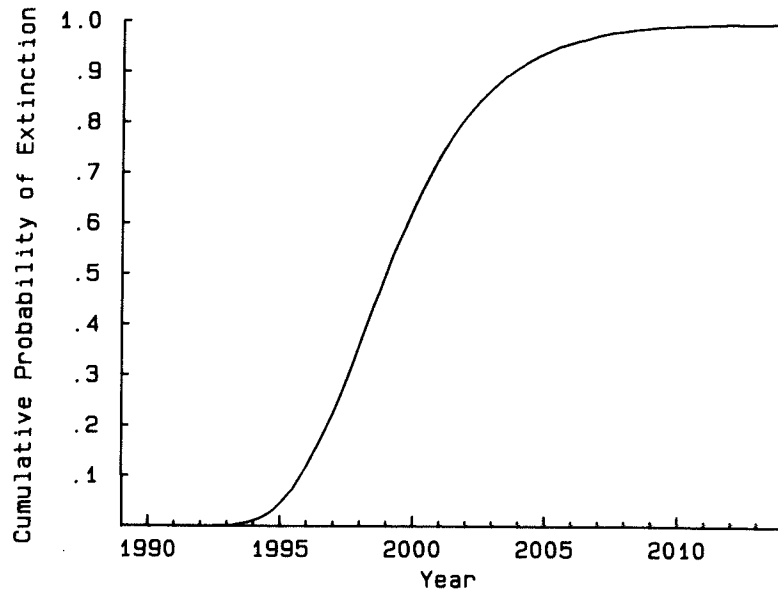


Figure 5.—Cumulative frequency distribution of times to extinction of the Hamilton population of the eastern barred bandicoot from 10,000 computer simulations, using population parameters estimated from data on the present Hamilton population, as described in the text and Table 1 (basic scenario).

PVA is a new tool for population management and conservation. We need refinements of the models (incorporating, for example, feedback between demographic fluctuations and random genetic changes), we need more precise data to feed into the models, and we need to monitor populations to confirm the predictive power of the PVAs. As the use of PVA has revealed the critical importance of random variation—in demographic events, in the environment, and in genetic processes—to the final extinction of many populations, it has become apparent that we lack an empirical understanding of the magnitude of such variation in natural systems. We do not know, for example, how reproductive rates and mortality rates vary seasonally and annually for the eastern barred bandicoot, nor do we know the extent of fluctuations in population numbers and density. The PVA of the Victoria population of the eastern barred bandicoot should be repeated,

as additional data improve our understanding of the dynamics of the population and, more importantly, as management actions change those factors affecting the probability of population persistence.

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