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MODELLING THE REINTRODUCTION OF THE GREATER BILBY *Macrotis lagotis* USING THE METAPOPULATION MODEL ANALYSIS OF THE LIKELIHOOD OF EXTINCTION (ALEX)

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Abstract

Population viability analysis of the greater bilby Macrotis lagotis *was conducted using the metapopulation model ALEX. ALEX was used to examine the effect of reintroduction configurations and potential manipulations on the extinction risk of the metapopulation. More specifically, the impact of patch separation, sporadic big rains and fire on population survival was investigated.*

Estimates of population parameters, including survival and fecundity, dispersal rate and home range size, were derived from a bilby reintroduction programme conducted in central Australia, as were parameters describing environmental quality and the impact of fire, drought and sporadic large rainfall events.

The modelling results indicated that local segregation of a population to achieve replication did not change extinction risk dramatically and that an experiment for a 2-year duration (equivalent to a generation time) could be achieved at low risk with a small population. Adult mortality was of key importance in determining population survival. With the release of 12 individuals, drought and sporadic high rainfall events limited the life of the reintroduced population to a median of 8 years. In the absence of these events, median extinction time was extended to 26 years. The modelling indicated that there was little scope to reduce environmental variation (and improve the population survival prospects) through manipulation or management of the environment. However, spatially subdividing subpopulations so that they should experience appreciably different big rainfall and drought events has potential to reduce metapopulation extinction risk.

Keywords: Population viability analysis, reintroduction, bilby.

INTRODUCTION

The application of a population viability analysis model in the formulation of a species reintroduction programme is discussed using the greater bilby *Macrotis lagotis* as an example. The bilby is a type of a bandicoot. It is nocturnally active, semi-fossorial, constructing a deep burrow for shelter, and omnivorous consuming predominantly seed, bulbs and invertebrates (Johnson, 1989). The species is strongly sexually dimorphic in size with adult males weighing 1500–2500 g and females 700–1100 g. It was once distributed over 70% of the arid and semi-arid parts of Australia but declined rapidly in the late 1800s and early 1900s and is now considered vulnerable to extinction by the IUCN (Kennedy, 1992). The remnant populations are restricted to relatively unproductive areas of the former range where stock, rabbits *Oryctolagus cuniculus* and foxes *Vulpes vulpes* are absent or rare (Southgate, 1990*a*). A programme was initiated in the mid 1980s to determine if reintroduction could be used to expand the species' current range.

The role of reintroduction in conservation is generally perceived to be one of providing a management tool for the creation of additional subpopulations or to bolster an existing population. This notion has been reinforced in a policy produced by the Reintroduction Specialist Group of the IUCN (1987), which advocates that reintroduction be used only when the limiting processes operating at a release site have been eliminated. This presupposes that original causes of decline can be clearly determined and that favourable habitat can be identified and managed effectively. However, it is rare for the habitat requirements of a threatened species to be thoroughly understood and frequently the threatening processes are not clearly evident (Scott & Carpenter, 1987; Griffith *et al.*, 1989; Short *et al.* 1992). Under these circumstances, the acceptability of habitat conditions must be investigated by monitoring the survival, fecundity and dispersal characteristics of the species. In other words, reintroduction must be used as a research tool to define habitat conditions and continue in that role until habitat favourability can be predicted with a high degree of confidence (Southgate, 1994). Once this information is known, site selection or management may be improved to provide the released animals with a higher probability of survival.

If reintroduction is to be used effectively as a research tool we must become familiar with the implications of a particular experimental design and the peculiarities of small population dynamics. Given a set of resources (e.g. a certain number of animals for release), attention must be given to how these resources can be divided to retain the integrity and function of the population but also provide replication to reduce the uncertainty of the experimental results. The impact of the released subpopulation size and distance between subpopulations on the extinction risk needs to be examined. Ultimately, the suitability of conditions at a release site will be reflected in growth of the population and the fate and fecundity of the animals born on site.

Population viability analysis (PVA) is being used more widely to identify threatened species, design programmes of further research and assess the efficacy of management options (Lacy & Clark, 1990; Shaffer, 1990; Beudels, *et al.*, 1992; Lindenmayer *et al.*, 1993; Possingham *et al.*, 1993). In this study, the metapopulation model Analysis of the Likelihood of Extinction (ALEX) described by Possingham *et al.* (1992) and Possingham and Davies (this issue) was applied to examine the outcome of alternative reintroduction experimental designs. ALEX was chosen because it accommodated metapopulation dynamics, environmental stochasticity and the option of exposing subpopulations to independent environmental events. In many simple population models developed to date, environmental variation affects all individuals similarly and simultaneously. This assumption contrasts with nature where spatial and temporal patchiness in the environment (differentially affecting individuals and subpopulations) may be the norm for most species (Wilcox, 1986; Gilpin, 1987; Goodman, 1987; Hanski & Gilpin, 1991; Stacy & Taper, 1992). In the formulation of a potential reintroduction programme, ALEX was used to investigate:

1. the influence of founding population size and subdivision on population viability;
2. the effects of the frequency and magnitude of environmental events on the population; and
3. the options for manipulating the environment or subdividing the population to realise a lower variance in population growth rate.

METHODS

Population parameters for the bilby were derived from a reintroduction programme at Watarrka National Park (WNP) situated 330 km south-west of Alice Springs. The park is about 34,000 ha in area and composed of prominent ranges, dissected valleys with shallow soils and sections with aeolian-deposited sand. The reintroduction site was situated in an area with sandy rises where the dominant vegetation was desert oak *Allocasuaria decaisneana* with an understorey of spinifex *Plectrachne schinzii*; mulga *Acacia aneura*, mixed grasses and herbs dominated the swales. The area chosen for the reintroduction was similar to habitat occupied by the bilby in parts of the Tanami and Great Sandy Desert (Southgate, 1990*b*). No bilbies have been recorded in this area for over 30 years (Finlayson, 1961) and the nearest known population was over 200 km away.

Animals were initially released in April 1988 and the population was intensively surveyed until March 1991. Fifteen captive-bred animals were released during this period (Table 1). Distribution and abundance of the population were obtained by monitoring burrow activity. Periodic tracking and recapture of radio-collared animals provided information on movements, social organisation and survival and fecundity rates. Food was augmented but only the released animals were skilled at using the food hoppers. Mean dispersal distance of the population was determined by averaging the distance between a release site and detected burrow and feeding evidence created by the progeny of released animals (referred to as *in situ* bred animals). The survival and fecundity parameter values used in ALEX were derived from the population prior to its collapse in mid-1990.

The probability of occurrence of major environmental events such as fire, drought and big rainfall are collectively referred to as 'catastrophes' in this paper. A drought catastrophe was deemed to have occurred when the 3-year rolling mean of precipitation was less than 150 mm; similarly, a big rain catastrophe occurred when the 3-year rolling mean of precipitation exceeded 350 mm. Meteorological data from Tempe Downs Station (which adjoins WNP) for the period 1888–1991 ($n = 99$) were used to determine the frequency of these events. The incidence of fire in spinifex grasslands is linked with intermittent large rains (Griffin, 1984; Stafford Smith & Morton, 1990).

PVA models provide a mathematical tool for estimating the probability of extinction of organisms. The probability is derived by simulating an array of interacting processes which is generated from the best available estimates of the life-history parameters of a species, the frequency and relative impact of catastrophes and a key range of environmental processes (Lindenmayer and Possingham, 1991). ALEX is a discrete time-driven model with a 1-year time step. Although a 6-monthly time step would be more appropriate for a species like the bilby, the generic structure of ALEX and the 1-year time step were maintained in lieu of constructing a specific model. Only the numbers of one sex are counted and in this case the female sex was chosen because it was likely to be most limiting to the population. Input mortality parameters were adjusted to reflect the 1-year time period and the fecundity of females less than 1 year old was ignored. In the model, patches may be configured with a unique habitat quality and founder population size, and catastrophes may be initiated to affect individual or all (global) patches. A simulated population may be subjected to

Table 1. Source and fate of animals radio-tracked in Hope Valley, Watarrka National Park (1988–1991)

Animal[a]	Source[b]	Induction date	Independence date	Last record	Age (months) last record	Days independent	Location records	Fate[c]
M79	AZRI	01.03.88	21.04.88	18.10.89	37	540	174	Disappear a
M78	AZRI	01.03.88	21.04.88	22.04.88	17	1	1	Disappear b
F70	AZRI	01.03.88	21.04.88	13.07.90	46	810	198	Dead c
F75	AZRI	01.03.88	21.04.88	17.05.89	25	390	135	Retrieved 1
M68	AZRI	01.03.88	20.10.88	07.03.89	33	150	24	Disappear b
M76	AZRI	01.03.88	20.10.88	29.10.90	49	720	247	Dead a
F71	AZRI	01.03.88	20.10.88	28.08.90	59	660	237	Dead b
F78	AZRI	01.03.88	20.10.88	06.03.89	22	150	59	Disappear b
F365	WNP	—	10.06.89	13.07.90	18	390	140	Dead e
F369	WNP	—	19.08.89	16.03.90	23	510	95	Disappear b
F1	WNP	—	21.04.90	16.05.90	6	30	11	Dead b
F2	WNP	—	20.04.90	28.08.90	~12	120	31	Dead b
F357	WNP	—	20.07.89	24.09.89	3	56	41	Disappear b
F358	WNP	—	20.07.89	24.09.89	3	56	45	Disappear b
M328	WNP	—	03.10.89	18.11.89	5	18	32	Disappear b
F329	WNP	—	03.10.89	20.12.89	6	56	26	Disappear b
M84	AZRI	03.11.89	01.01.90	03.08.90	40	210	41	Dead d
M90	AZRI	03.11.89	01.01.90	10.06.90	33	150	33	Dead c
M350	WNP	—	12.05.90	16.05.90	3	5	4	Dead e
M352	WNP	—	12.05.90	16.05.90	3	3	3	Dead d
M395	WNP	—	11.06.90	11.06.90	3	1	1	Dead d
M346	WNP	—	31.01.91	09.02.91	~12	10	3	Dead e
MA5	AZRI	31.10.90	06.12.90	07.12.90	10	1	1	Dead a
MA15	AZRI	03.12.90	30.01.91	20.02.91	22	21	3	Retrieved 2
F89	AZRI	31.10.90	06.12.90	15.12.90	28	9	6	Dead e
F90	AZRI	09.01.91	30.01.91	31.01.91	16	1	1	Disappear a
FA2	AZRI	31.10.90	06.12.90	14.12.90	14	8	5	Dead b

[a] F, female; M, male in the animal code.

[b] AZRI, Arid Zone Research Institute; WNP, Watarrka National Park.

[c] Disappear a, without trace, functional collar presumed.
Disappear b, without trace, no collar or collar not functioning.
Retrieved 1, eye abscess, death imminent.
Retrieved 2, returned to AZRI.
Dead a, whole or near whole remains found on surface.
Dead b, part or piece remains found on surface.
Dead c, cached remains found.
Dead d, remains found down burrow.
Dead e, collar only found on surface.

the occurrence of up to three independent types of catastrophe and these may be invoked individually or in concert. A catastrophe may be configured to affect population size by nominating the probability of occurrence of a catastrophe and extent to which a population is reduced if a catastrophe occurs. Alternatively, a step-wise state function may be used to link fecundity to habitat quality and habitat quality to catastrophe. In the version of ALEX used in this paper, the number of females that bred each year was derived from the quality of the patch multiplied by the number of females present.

The persistence time for the population was examined in response to several scenarios. In each, the configuration of a population or the magnitude of an environmental variable was systematically altered while keeping the other parameter settings constant to determine the population sensitivity. In Scenario 1 the impact of founder population size on the survival of the population was examined by altering the founder population size in a patch of constant size. The effect of segregation on the population was examined in Scenario 2 by altering the number of patches and the initial founder population in each patch but keeping the overall population size and the amount of habitat occupied constant. The impact of population isolation on extinction risk (Scenario 3) was investigated by altering the 'width' of the connecting corridor between a set number of patches of equal size and composition. ALEX attaches no specific risk of mortality to diffusion; improvement in metapopulation survivorship would result from animals being able to move or re-invade habitats of better quality. In Scenarios 4–8, a configuration consisting of four patches each containing three founder animals was used to examine the effect of varying mortality rates, catastrophe properties and catastrophe combinations on population extinction risk. Sensitivity analysis was conducted by tagging specific parameters including adult and juvenile mortality, catastrophe frequency and the magnitude of effect. A total of 500 simulations over a period of 20–100 years was completed for each parameter variation in each scenario.

RESULTS

Characteristics of the reintroduced population

Table 2 presents representative survival and fecundity data for females in the absence of catastrophic events. It should be noted that these data were gathered over a short period from a small reintroduced population which eventually declined to extinction. They are presented here in outline to provide a starting point to conduct simulations. Their broader relevance to natural populations in other environments and time frames therefore remain ambiguous. The data on the population dynamics and life history of the bilby were translated to form input to ALEX (Table 3). The population increased in 1988 and 1989 but declined dramatically in 1990 (Fig. 1). Released males and females maintained fidelity with the release pens (and feeding sites); however, the males had large home ranges and frequently occupied burrows situated over two 2 km apart on consecutive days. Females were less adventurous and generally occupied burrows within 500 m of their respective release pen. The area occupied expanded with the growth of the *in situ* component of the population, and 24 months after release evidence of bilby activity had been recorded over an area of 8800 ha. Average dispersal distance of females in the population was 2·3 km year^{-1}; one group had become established 10·5 km away from the release site at the end of the study.

The bilby, in common with other bandicoots, has a short gestation period (14 days) and a short period of lactation. Females become sexually mature at the age of 6 months; pouch-life takes between 71 and 80 days and young remain dependent on the mother for another 10–14 days. There was no seasonality in breeding and up to four litters were produced by a female per year. The mean litter size for animals at WNP was 1·7, distributed as 38% litters of one, 54% litters of two and 8% litters of three. The sex ratio of captive-bred in-

Table 2. Population and environmental parameters from a reintroduction programme at Watarrka National Park (April 1988–May 1990) and captive population located at the Arid Zone Research Institute, Alice Springs

The time unit used in the calculation of the survival and fecundity parameters is 3 months

	Reintroduced	(*n*)	Captive	(*n*)
Juvenile				
Survival	0·91	(38)	0	(32)
Fecundity	0		0	
Immature				
Survival	0·25	(12)	0·91	(22)
Fecundity	0		0	
Subadult				
Survival	1·0	(3)	0·94	(17)
Fecundity	0·5	(3)	0·16	(24)
Adult				
Survival	0·89	(7)	0·81	(16)
Fecundity	0·88	(23)	0·33	(74)
Longevity (years)	5		7	
Density of females (individuals ha^{-1})				
High	0·042		—	
Low	0·004		—	
Annual probability of the occurrence of drought[a]	0·1		—	
Annual probability of the occurrence of high rainfall[b]	0·1		—	

[a] Drought period (<150 mm rainfall on average for 3 consecutive years).

[b] High rainfall period (>350 m on average for 3 consecutive years).

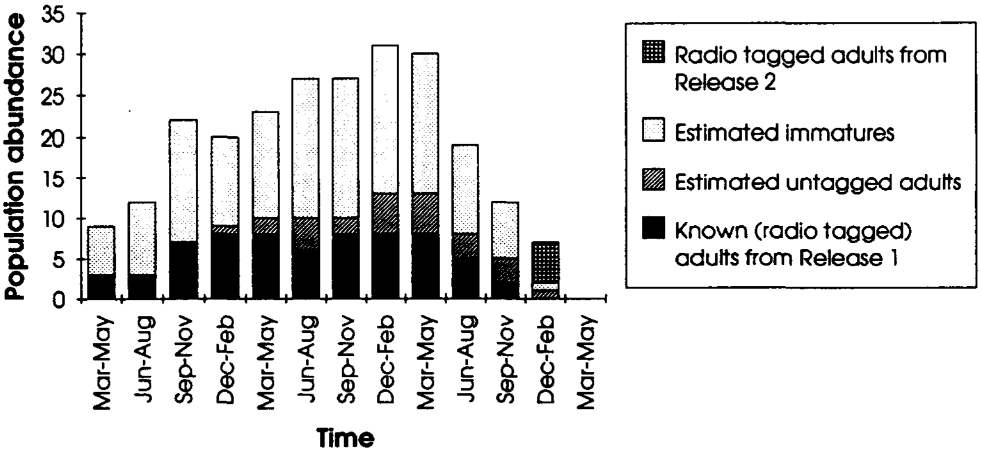

Fig. 1. Abundance of the reintroduced bilby population at Watarrka National Park between March 1988 and February 1991.

Table 3. Values of the life history and environmental parameters used in ALEX for the metapopulation analyses of the bilby *Macrotis lagotis*

Annual probability of litters	
0 litters per year	0
1 litters per year	0
2 litters per year	0·17
3 litters per year	0·33
4 litters per year	0·5
Probability of young per litter	
0 young per litter	0·11
1 young per litter	0·19
2 young per litter	0·61
3 young per litter	0·08
Young per year	
0 female young	0·05
1 female young	0·159
2 female young	0·247
3 female young	0·244
4 female young	0·170
5 female young	0·087
etc.	
Annual probability of death	
Newborn (juveniles)	0·79
Adult	0·09
Density in high-quality habitat	
Minimum living area	24 ha
Minimum breeding area	24 ha
Extinction threshold	1
Low patch population threshold	3
Movement	
Mean migration distance	0·0
Probability of diffusion	
Adults	0·8
Newborn (juveniles)	1·0
Effect of environmental quality on diffusion	1·0
Minimum population for diffusion (proportional)	0·02
Catastrophe characteristics	
Annual probability of the occurrence of drought	0·1
Annual probability of the occurrence of high rainfall	0·1
Patch characteristics	
Total area (ha)	7200
Maximum quality of patch	100%
Maximum biomass of patch	100%
Initial biomass	50%
Growth rate of biomass (annual increment)	10%
Patch quality of environmental variable	
Mean	0·75
Standard deviation	0·25
Correlation of patch quality between patches	1·0
Corridor width (proportion of patch circumference)	>30%

dividuals and the captured young of released animals was close to parity.

Adults (>7 months) and pouch young (0–3 months) had a high survival rate (p = 0·89 and p = 0·91, respectively) while immatures (4–6 months) had low survival (p = 0·25). The fecundity of subadult females (6–9 months age) was less (m_x = 0·5) compared to individuals older than 9 months age (m_x = 0·88) and far greater than the fecundity of captive adults (m_x = 0·33) managed with an aim to increase population size (Conservation Commission of the Northern Territory, unpublished records).

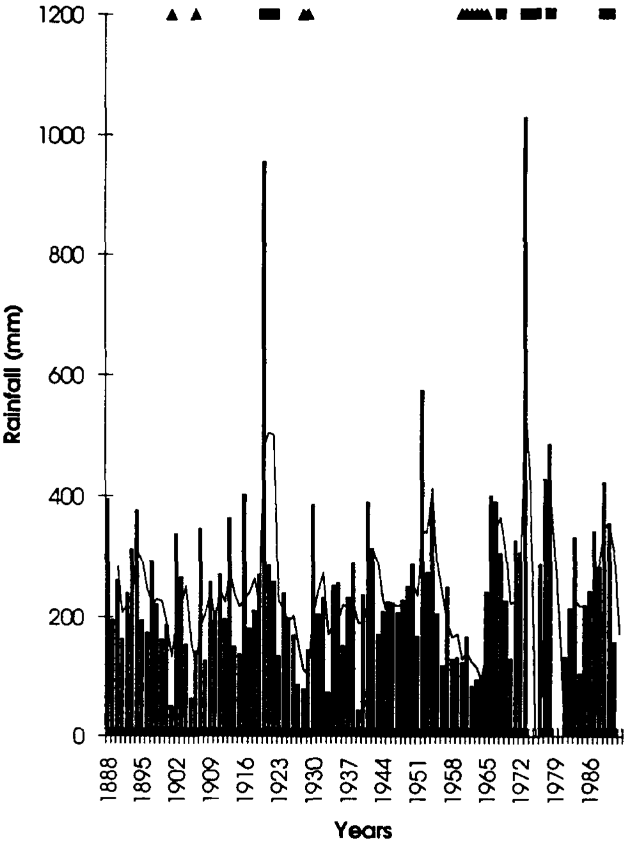

Fig. 2. Annual rainfall (▬) for Tempe Downs Station indicating periods of drought (3-year rolling mean (—) with <150 mm precipitation, ▲) and big rain (3-year rolling mean >350 mm, ■). Note: data for years 1981–83 and 1988–91 were derived from Watarrka National Park records; no data available for 1975–76 and 1981–82.

Characteristics of the release environment

The reintroduction programme commenced at the end of 3 years of below-average rainfall (mean: 205 mm compared to average annual rainfall: 238 mm). Rainfall during the study was well above average (3-year mean: 351 mm). The exceptional rainfall at the start of the study triggered a major biotic change; a flush of annuals resulted in an eruption of rodents (*Mus, Notomys* and *Pseudomys* spp.) and an increase in predator abundance (*Felis catus, Vulpes vulpes* and *Canis familiaris*). The mortality of radio-tracked bilbies in the late part of 1990 was primarily from predation, and the decline of the entire population was associated with an increase in predator activity.

The impact of severe drought on bilby populations is not clear. Anecdotal records indicate that bilby populations decline substantially in response to dry conditions in the Tanami Desert (Conservation Commission of the Northern Territory, unpublished records). The occurrence of low and high rainfall periods at the study site is shown in Fig. 2. Both the defined drought and big rain catastrophe had a probability of occurrence of 0·1. The random proportion of the population killed during a catastrophe was set at between 0·5 and 0·9 for a big rain event and between 0·0 and 0·5 for drought.

Most of the study area had been burnt during a summer fire in 1985; however, biomass had accumulated sufficiently to carry several patch burns within the release area at the end of 1989. Signs of bilby feeding

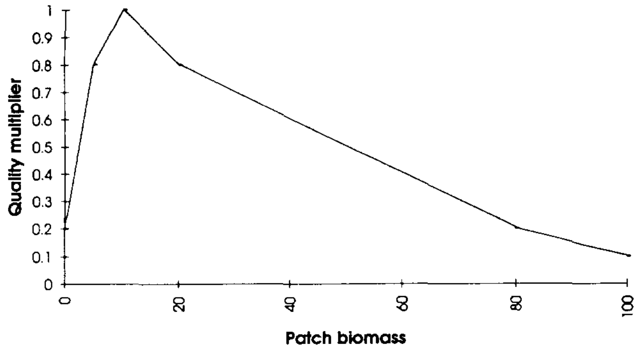

Fig. 3. The postulated relationship between habitat biomass and the value of the patch quality. The number of breeding females is multiplied by the habitat quality multiplier.

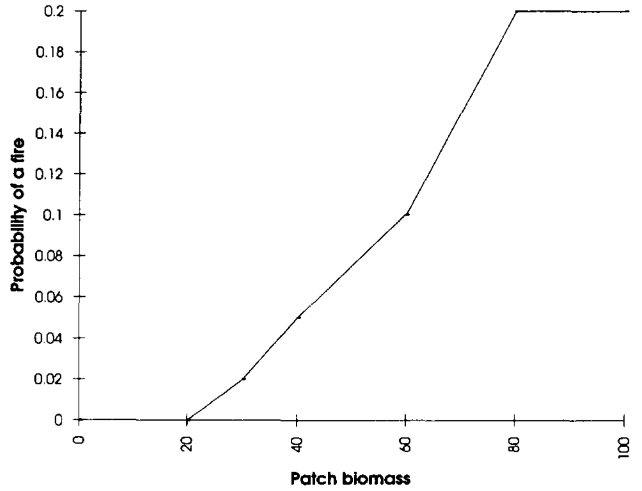

Fig. 4. The postulated functional relationship between the patch biomass and the probability of a fire.

activity were very conspicuous on some of the burnt patches and absent in areas where spinifex cover was high. The animals were attracted to the burnt areas because of the seed surfeit following post-fire ephemeral plant growth. It was postulated that least favourable conditions (and presumably lowest fecundity) occur in late successional stages when biomass is high, and this notion was incorporated in the habitat state function shown in Fig. 3. A dependence function to describe the occurrence of fire catastrophe is shown in Fig. 4. There was no chance of a fire occurring when biomass was 20% of maximum but a 0·2 probability when exceeding 80% of maximum. Growth rate of biomass was stated as 10% per annum with a maximum of 100.

The environmental parameters presented in Table 3 represent the range of conditions a population at WNP may encounter. They formed the set of background input values for ALEX unless stated otherwise.

Simulation: population size and segregation of sample units

Scenario 1: Modifying the founder population size

The initial population size was altered from 3 to 60 animals in a patch of 7200 ha. Extinction risk declined rapidly with increased founder population size (Fig. 5); however, the effect was asymptotic and increasing the founder population size above 30 individuals did not substantially improve population survivorship. A founder population of 60 had an 8% chance of extinction in 10 years. A founder population of three individuals had a 15% chance of becoming extinct in 2 years; with 12 individuals the extinction risk was reduced to 2% over the same period.

Fig. 5. The probability of extinction at 5 (♦), 10 (▲) and 20 (■) years for a founder bilby population of various sizes.

Scenario 2: Subdivision of the population into replicates

A founding population size of 12 was selected to examine the effect of subdivision of this population on metapopulation survivorship. One to six replicate patches (total area same as the founder release area of 7200 ha) were tested containing numbers of animals amounting in total to the founding population size. A marked increase in the median probability of extinction was evident when replicates contained less than three individuals (Fig. 6).

Scenario 3: Modifying diffusion between the replicates

Four replicates each containing three individuals were selected to investigate the impact of diffusion between subpopulations on metapopulation survival. Once diffusion between patches was made possible, increasing corridor width (allowing more animals to move between patches) corresponded with no improvement in metapopulation survivorship (Fig. 7).

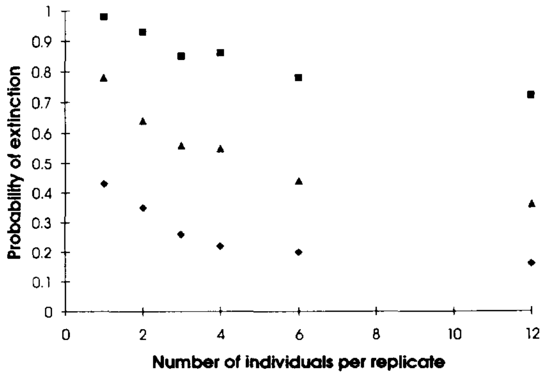

Fig. 6. The probability of extinction for a founding population of 12 individuals segregated into possible sample unit configurations which additively amounted to the founding population size. ♦, 5-years; ▲, 10 years; ■, 20 years.

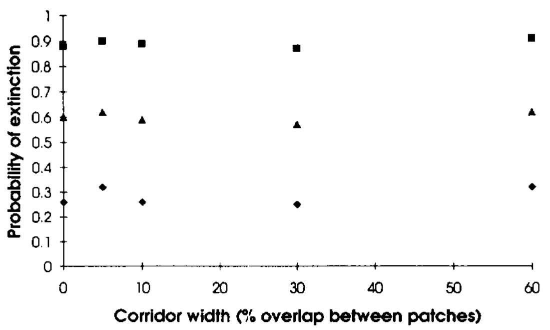

Fig. 7. The influence of corridor width (touch distance) between four replicates each containing three individuals and the probability of extinction over a 5 (◆), 10 (▲) and 20 (■) year period.

Simulation: environmental conditions and population parameters

Scenario 4: Inclusion and exclusion of catastrophes

A founder population of 12 individuals equally divided between four replicates with a touch distance of greater than 30% of the patch circumference was used to examine the impact of the environment on metapopulation survival. The survival and fecundity data derived from WNP resulted in a population growth of $\lambda = 1{\cdot}49$. In the absence of environmental catastrophes, the median extinction time was 26 years. Inclusion of all three catastrophes (drought, big rain and fire) produced a median time to extinction of 8 years.

Scenario 5: Alteration of population parameters

There was relatively little scope for increasing adult survivorship or improving fecundity; both were close to maximum. A reduction of juvenile mortality to 0·35 (less than half the input value) increased annual growth rate to 2·71 and improved the median time to extinction to 12 years. Further reduction of juvenile mortality to 0·1 (similar to the adult value) resulted in a growth rate of 3·4 and a further increase in the median time to extinction time (17 years). Population survival was extremely sensitive to adult mortality, more so than juvenile mortality (Fig. 8). Increasing the probability of annual adult mortality from 0·09 to 0·58 or juvenile mortality from 0·79 to 0·96 reduced the annual growth rate to 1·0. When adult mortality was increased to this level, the median time to extinction was 3 years.

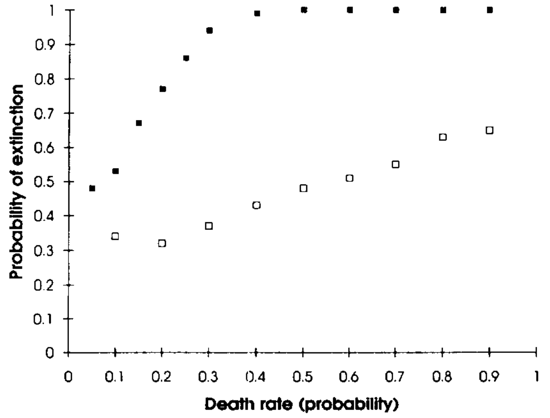

Fig. 8. The effect of juvenile (□) and adult (■) mortality on population extinction risk. The population consisted of four replicate patches each with three founder individuals.

Scenario 6: Impact of big rain and drought

The probability of extinction was very sensitive to frequency of big rain and drought events, whereas altering the magnitude of effect of these events had less impact on the population (Figs 9 and 10). Specifying big rain or drought as the only catastrophe produced a median extinction time of 9 and 15 years, respectively. Inclusion of drought and fire but elimination of big rain events increased the median time to extinction to 29 years; similarly, in the absence of drought but with the inclusion of big rain and fire events, the median time to extinction was 12 years.

Scenario 7: Impact of fire

Fire in isolation resulted in a risk of extinction reaching a plateau of 13% at around 60 years. Elimination of fire but inclusion of big rain and drought events produced a median extinction time of 8 years for the population. There was no substantial change to the

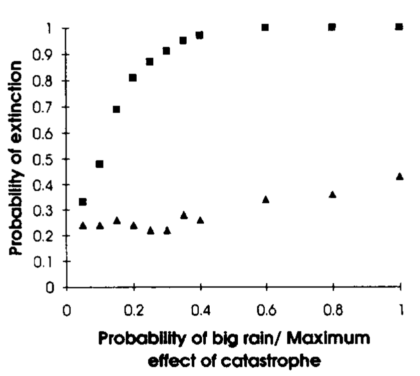

Fig. 9. The influence of big rain frequency (■) and the magnitude of effect (▲) on population extinction risk over a 10 year period. The population consisted of four patches each with three founder individuals.

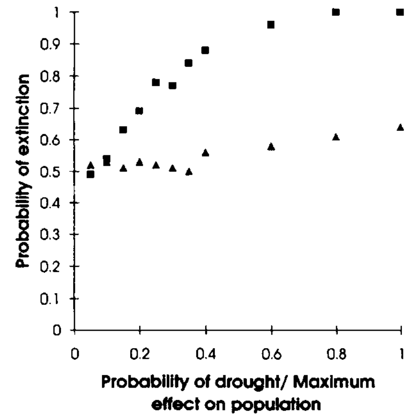

Fig. 10. The influence of drought frequency (■) and the magnitude of effect (▲) on population extinction risk over a 10 year period. The population consisted of four patches each with three founder individuals.

extinction risk when the maximum biomass of each patch or the growth rate of biomass was altered.

Simulation: the metapopulation and environmentally driven variance

Scenario 8: Exposing sample units to asynchronous environmental variance
The impact of asynchronous environmental variance on metapopulation persistence was investigated by (1) altering the extent to which environmental quality was correlated between each habitat patch; and (2) disengaging the 'global' effect of catastrophe within ALEX so that catastrophes act independently on each patch or subpopulation. Whether the environmental quality in each patch was correlated, set at independence or negatively correlated, all simulations of the population resulted in the median time to extinction remaining constant at around 8 years. Disengaging the global effect of catastrophes increased the median time of extinction to 11 years.

DISCUSSION

Population viability analysis is important in the conservation of threatened species because first, the models focus attention on the parameters that are likely to be critical to the dynamics of a population (Lacy & Clark, 1990) and therefore, indicate information of greatest importance to collect in the field (see Tables 2 and 3), and secondly, they provide an opportunity to assess the validity of these data in hypothetical situations (Shaffer, 1990).

The reintroduction programme at WNP showed that it was possible to transfer bilbies from a captive to a free-range existence successfully. However, the programme demonstrated the deficiency in our knowledge concerning the environmental conditions that enabled a population to persist. We lack cues to accurately predict changes in habitat over time and to identify and manage the impending conditions that appear hostile to the bilby. Reintroduction as a management tool would be premature under these circumstances, since there would be little likelihood of a self-sustaining population resulting from the release of a founder population. The population at WNP persisted for less than 3 years. A hypothetical population with an equivalent founder base that was modelled in ALEX had a median extinction time of 4 years.

In the absence of adequate ecological information or opportunities to study wild populations, reintroduction needs to be tempered to perform a research role. The behaviour and growth of released populations need to be contrasted against environmental variables, including predation pressure and food limitations. Ideally, this process should be continued until the fate of a population may be predicted accurately from the assessment of environmental conditions.

The practicality of experimentally examining these issues by species reintroduction is contingent upon (a) the sample units (i.e. subpopulations) being of sufficient size to retain population processes and of sufficient number to permit estimation of their variance under experimental conditions; (b) metapopulation persistence being of adequate duration to permit assessment of environmental impacts; (c) the selection of a suitable spatial scale to avoid experimental pseudoreplication (Hurlbert, 1984); and (d) the potential to test whether manipulation of the population or the environment improves population survival. With a finite number of individuals available for release, careful consideration needs to be given to the best use of this limited resource. For example, the desire to maintain population size and integrity conflicts with the need to subdivide the population to achieve replication of sample units.

The importance of founder population size on the extinction probability of the population has been reported by Lande (1988) and the theory predicts that extinction risk will decrease with increasing founder population size but quickly become asymptotic (Griffith *et al.*, 1989). Scenario 1 supported this prediction and the extinction risk for the species began to plateau once founding population size exceeded 30 individuals. The extinction risk for a population of this magnitude was still appreciable (p = 0·18 chance of extinction in 10 years). For a shorter period and a smaller population the extinction risk decreased sufficiently to become an acceptable risk with which to run an experiment to learn more about age-specific rates of fecundity and mortality in relation to a set of environmental conditions. A population of 12 individuals had a p = 0·02 extinction risk in 2 years.

Increased local subdivision of the bilby population (Scenario 2) caused an increase in the extinction risk. However, the relationship was asymptotic and the most severe inflection occurred when a sample unit consisted of only one or two individuals. In terms of field logistics, sample unit composition consisting of two or three females per locality was practical; the home range of up to three females could be stabilised around a feeding station at WNP. While there is a threshold density necessary for some species to enable social behaviour such as group defence, group mating or schooling to take place (Andrewartha & Birch, 1954), bilby populations can evidently function reproductively at very low densities; sparse populations consisting of a few adults and young are generally encountered and concentrations of wild bilbies in excess of 20 individuals km^{-2} are rare (Conservation Commission of the Northern Territory, unpublished records). The arrangement and separation distance between sample units had very little impact on metapopulation resilience (Scenario 3), presumably because each sample unit was being affected simultaneously by a set of environmental conditions unsuitable for the long-term persistence of the population.

Goodman (1987) suggested that the key to a dramatic improvement for the survival prospects of a population rests in reducing variance in the population growth rate. This may be achieved by (a) manipulating environmental variance to realise a lower variance in growth rate by means such as temporary disease control, predator control, and supplemental feeding at those times only; (b) manipulating patch or reserve design to realise a lower environmentally driven variance (i.e. opting for a system of several reserves at a sufficient distance so that they experience independent environmental variation); and (c) directing manipulation of the population so as to realise lower variance of growth rate when the population is low by releases from captive breeding or introductions from other populations.

Mortality of adults and juveniles had greatest impact on population growth (Scenario 5) and big rain and drought were the most influential environmental conditions affecting mortality. In isolation, both drought and big rain at the selected frequency settings caused the extinction of the population. In concert, the effects of drought and big rain increased extinction risk further. Although the incidence of fire was configured to play a beneficial role in increasing population growth, its presence produced little improvement to population extinction risk while the other two factors operated. These results suggest a rather limited scope for manipulation of the environment to enhance subpopulation survival. Drought and big rains cannot be predicted accurately in arid Australia (Stafford Smith and Morton, 1990) and are independent of manipulation leaving amelioration of the magnitude of impact by strategic supplementation of food or reduction of predator pressure as the only means to reduce population variance. However, altering the maximum effect of individual drought or big rain events had little effect; most sensitivity was related to the frequency of the big rain or drought events.

The effect of increasing the separation distance (decreasing movement) between sample units until the local environments become uncoupled and experience independent variation may result in separate subpopulations experiencing asynchronous patch quality and asynchronous catastrophes. Scenario 8 indicated that varying patch quality between subpopulations resulted in no improvement to the extinction risk of the population. Exposing subpopulations to asynchronous big rain and drought events, however, marginally increased metapopulation survival. These results support the suggestions of Goodman (1987) regarding greater resilience of a subdivided population compared to one which is lumped, and are consistent with the findings of Stacy and Taper (1992).

The application of population viability analysis has been valuable for elucidating options for planning reintroduction experiments and generating hypotheses to test in the field. Despite the high risk of catastrophic events in arid Australia, there is a high probability that a subdivided (replicated) reintroduced population of the bilby will survive for sufficient duration to permit the investigation of the growth and fate of a released population. Adult mortality is of key importance to monitor. There is apparently little scope to reduce environmental variation through manipulation or management of environmental effects. For example, the logistics of manipulating predation pressure over hundreds of square kilometres to accommodate each bilby subpopulation would be enormous. The reduction of metapopulation extinction risk by spatially segregating subpopulations to experience appreciably different big rainfall and drought events needs to be investigated more thoroughly. Experimentally investigating this issue in arid Australia would need sample units to be spatially separated in the order of 300–400 km. A recapture and re-release operation over a wide metapopulation arc may cost less and may be a more reasonable conservation option compared to improving conditions for a localised population via intensive environmental management.

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