

## **A method for validating stochastic models of population viability: a case study of the mountain pygmy-possum (*Burramys parvus*)**

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### **Summary**

**1.** A method of validating stochastic models of population viability is proposed, based on assessing the mean and variance of the predicted population size.

**2.** The method is illustrated with a model of the population dynamics of *Burramys parvus* Broom 1895 (the mountain pygmy-possum), based on annual census data collected from a single population in the Snowy Mountains of New South Wales, Australia between 1986 and 1997. The model incorporates density-dependence in survivorship and recruitment, and demographic and environmental stochasticity.

**3.** The model appeared to make reasonable predictions for the three populations that were used for validation, provided the equilibrium population size was estimated accurately. This may require that differences in habitat quality between populations be taken into account.

**4.** Following validation, the model was re-parameterised using the additional data from the three populations, and the risk of population decline within the next 100 years was assessed. Although populations as small as 15 females are predicted to be relatively safe from extinction caused by stochastic processes, *B. parvus* appears vulnerable to loss of habitat and reductions in the population growth rate.

**5.** The approach used in this paper is one of few attempts to validate a model of population viability with field data, and demonstrates that some aspects of stochastic population models can be tested.

*Key-words:* *Burramys parvus*; extinction risk; population viability analysis; stochasticity; validation

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## Introduction

Population viability analysis (PVA) typically uses stochastic population models to estimate minimum viable population sizes (Shaffer 1981; Gilpin & Soulé 1986), and assist management of threatened (Burgman, Ferson & Akçakaya 1993; Possingham, Lindenmayer & Norton 1993) and abundant species (McCarthy 1996). The accuracy of population viability analysis has been questioned recently by several authors, who have suggested that the predictions may be subject to substantial error (Possingham *et al.* 1993; Taylor 1995; McCarthy, Burgman & Ferson 1996). While such concerns are relevant to population viability analysis, they could be directed equally toward any modelling exercise that is based on less than perfect information. Population viability analysis differs from most other types of predictive modelling by accounting for variability and making predictions about extreme values (such as extinction) rather than central tendencies (such as median and mean population sizes). Such characteristics pose particular challenges for model development.

By definition, no model will ever be a perfect representation of reality. Therefore, it is important to validate models to determine their limits of accuracy. Despite the proliferation of models of population viability, most have not been validated with field data (Lacy 1993; Brook *et al.* 1997). One reason is that data are usually scarce and any available data are used for parameterisation rather than validation. An additional challenge is that the predictions of population viability analysis are characterised by probability distributions, while observations that could be used for validation are typically point values (e.g., population size). Comparing the two may require considerable amounts of data so that the point values can be compared in terms of probabilities (Burgman *et al.* 1993). There are no established methods for validating stochastic population models, but useful methods are required.

In this paper, a method for validating stochastic population models that are used in PVA is proposed. The method is illustrated with a stochastic model of the population dynamics of *Burramys parvus* Broom 1895 (the mountain pygmy-possum). The model is parameterised with 12 years of data from one population, and then validated using data from three other populations of *B. parvus*. After validating the model, it is used to predict the viability of mountain pygmy-possums in small isolated populations. This represents one of few attempts at validating a stochastic population model with field data.

## Methods

### *The standard deviates test*

Stochastic population models that are used in PVA typically predict a probability distribution of population sizes rather than a single population size. Ideally, the predictions would be validated by comparing the predicted distribution to an observed distribution. This requires replicate observations for each prediction, which are rarely available, especially for endangered species. Separate observations may be available for different times or in different places, but the predictions are likely to vary in space and time. To make these predictions equivalent so that the different observations can be used as replicates, it is necessary that they be re-scaled. The observations can be compared on the same scale by expressing them in terms of the number of standard deviations away from the mean. This can be achieved by subtracting the observed population size from the mean predicted population size and dividing by the predicted standard deviation in population size to generate a “standard deviate” for each year (Sokal & Rohlf 1981). If the mean population size is predicted accurately, the standard deviates will have a mean equal to zero. If the standard deviation (or variance) of the population size is predicted accurately, the standard deviates will have a variance equal to 1. A t-test may be used to test whether the mean of the standard deviates is significantly different from zero, and a chi-squared test is used to test whether the variance of the standard deviates is significantly different from 1 (Sokal & Rohlf 1981). If the level of variation predicted by the population model is too large, then the variance of the standard deviates would be less than 1. It would be greater than 1 if the level of variation predicted by the model is too small. To ensure a proper statistical test, the predictions of the model must be independent, which can be achieved by basing the predicted population size only on the previous year’s abundance. Thus, the method tests the mean and variance of the predicted annual change in population size.

### *Burramys parvus*

The standard deviates test was illustrated using a population model of *Burramys parvus*, a small (adult body weight of 40–45 g) terrestrial possum inhabiting alpine regions of south-eastern Australia. The species occurs in the Snowy Mountains in New South Wales, the Hotham/Bogong region in Victoria, and in the vicinity of Mt Buller in Victoria. Populations in these regions are variously fragmented. Typical breeding areas are boulder fields above the snowline (approximately 1500 m above sea level). *Burramys parvus* is an omnivore, eating a range of invertebrates (Bogong moths in particular) and plant matter

(Mansergh *et al.* 1990; Smith & Broome 1992). Breeding occurs in spring, with a single litter of four offspring being produced. Males migrate from the breeding areas by the end of summer, and typically over-winter in areas up to several kilometres away. Females are comparatively sedentary (Mansergh & Broome 1994; Broome, unpublished). *B. parvus* hibernates over winter in crevices below the snow (Broome & Geiser 1995; Körtner & Geiser 1998).

In the Snowy Mountains, the area of this study, distances of up to several kilometres separate suitable habitat for *B. parvus* (Caughley 1986). Populations in four separate areas were surveyed. Males are capable of moving between these areas, although migration by adult females is rare (Broome, unpublished). Because males are apparently polygynous, only the female component of the population was modelled, and populations in each of the four areas were treated separately.

#### Data

Four localities were surveyed, and were given the names Blue Cow, Charlotte Pass, Paralyser, and Summit Road. Surveys of *B. parvus* were conducted annually from 1986 at Blue Cow, and from 1987 at the other three sites until 1997. Trapping was conducted annually in the first two weeks of December for 3-4 nights. Individuals were marked with fish fingerling ear tags (Utah Stamp Co.). Population sizes were estimated using the program CAPTURE (White *et al.* 1978) at the larger sites (Blue Cow and Charlotte Pass) where the data were sufficient (Broome, unpublished). Differences between these estimates and the number of females known to be alive were only slight and mark-recapture estimates could not be obtained for two populations (Broome, unpublished), so the numbers known to be alive were used for subsequent analyses (Fig. 1). It was assumed that unmarked *B. parvus* were new recruits in the population. Data from the Blue Cow population were used initially to estimate the model parameters, and data from the other three populations were used for validation.

#### The model

To reflect the annual breeding cycle of *B. parvus*, a discrete time step of one year was used. The model population was censused immediately prior to breeding in spring. Because *B. parvus* breeds as a one-year-old, only a single age class was required. Annual survival and recruitment were both modelled as a function of population density, and the density-dependent relationships were estimated using regression analysis. Recruitment was defined as the mean number of female offspring raised to adulthood by each female, thus incorporating the survival of the offspring over

the winter period. Recruitment was modelled using a Ricker (1975) function, to ensure positive values were retained when population size was high (Fig. 2). Annual survival of adults was modelled as a simple linear function of population size. In this case, values in the interval [0-1] were retained over the range of all feasible population sizes (Fig. 3). The model was scaled against population density by modifying the parameters that described the strength of density dependence. Thus, recruitment was modelled as

$$r = \exp(1.5 - 2.09N/N^*),$$

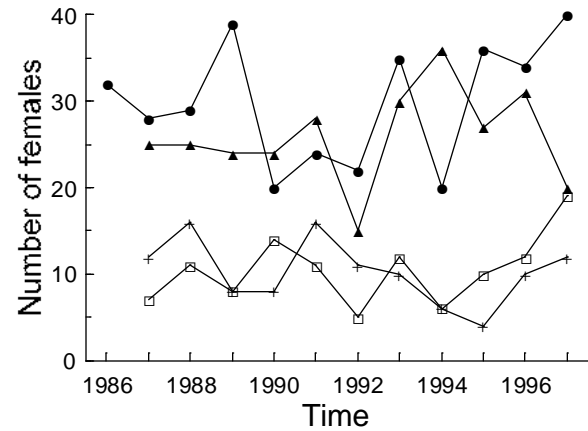


Fig. 1. Observed population trajectories of *B. parvus* in the 4 populations: Blue Cow, circles; Charlotte Pass, triangles; Paralyser, squares; and Summit Road, crosses.

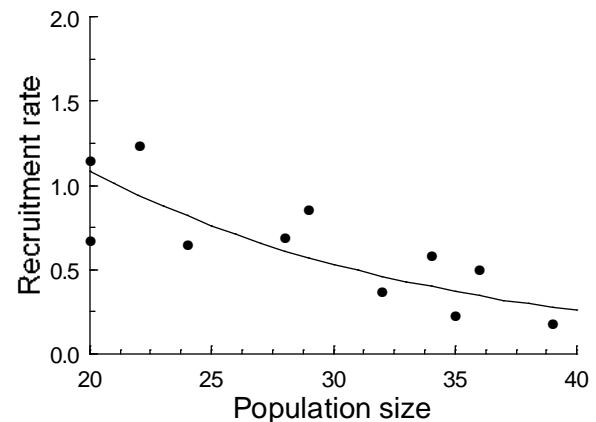
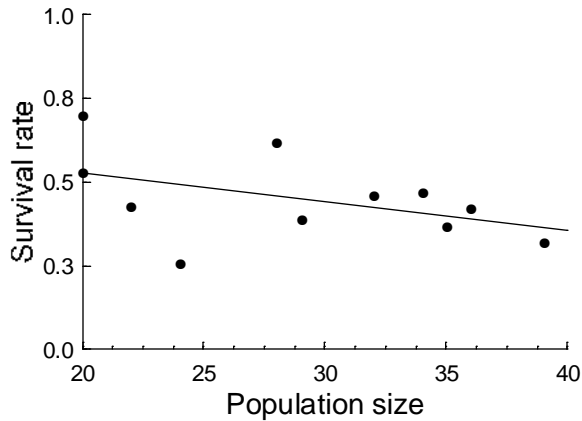


Fig. 2. Recruitment rate of females versus the number of females in the Blue Cow population of *B. parvus*. The fitted Ricker (1975) function was estimated by regression analysis:  $r = \exp(1.5 - 0.071N)$ , where  $N$  is population size.



**Fig. 3.** Survival rate of adult females versus the number of females in the Blue Cow population of *B. parvus*. The fitted line was estimated by regression analysis:  $s = 0.70 - 0.0086N$ , where  $N$  is population size.

and survival was modelled as

$$s = 0.70 - 0.253N/N^*$$

where  $N$  is the population size, and  $N^*$  is the equilibrium population size, *i.e.*, the population size at which the mean growth rate ( $r+s$ ) equals 1. In the case of the population at Blue Cow, the equilibrium population size was 29.4.

Demographic stochasticity was modelled by randomly determining the annual survival of individuals and drawing the number of recruits from a Poisson distribution (Shaffer 1981; Akçakaya 1990; McCarthy, Franklin & Burgman 1994). Environmental stochasticity was modelled by drawing the annual recruitment and survival rates from a normal distribution with a specified coefficient of variation. The level of environmental stochasticity may be estimated from the variation around the regression lines (Figs 2 and 3), but this variation will be due, in part to measurement error and demographic stochasticity (McCarthy 1996; Kendall 1998). To avoid this systematic error, different levels of environmental stochasticity were used until the predicted level of variation in population size (due to density dependence, and demographic and environmental stochasticity) matched the observed level of variation in the Blue Cow population. This resulted in the coefficient of variation in survival and recruitment being estimated as 20%, with perfect correlation between survival and recruitment rates. Only the female component of the population was modelled because *B. parvus* is polygynous and males are highly mobile on a nightly basis (Mansergh & Scotts 1990; Mansergh & Broome 1994; Broome, unpublished).

### Validation

For each of the three populations used for validation, the equilibrium population size was estimated by adjusting the value for the Blue Cow population on the basis of the area of suitable habitat. At Blue Cow, the area of available habitat is 5.0 ha, which corresponds to an estimated equilibrium population size of 29.4 (Figs 2 and 3). On this basis, the equilibrium population size was estimated as 20.0 for the Charlotte Pass population (3.4 ha), 13.5 for the Paralyser population (2.3 ha), and 11.8 for the Summit Road population (2.0 ha). Scaling the equilibrium population size in this way requires the assumption that the habitat quality is equivalent in all localities. The equilibrium population size was also estimated by scaling it against the average population sizes that were observed during the surveys. At Blue Cow, the average population size over 11 years was 28.6, which corresponds to an estimated equilibrium population size of 29.4 (Figs 2 and 3). On this basis, the equilibrium population size is 24.4 for the Charlotte Pass population (mean population size of 23.7), 10.8 for the Paralyser population (mean population size of 10.5), and 10.8 for the Summit Road population (mean population size of 10.5).

For each of the populations, the mean and standard deviation of the predicted population size was determined for each yearly time step, and the standard deviates were calculated. To test whether the mean population size is being predicted accurately at both large and small population sizes, the correlation between the standard deviates and the initial population sizes was examined. A correlation that is significantly different from zero indicates that the standard deviates are dependent on population size, which suggests that the density dependence mechanisms are not being modelled properly. Additionally, the magnitude of the standard deviates should not be correlated with population size if the variance in population size is being predicted accurately at both small and large population sizes. This was tested by determining if the square of the standard deviate was significantly correlated with population size.

### Viability

Following validation, the model was re-parameterised using the additional data from the Charlotte Pass, Paralyser and Summit Road populations. Differences in population sizes were accounted for by scaling the observed population sizes by the mean population size at each location. The density-dependent relationships for recruitment and annual survival were re-parameterised using these data (Figs 4 and 5). On average, 2 female offspring are produced in each litter of *B. parvus* (Mansergh & Scotts 1990; Broome, unpublished). To

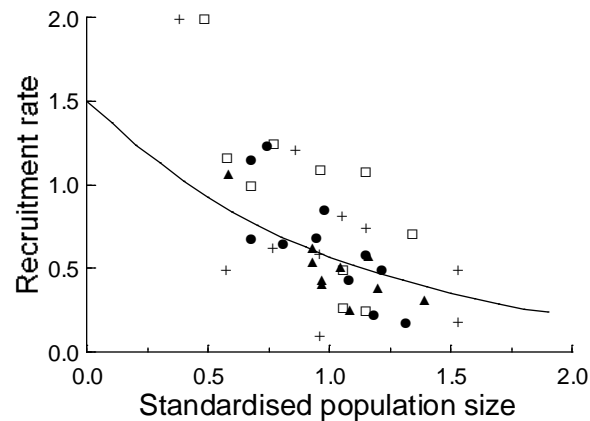
ensure that recruitment was not unrealistically high at low population densities, the regression relationship for recruitment was forced through the y-axis at a value of 1.5 (Fig. 4). This led to weaker density dependence than used in the initial model, but is a more plausible relationship because the average number of female recruits should not exceed the average number of females per litter. Thus, recruitment was modelled as

$$r = \exp(0.41 - 0.96N/N^*)$$

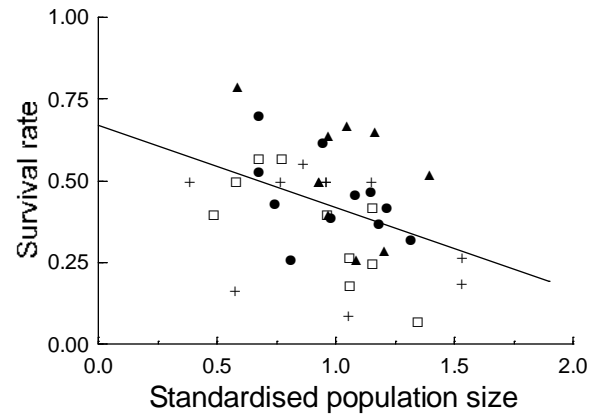
There are two apparent outliers at small population sizes when using this relationship (Fig. 4), but these *per capita* recruitment rates are subject to greater error because the population sizes (*i.e.*, the sample size of the estimates) are small. The fitted regression line falls within the 95% confidence intervals for these estimates. The sensitivity of the predictions to changing the strength of density dependence was assessed by also conducting simulations in which the recruitment function was forced through an intercept of 1.6.

Survival was modelled using the relationship

$$s = 0.67 - 0.25N/N^*$$



**Fig. 4.** Recruitment rate of females versus the number of females in the four populations of *B. parvus*: Blue Cow, circles; Charlotte Pass, triangles; Paralyser, squares; and Summit Road, crosses. Population sizes were standardised across sites by dividing the actual values by the mean population sizes in each of the four sites. The fitted Ricker (1975) function was estimated by regression analysis:  $r = \exp(0.41 - 0.97N_{std})$ , where  $N_{std}$  is the standardised population size.



**Fig. 5.** Survival rate of adult females versus the number of females in the four populations of *B. parvus*: Blue Cow, circles; Charlotte Pass, triangles; Paralyser, squares; and Summit Road, crosses. Population sizes were standardised across sites by dividing the actual values by the mean population sizes in each of the four sites. The fitted line was estimated by regression analysis:  $s = 0.67 - 0.25N_{std}$ , where  $N_{std}$  is the standardised population size.

The viability of isolated populations of *B. parvus* was assessed by determining the risk of population decline for populations with different equilibrium population sizes. There is concern that climate change will reduce the amount of snow cover (Whetton, Haylock & Galloway 1996), which acts as a thermal insulator over winter (Walter & Broome 1998). This may cause a reduction in survival of adults and juveniles over winter. To assess the threat posed by reduced survival, simulations were conducted with reduced values for recruitment and survival, and with an equilibrium population size of 20.

The equilibrium population size was used as the initial population size in all simulations. For each set of parameters, 10,000 iterations were conducted to predict the probability of population extinction, and the expected minimum population size within a 100 year period. Differences in the expected minimum population size correspond to the area between two quasi-extinction risk curves (Burgman et al. 1993, McCarthy 1996) and indicate how close the population is being moved towards or away from extinction (McCarthy 1996). To assess the risk of the population declining to a dangerously small population size, the probability of decline to 5 females or fewer at some stage within the 100 year simulation was also predicted.

**Results**

*Validation*

When the equilibrium population size was scaled against habitat area, the predictions of the model were not significantly different from the observed population size of *B. parvus* at the Summit Road site. However, the model under-predicted population size for the Charlotte Pass population, and over-predicted population size for the Paralyser population (Table 1). The model assumed equal habitat quality, but, based on observed population densities, there is evidence that habitat quality is highest at Charlotte Pass and lowest at Paralyser (Broome, unpublished). When the equilibrium population size was scaled against the observed population size, the predictions of the model were not significantly different from the observations for all three populations (Table 1). For the cases in which the mean and variance of the standard deviates were not significantly different from the expected values (0 and 1 respectively), the standard deviates and their squares were not significantly correlated with population size.

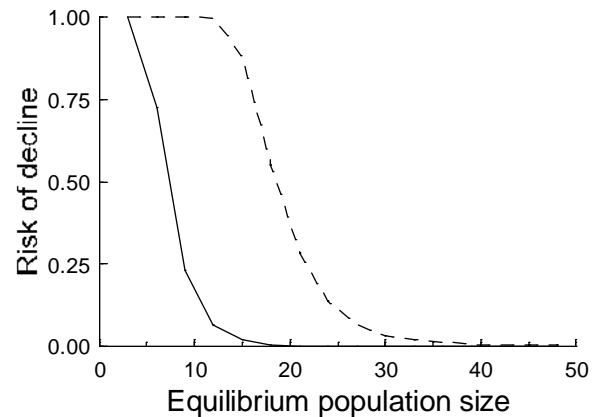
**Table 1.** Results of validating the model using three populations of *B. parvus*: Charlotte Pass, Paralyser and Summit Road. Results are shown for cases in which the equilibrium population size was scaled against both habitat area and the observed population size. The mean and variance of the standard deviates are given.

Population	mean <sup>1</sup>	variance <sup>1</sup>
Scaled by habitat area		
Charlotte Pass	-1.8*	1.9
Paralyser	0.76*	0.85
Summit Road	0.43	1.0
Scaled by population size		
Charlotte Pass	-0.41	0.99
Paralyser	0.025	1.3
Summit Road	0.098	1.3

1. The predictions are significantly different from the observations if the mean of the standard deviates is significantly different from zero, or if the variance of the standard deviates is significantly different from 1. Significant differences ( $P < 0.05$ ) are indicated by an asterisk (\*).

*Viability*

The model predicted that small isolated populations of *B. parvus* are relatively safe from extinction. The risk of extinction within 100 years was predicted to be less than 1% when the equilibrium population size was larger than about 18 females (Fig. 6). The risk of declining to 5 females or fewer was predicted to be less than 1% when the equilibrium population size was greater than about 38 (Fig. 6). The expected minimum population size decreased approximately linearly with the equilibrium population size, from a value of 20 when the equilibrium population size was 50, to 0.3 when the equilibrium population size was 6. Increasing the intercept of the recruitment function from 1.5 to 1.6 decreased the risk of falling to small population sizes. When the equilibrium population size was 30, this change caused the expected minimum population size to increase from 10.7 to 11.2.



**Fig. 6.** The predicted risk of decline within 100 years of isolated populations of *B. parvus* versus the equilibrium population size. Results are shown for the risk of extinction (continuous line) and the risk of decline to 5 individuals or fewer (broken line).

Extinction of *B. parvus* within 100 years was almost certain when the equilibrium population size was 20 and survival and recruitment were reduced by 40% (Fig. 7). The risk of extinction was greater than 1% when survival and recruitment were reduced by more than 6%. The model predicted that the population would almost certainly decline to 5 females or fewer at some time within 100 years when survival and recruitment were reduced by 20% (Fig. 7). The expected minimum population size declined approximately linearly with reductions in the survival and recruitment rates, from a value of 6 when there was no change in survival or recruitment to 0.8 when survival and recruitment were reduced by 30%.

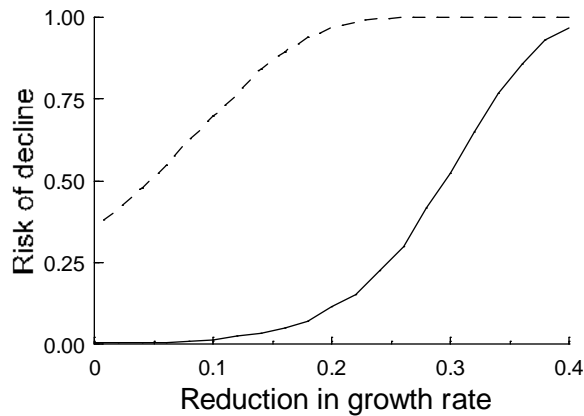


Fig. 7. The predicted risk of decline within 100 years of isolated populations of *B. parvus* versus the proportional reduction in the population growth rate. Results are shown for the risk of extinction (continuous line) and the risk of decline to 5 individuals or fewer (broken line).

## Discussion

Probabilistic predictions of stochastic metapopulation models have been tested previously using data on observed local extinction and colonisation events (e.g., Hanski 1997, McCarthy, Lindenmayer & Possingham in press) and patterns of patch occupancy (e.g., Hanski 1997, Lindenmayer, McCarthy & Pope 1999, McCarthy, Lindenmayer & Possingham in press). Such methods are suitable when presence absence data are available. In contrast, our method of validating stochastic population models is suitable using time series data on population size in individual areas. In this paper, the validation dataset was obtained using other populations, but it could also consist of new data from a single population in the years after the stochastic model was developed.

In most circumstances, sampling error would contribute to some of the variation in the observed population sizes, and influence comparisons of the predicted and observed population sizes. For example, unbiased sampling error would tend to make the observed variation in population size larger than reality. Such errors could be accommodated in the validation method by explicitly modelling the data collection process in the stochastic simulation. The drawback is that it would be difficult to distinguish between errors in the population model and errors in the model of the data collection process. A separate test of the data collection model would be warranted in these circumstances to help identify errors in the population model *per se*.

Validation of the population model of *B. parvus* demonstrated that it was reasonably accurate within the

range of the data, provided the equilibrium population size was sufficiently accurate. The mean and variance of the population growth rate were validated for the *B. parvus* model, but the predicted risk of extinction remained untested because extinctions did not occur. Validating such predictions requires data from a considerable number of populations and over a sufficiently long period such that some extinctions are likely to be observed (e.g., Hanski 1997). Although small population sizes were observed in our study, with as few as 4 individuals, it is possible that the dynamics of the population may change at small population sizes. The relatively infrequent passage to small population sizes may have contributed to the apparently good fit. Stronger density dependence, changed levels of stochasticity, or an Allee effect (Allee, 1938; McCarthy, 1997) may occur but remain undetected, leading to a change in the population dynamics and an abrupt change in the risk of extinction. Predictions of the risk of the population falling to as few as 5 individuals may be reasonable, given that this is within the range of the observed data. However, as with any model, multiple compensating errors may contribute to the congruence between the predictions and observations. Therefore, it is important to note that a validated model remains an imperfect description of reality that has yet to be falsified (Rykiel 1996).

The model predicted that populations as small as 15 individuals are relatively safe from extinction. This result depends in part on the strength of density dependence. As the population falls closer to extinction, the recruitment and survival rates increase, helping to rescue the population from collapse. The density dependence is likely to be due to the availability of suitable sites for hibernation during winter or nesting sites during summer (Körtner & Geiser 1998; Broome, unpublished). Aggression among females means that these sites are rarely if ever shared and the number of suitable hibernacula and nest sites is likely to be limiting. Only certain places will be sufficiently insulated to allow *B. parvus* to remain in torpor and conserve energy over winter. The limited availability of suitable habitat means that current areas are critical for the persistence of *B. parvus*, and conservation of these areas must be a priority.

The recently discovered population of *B. parvus* at Mt Buller in Victoria has a population size of approximately 300 individuals (Heinze & Williams 1998). Based on the availability of habitat, it is likely to have remained at approximately this size for the past 10,000 years or more (Megan Osborne pers. comm.). The persistence of such a small population is consistent with predictions of the model. However, there is some concern that *B. parvus* is vulnerable to climate change (Geiser & Broome 1993; Brereton, Bennett & Mansergh, 1995). Snow provides important thermal insulation, maintaining temperatures above freezing in hibernacula (Körtner & Geiser 1998; Walter & Broome 1998). Projected reductions in snow

accumulation (Whetton *et al.* 1996; Whetton, 1998) may lead to reduced survival and recruitment rates of *B. parvus*, and increased risks of population decline. There is some uncertainty about the magnitude and effects of climate change. However, the absence of *B. parvus* from boulder fields at lower elevations suggests that the species is vulnerable to reduced snow cover. The model predicted that smaller populations are most likely to go extinct in response to climate change, suggesting that these populations may be a suitable focus for monitoring such effects.

Previous attempts to validate stochastic population models have ignored variation (Brook *et al.* 1997). Because the mean growth rate and its variance are important parameters of stochastic population models, validation should account for both these attributes. Similarly, it is important to test whether the predictions of the model (mean and variance of the population size) depend on population size. The validation methods that were used in this paper tested specific aspects of the population model. Significant differences for these tests would suggest specific aspects of the model that were inaccurate. For example, if the population growth rate is underestimated when population size is small and overestimated when population size is large, the standard deviates will tend to be correlated with population size. A positive or negative correlation between the standard deviates and population size suggests that density dependence is not being modelled accurately. A good model should accurately predict the variance in the population growth rate at all population sizes. A positive or negative correlation between the square of the standard deviates and population size would demonstrate that the accuracy of the variance depends on population size, suggesting that the stochastic processes (demographic and environmental) are not being modelled accurately at all population sizes.

The validation of the model indicated that the habitat quality varied among populations, but, despite occurring at different densities, the effect of density dependence was similar in the different areas. Once scaled to account for different densities by modifying the slope of the density dependent relationships, the recruitment and survival functions were similar for the different populations (Figs 4 and 5). The form of density dependence is likely to vary to at least some extent between populations, but the standard deviates test has insufficient power to detect small differences. This lack of power occurs partly because the average population densities vary over only a small range between different populations (from 4.6 females ha<sup>-1</sup> at Paralyser to 7.0 females ha<sup>-1</sup> at Charlotte Pass). In some areas of Victoria, population densities are an order of magnitude greater than observed in this study, and the form of density dependence may be distinctly different in these circumstances.

Stochastic population models have been used for almost 20 years to predict risks of extinction (Shaffer 1981). In this time, many models have been developed but few have been validated. The methods of validation that were used in this study were applied to observed population trajectories. These are the kinds of data that are likely to be available for many species for which population viability analyses have been conducted. Validation of these models is important to determine their limits of accuracy. The tests can also help to identify model errors, which may be subsequently corrected to provide improved predictions.

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