http://dx.doi.org/10.1071/PC17002

Pacioni, C., Williams, M.R., Lacy, R.C., Spencer, P.B.S. and Wayne, A.F. (2017) Predators and genetic fitness: key threatening factors for the conservation of a bettong species. Pacific Conservation Biology, 23 (2). pp. 200-212.

Predators and genetic fitness: key threatening factors for the conservation of a bettong species.

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Running title (<50 letter spaces): Interaction effects of predation and genetic fitness

Summary on line table of contents (<50 words):

Abstract

Globally, many wildlife species are declining and an increasing number are threatened by extinction or are extinct. Active management is generally required to mitigate these trends and population viability analysis (PVA) enables different scenarios to be evaluated and informs management decisions. Based on population parameters obtained from a threatened bettong, the woylie (*Bettongia penicillata ogilbyi*), we developed and validated a PVA model. We identified the demographic and genetic responses to different threatening factors and developed a general framework that would facilitate similar work in other bettong species. The two main threatening processes are predation by introduced animals and its interaction with reduced fitness (for example due to inbreeding depression). Although predation alone can drive a decline in certain circumstances (e.g. when predation success is independent from population density), synergistically, predation and reduced fitness (which can be caused by inbreeding depression stress, or a disease) can be particularly relevant, especially for small populations. The minimum viable population size was estimated at 1 000-2 000 individuals. In addition, the models identified that research into age-specific mortality rates and predation rates by introduced animals should be the focus of future work. The PVA model created here provides a basis to investigate threatening processes and management strategies in woylie populations and other extant bettong species, given the ecological and physiological similarities amongst these threatened species.

Keywords

Population dynamics, Population Viability Analysis, Vortex, Minimum population size, Individual-based model, woylie

Introduction

The persistence of declining populations has benefited from the use of population viability analysis (PVA) to identify key threatening processes between different populations and determine the driving forces causing the decline (Lindenmayer *et al.* 1993; Morris and Doak 2002). It has played an important role in quantifying risks (Haydon *et al.* 2002; Armstrong *et al.* 2003), the establishment of research priorities, refining the aims of monitoring programs and the evaluation of different management strategies (Lindenmayer *et al.* 1993; Starfield 1997; Morris and Doak 2002). To ensure PVA models are valid, their accuracy and assumptions need to be rigorously scrutinised and the conclusions drawn from them must have a sound biological basis (Lindenmayer *et al.* 1993; Bart 1995; Caughley and Gunn 1996; Lacy 2000). Bart's (1995) review criteria for the acceptance of models in wildlife conservation are particularly useful in this regard. These include: i) *Structure of the model* - a full disclosure of the model structure and underlying assumptions to evaluate their compatibility to the biology and ecology of the species under study (see also Lindenmayer *et al.* 1995; Starfield 1997); ii) *Parameter values* - a thorough analysis of the consequences of possible measurement errors (also defined as sensitivity testing, Lacy 1993; Starfield 1997; Lacy 2000); iii) *Secondary predictions of the model* - Evaluation of secondary, non standard outputs of the model; iv) *Primary predictions of the model* - validation of the model comparing the predictions with real data (but notably Starfield (1997) considered this implicit in the validation of the assumptions).

Clearly, the quality and value of a PVA model is dependent on the quality of the data upon which it is built. However, often alternative approaches do not offer a higher confidence and, as is common in crisis conservation management, urgent decisions need to be taken based on the best available data. At a minimum, PVA represents a tool capable of quantifying the extent of the lack of knowledge (Lindenmayer *et al.* 1993; Starfield 1997). Moreover, new technology improvements and experience gained facilitate the correct use of this relatively modern approach as demonstrated by Brook *et al.* (2000).

In this study, we used PVA to investigate the relative effects of different variables (population size, predation by introduced predators, introduced predator control (fox-baiting), initial heterozygosity and inbreeding depression) to the population demography and genetic diversity of woylies (*Bettongia penicillata ogilbyi*). The woylie is an Australian macropod that experienced a spectacular recovery following a introduced predator control program (Orell 2004), but subsequently has undergone a second dramatic decline during which all large woylie populations in Western Australia had >90% decline since 1999 (Wayne *et al.* 2013). We aimed to evaluate the relative importance of these factors as well as estimate the minimum viable population size and a minimum viable heterozygosity.

The development of a PVA model for the woylie is intended to inform management actions that will maximise the conservation outcomes for the species. The woylie has also been suggested as an ecological model for macropod conservation (Mawson 2004; Finlayson *et al.* 2010; Pacioni *et al.* 2013) since it shares many ecological, reproductive and genetic features with other potoroids and the species has been comparatively more extensively studied (Parsons *et al.* 2002; Pizzuto *et al.* 2007; Pacioni 2010; Haouchar *et al.* 2016). Therefore, identifying demographic and genetic responses to different scenarios for the woylie may be of substantial support to the management and conservation of other species, particularly those for which less information is currently available. In particular, once appropriate modifications are made on the base of biological differences between species, the model can be used as a 'template' for work on other similar species for which such detailed information may not be equally available.

Materials and Methods

VORTEX (Lacy and Pollak 2013) was used to model genetic and demographic dynamics associated with different scenarios. VORTEX is an individual-based model that allows examination of the consequences of various demographic, genetic, and management processes and, most importantly, examining their interactions, therefore, overcoming one of the most important limitations of state-variable models (Huston *et al.* 1988; Lacy 2000). Individual-based models do not require simplified assumptions to describe complex phenomena that could incur the risk of over- or under-estimating the probability of extinction and other outcome metrics (Huston *et al.* 1988; Lacy 2000). The input values of demographic and other parameters for the baseline Vortex model are listed in Appendix A. Justifications for the values of the more important parameters are described below.

Model parameters

In order to accommodate the fast generation time, the VORTEX time-unit was set to 91 days (hereafter time-unit). At approximately 100 days, joeys leave the pouch but remain dependent on their mother until around 180 days. Females start reproducing between 180 and 240 days of age, while males start after 270 days (Sampson 1971; Christensen 1980). Consequently, for modelling purposes, females can be considered adults after two time-units (i.e. age 1 (first time-unit after birth)=pouch young; age 2=juvenile; age 3 and afterwards=adult), while males have an additional sub-adult stage and become adults after the third time-unit following birth (i.e. age 1=pouch young; age 2=juvenile; age 3=subadult; age 4 and afterwards=adult). Broadscale baiting to control introduced predators (mainly foxes, *Vulpes vulpes*) is carried out four times per calendar year (hereafter year) across more than 3.4 million hectares of conservation estate, including key woylie populations, in south western Australia, with a regular target interval of 90 days between baiting events (Armstrong 2004). Hence, the chosen time-unit also easily allowed the inclusion of an introduced predator control program (i.e. one baiting session per time-unit).

When the exponential maximum growth rate (Caughley 1971; Caughley 1977) was calculated from trapping data (see below) the different times between trapping intervals was standardised as recommended (Morris and Doak 2002). This was achieved using the linear regression method described by Dennis *et al* (1991) implemented in a customised version of the "Schlinger Tool G" (SCMG 2009) for Microsoft® Excel 2007, where the square root of the length of the time intervals ($\sqrt{(t_{i+1}-t_i)}$) was used as the independent variable. The density independency of the section of data under analysis was confirmed through a linear regression analysis with $\alpha=0.05$ in the "Schlinger Tool G" (SCMG 2009).

Baseline scenario

A baseline scenario was created to describe demographic dynamics in the absence of inbreeding depression, as well as in the absence of any additional mortality caused by predation or catastrophic events (e.g. bush fires). The maximum age of reproduction in the model was defined as the maximum life expectancy because there is evidence that woylies reproduce throughout their life (Christensen 1980; Delroy *et al.* 1986). Life span in the wild was determined using trapping records (>26 000 woylie records spanning 34 years; Wayne *et al.* 2013), where animals trapped for the first time were sexually immature (i.e. known age). Because females can give birth to up to three successive young per year (Sampson 1971; Christensen 1980), to adjust for the 91 day time-unit, 75% breeding females were set as having one pouch young and 25% none.

Reproductive success was modelled as density dependent as suggested by data collected from a woylie population that reached carrying capacity at Karakamia Sanctuary (Western Australia)

(Ward *et al.* 2008) and Venus Bay Island A (South Australia) (Delroy *et al.* 1986) using the formula:

$$P_N = (P_0 - [(P_0 - P_K)(N/K)^B])N/(N + A) \qquad \text{(Miller and Lacy 2005)}$$

Where N is the population size, P_N is the proportion of breeding females when the population is N, P_K is the proportion of breeding females at carrying capacity and P_0 is the proportion of breeding females when the population is close to zero. The parameter B describes the effect that the density has on the reproductive success and A is the Allee effect. An average of 89.3% of females were found with pouch young at any point in time in Upper Warren (Christensen 1980; Ward *et al.* 2008). This value was used as P_0, while 57% was used for P_K based on Karakamia estimations. The value B=16 and A=0.1 were arbitrarily chosen so that the density effect was limited to the extreme of the distribution – very low and very high density (Miller and Lacy 2005).

Trapping data were used to determine woylie exponential maximum growth rates and (indirectly) juvenile and subadult mortality rates. Trapping success (the proportion of woylie captures over the total number of available traps) is considered to adequately represent woylie relative population size (Wayne *et al.* 2013). However, 'trap learning' may initially increase the proportion of trappable individuals within the population and generate a significant bias. Discarding the data from the first year of trapping (4-6 sessions) was considered sufficient to adjust for this bias.

Since fox control by baiting in Upper Warren began, woylie populations have shown a substantial growth (Burrows and Christensen 2002; Orell 2004). The maximum values of exponential growth rate calculated from trapping data were used as an approximation of the intrinsic growth rate in the model (as defined by Caughley 1971; Caughley 1977), which was then used to approximate the mortality rate of juvenile and subadult age classes as explained below.

The only available estimation of mortality rates for different age classes was obtained from sites in Upper Warren when very limited fox control occurred (Christensen 1980). A direct quantification of the additional mortality caused by foxes was not available. However, Christensen (1980) reported that more than 50% of mortality cases were caused by foxes. A similar proportion was reported in other studies of small marsupials (Freegard 2000; Short *et al.* 2002). Consequently, Christensen's (1980) mortality rates were halved and used as starting values for adults and pouch young age classes in the baseline scenario (which models the population dynamics in the absence of fox predation).

Juvenile and subadult are the age classes whose survival rates are more difficult to establish as a consequence of their reduced trappability, dispersal - which occurs mainly at this age (Christensen 1980; Pacioni 2010), and the rapidity at which animals progress through these age classes (Sampson 1971; Christensen 1980; Ward *et al.* 2008). Additionally, in woylies, as well as in other macropods, these classes are considered to be more affected by predation (Christensen 1980; Spencer 1991; Freegard 2000) and consequently Christensen's (1980) mortality rates for juveniles and subadults would most likely lead to overestimates of mortality of these age classes if used in the baseline scenario (in which no fox predation is modelled). Therefore, in the model, mortality rates for juveniles and subadults were progressively reduced until the maximum yearly exponential growth rate generated by the model matched the observed exponential maximum growth rate over a four year period (Appendix B).

Following broadly accepted recommendations (Lacy 1993; Bart 1995; Starfield 1997; Lacy 2000), several population parameters were altered to investigate the influence that these have on demographic projections (i.e. sensitivity testing; Table 1). Mortality rates for all age classes were tested independently, progressively increasing the baseline values up to six fold. For each time-unit VORTEX draws a value from a normal distribution with a mean equal to the mortality rates entered. The standard deviation of these distributions was set to 10% of the mean, and was tested with a range between 10 and 30 % in the sensitivity testing. Additionally, different carrying capacity values and initial population sizes were tested. Among the reproductive parameters, only the percentage of breeding males (60%, 90% and 100%) was tested because of the confidence in the other reproductive variables due to extensive and long term field data collection (Sampson 1971; Christensen 1980; Delroy *et al.* 1986) and investigations carried out on both captive and wild woylie populations (Smith 1992; 1994; 1996; Johnson and Delean 2001). Lastly, all the parameters listed above were also let vary concurrently to explore their interaction collecting 500 samples, each with 200 replicates, using a Latin Hypercube Sampling scheme.

Additional modelling scenarios

Several scenarios were also modelled to investigate the effects that different processes would have on projections of population demography and genetic diversity (Table 1).

Predation by introduced foxes and cats is a significant component of mortality in all age classes (Freegard 2000; Short *et al.* 2002), so scenarios that included predation by introduced predators with and without the mitigation effect of the fox-baiting program were incorporated into the model to investigate how these influence population dynamics. In Upper Warren, as well as in most other Western Australian locations where woylies occur (e.g. Batalling State Forest, Tutanning Nature Reserve, Dryandra woodland), fox-baiting is carried out under the Western

Shield program (Armstrong 2004; Wyre 2004). Efficacy of the control of introduced predator control is influenced by the timing of the bait distribution, weather conditions (rain dilutes sodium monofluoroacetate – the active ingredient of the fox baits – reducing the doses ingested) and prey availability (Saunders *et al.* 2000). No quantification of the efficacy fluctuations was available because this is monitored through indirect evidence based on mammal abundance (Armstrong 2004; Orell 2004; Wyre 2004). The modelling of the variable efficiency of the fox-baiting program was achieved using the catastrophe option available in VORTEX, which enables the survival rates and fecundity to be proportionally reduced. Christensen's (1980) data were used to quantify the effect of predation in the absence of the introduced predator control program. Given the rationale that foxes do not necessarily kill woylies each time they attack, but they are likely to cause pouch young ejection, predation was modelled as reductions in both survival and fertility (Appendix C). A random effect (using a uniform random function) was used to express the variability in fox-baiting efficiency. Lastly, these parameters were included in a density dependent function based on the following rationale.

Despite the presence of foxes, woylies did not disappear from Upper Warren, Dryandra and Tutanning for various hypothesised reasons. For instance, much of the sympatric native marsupial fauna consume *Gastrolobium* plants that naturally contain sodium monofluoroacetate. Therefore, while native fauna have a higher tolerance towards the toxin, introduced eutherian predators were likely to have undergone secondary poisoning, providing protection to woylie populations (Christensen 1980). An alternative hypothesis, at least in the open woodlands, was suggested by Sampson (1971) who believed that the thick scrub offers protection from predation to woylies; however, as the population density increases, animals are forced into less optimal, open areas where they are quickly predated, limiting the population growth in more open areas. The two hypotheses are clearly not mutually exclusive and possibly both phenomena were responsible for the survival of woylies (perhaps with a different proportional contribution depending on the area). Either way, woylie density would appear to be the driving factor; consequently, the variable predation success was also modelled as density dependent (Appendix C).

Inbreeding depression may become a significant component in reducing population fitness especially when the effective population size is small; therefore the investigation of its effect on the projections of population viability is recommended (Lindenmayer *et al.* 1995; Caughley and Gunn 1996; Lacy 2000; Allendorf and Luikart 2007). This is particularly relevant in the woylie, as it is for many other endangered species, given the recent decline and that several populations have been at very small numbers for several years. For example, the population at Tutanning Natural Reserve had an estimated population size of about 300 individuals for the last 40 years (Sampson 1971; Groom 2010; Wayne *et al.* 2013). VORTEX uses two models to simulate inbreeding depression: the heterosis model (where inbred individuals have lower survival, with severity of this inbreeding depression expressed in “lethal equivalents”) and the recessive lethals model (where animals are killed when they are homozygous for lethal recessive alleles at simulated loci). Because there are no studies on the number of lethal equivalents in wild woylie populations, we explored a range of values as suggested by the literature (Ralls *et al.* 1988; Lacy 1993; Crnokrak and Roff 1999; O'Grady *et al.* 2006; Traill *et al.* 2009). Inbreeding depression was modelled with a heterosis effect from 3.14 to 10 lethal equivalents and an additional 1.57 to 3.5 lethal recessive alleles per diploid. Both mechanisms were modelled separately and concurrently.

We used VORTEX default implementation for the recessive lethal model. However, VORTEX initialises (by default) the simulations with a level of inbreeding equal to zero. Therefore, to assess the interactions between inbreeding and other factors evaluated in this study, it was necessary to initialise the populations to a certain level of inbreeding. Homozygosity values found in natural occurring populations (16.5% Dryandra and Upper Warren, 36% Tutanning; Pacioni *et al.* 2011) were used as proxy to set the set initial level of inbreeding. A heterosis model was implemented by firstly assigning to each individual a starting inbreeding value drawn from a normal distribution truncated to zero and a mean equal to the initial homozygosity of the population. The additional mortality caused by inbreeding depression was then imposed to the first age class using the formula:

$$100 \times \{1 - [(1 - (m_b \times 0.01)) \times e^{-LEq \times MIN(1; (Iv + Is))}]\}$$

Where m_b is the mortality value used in the baseline model, *LEq* is the lethal equivalents, *Iv* is the inbreeding coefficient calculated by VORTEX and *Is* is the starting inbreeding value assigned to each individual (note that the current release of VORTEX 10 provides the ability for users to set an initial inbreeding coefficient greater than 0, so the above heterosis model could now be implemented within the standard inbreeding model.).

The effect of the parameters used to model predation, introduced predator control program and inbreeding depression (Table 1) were evaluated by varying them independently (i.e. one at a time), replicating the simulations 1 000 times. In addition, a Latin Hypercube Sampling scheme was used to examine all possible combinations of these sampled input parameters, allowing for analysis of interaction as well as main effects. For this analysis, we sampled 500 parameter combinations and repeated each case for 200 replicates. In all these simulations, the carrying capacity was set to 2 000, except for simulations where inbreeding depression was modelled independently. In the Latin Hypercube Sampling, we also varied the initial population size to estimate the minimum viable population as explained below.

[INSERT TABLE 1 ABOUT HERE]

Each scenario was simulated for 100 years. A length of 100 years was arbitrarily chosen in line with the IUCN time frame for classification of extinction risk (IUCN 2001).

Statistical analysis

To evaluate the effect of different model settings, key outcome variables (the final mean population size (N), final heterozygosity (H_t), and the growth rate ($r_{(ts)}$) calculated in last time-step of the simulations before carrying capacity truncation was applied) were compared statistically against the baseline scenario using the strictly standardised mean differences (SSMD, Zhang 2007) as implemented in the function *pairwise* in *vortexR* (Pacioni and Mayer in prep). The SSMD statistic offers the advantage of allowing a statistical test without being influenced by the sample size (Zhang 2007), and it is a recommended statistic for simulation studies with a large number of iterations (Pacioni and Mayer in prep). While H_t and $r_{(ts)}$ are technically undefined when the population goes extinct, in these cases we set H_t and $r_{(ts)}$ to zero in order to allow statistical comparisons. The *pairwise* function was also used to rank the population parameters that were changed in the sensitivity analysis based on the mean SSMD values and to calculate the Kendall's coefficient of concordance to verify whether the order of ranked factors was statistically consistent across the considered final outcome variables (i.e. N, H_t, $r_{(ts)}$).

We also needed a statistic that would capture population dynamics' trends on a longer term rather than limit the comparisons to a point in time at the end of the simulations. To this end, we used the 'recovery rate' ($r_{(Rec)}$) and the cumulative probability of extinction ($P_{(Ext)}$). We defined the $r_{(Rec)}$ as the average $r_{(ts)}$ in the first five years of the simulations. $r_{(Rec)}$ provides an indication of the capacity of the population to recover from low density (i.e. the beginning of the simulations) or its lack thereof. A population was considered (functionally) extinct when $N < 50$ and $P_{(Ext)}$ was defined as the proportion of times that a population would become extinct at the end of the simulations. These statistics were calculated and compared against the ones of the baseline scenario with the SSMD using the *vortexR* functions *rRec* and *Pextinct*.

The main purpose of the simulations conducted with the Latin Hypercube Sampling was to evaluate the interaction between predictors, in addition to further explore their main effects. These data were analysed by fitting a Generalised Linear Model using N as a dependent variable. We initially fitted a model with a Poisson error distribution. When over dispersion was identified, we used a negative binomial error distribution using the R package MASS (Venables and Ripley 2002). When necessary, we used a zero-inflated model as implemented in the R package pscl to deal with the excess of zeros caused by several parameter combinations that were responsible for population extinction (Zeileis *et al.* 2008). The zero-inflated models have two components: one caters for the probability of having $N=0$ and the second for the predicted value of N when the population does not go extinct. While our definition of population extinction was $N < 50$, in all simulations where extinction occurs N becomes eventually zero. Therefore, by using a zero-inflated model, the zero component of the model approximate the probability of extinction. In the simulations that included predation, not all predictors could be considered concurrently in the count component of the zero-inflated model because of quasi-complete separation of the data (in most simulations without baiting and non-density dependent predation, the population would go extinct). Therefore, we initially confirmed the significance of predation as a predictor, and then analysed separately simulations with and without predation. Despite this, only first order interactions could be included in the regression models. Beta regression models (Cribari-Neto and Zeileis 2010) were used when H_t was the dependent variable. It should be noted that VORTEX normally monitors heterozygosity using one locus, which is initialised with a heterozygosity of 100%. So, effectively, the values reported by H_t are the proportion of the initial heterozygosity that would be retained at the end of the simulations. As H_t is undefined when the population is extinct and these cases were already dealt with by the zero component of the zero-inflated models, we used a subset of the data that included only simulations where $H_t > 0$ for this analysis. Further details on these analyses are provided in the Appendices D - G. Results from the regression models were further explored by generating interaction effect plots for selected terms. These were generated by plotting the response variable with an initial population size of 500 individuals and density dependent predation. When evaluating the interaction between predation in the presence of the baiting program and inbreeding depression, the initial heterozygosity was fixed to 83.5%, while in the interaction between the baiting program and the initial heterozygosity, the number of lethal equivalents used to model heterosis was fixed to 4 and the number of lethal alleles to 3.

To establish the minimum viable population size and the minimum recommended initial heterozygosity, we calculated $P_{(Ext)}$ with the data generated with the Latin Hypercube Sampling and fitted a logistic regression model with either initial population size or initial heterozygosity as the only predictor.

Results

The model used in this study fulfilled the four criteria (Bart 1995) necessary to be considered a reliable technique for investigating and inferring general population trends over time (see Appendix H).

Sensitivity testing and model validation

Sensitivity testing was conducted to analyse the influence of variations in the demographic parameters on the results of the PVA. Based on the pairwise comparisons, the model was quite robust to changes in mortality rates in adult and pouch young age classes. Significant differences were found in the pairwise comparisons in *N* when the mortality rate of the adult was increased by six fold relative to the baseline model. Variation of mortality rates of juveniles and subadults had also a substantial effect causing population extinction when it was increased by six folds (Table 2). As expected, a lower carrying capacity was responsible for a lower *N*.

It is interesting to note that changes of pouch young mortality had the least effect on $r_{(ts)}$. In fact, while a decreasing trend was detectable (Fig. 1) differences were not significant. On the contrary, a substantial reduction of $r_{(ts)}$ was observed with most modifications of the mortality rates within the adult, and juvenile and sub-adult age classes (Table 2, Fig. 1).

[INSERT TABLE 2 AND FIG. 1 ABOUT HERE]

Genetic diversity was statistically different from the baseline scenario when the juvenile mortality was increased by six fold. Genetic diversity was also statistically different from the baseline scenario when the adult mortality was increased by six fold (Table 2). However, the biological importance of the latter difference is doubtful given there was approximately only a reduction of 5% in genetic diversity as a result. Similarly to what was observed for *N*, a lower carrying capacity was also responsible for a lower H_t

$P_{(Ext)}$ was different from 0% only when juvenile and subadult mortality was increased by six fold ($P_{(Ext)}$=100%) and $r_{(Rec)}$ was significantly lower when adult mortality was increased by five or six fold and when juvenile and subadult mortality was increased by four, five or six fold relative to the baseline model. While the other parameters tested alone (SD of mortality rates, initial population size and percentage of males breeding) did not appear to significantly influence any of the monitored parameters.

When the sensitivity testing parameters were ranked based on the mean SSMD, the ranks were consistent across the three key outcome variables (N, $r_{(ts)}$ and H_t; p=0.008) with the carrying capacity, the juvenile and adult mortality rates being within the first three ranks.

The results obtained from fitting a zero-inflated regression model to the sensitivity testing data obtained with the Latin Hypercube Sampling were consistent with the pairwise comparisons. In fact, the juvenile, adult mortality rates and their interactions were the most important predictors in the zero component of the model (Table 3). The juvenile and adult mortality rates, together with the carrying capacity were the three most important main effects also in the count component of the model. However, this analysis highlighted that interaction terms have a substantial effect on the final count component (Table 3), which was not possible to appreciate from the pairwise comparison.

[INSERT TABLE 3 ABOUT HERE]

The results obtained from the beta regression indicated that the genetic diversity was mostly influenced by the interactions of the carrying capacity with the mortality rates and with the initial population size (Table 4).

[INSERT TABLE 4 ABOUT HERE]

Additional scenarios

Predation significantly reduced N and significantly affected final heterozygosity (Table 2). $r_{(Rec)}$ was also reduced in all scenarios that included predation, however it was only significantly so when no baiting was implemented. $P_{(Ext)}$ was 100% when a non-density dependent predation was modelled, while the population stabilised to a lower N when predation was density dependent.

Inbreeding depression, when acting alone, did not significantly modify any parameters, although a general reduction trend in N, $r_{(ts)}$ and $r_{(Rec)}$ was evident when the model included lethal recessive alleles (which was worst when the starting heterozygosity value was 64%; Table 2). None of these scenarios obtained a $P_{(Ext)} > 0$.

Analysis of the data obtained with the Latin Hypercube Sampling revealed much more complex dynamics. In the scenarios where introduced animal predation was modelled, the interaction of the initial population size with both the number of lethal recessive alleles and the baiting program were the most important predictors for the zero component of the model (Table 5). The most important predictors for the final population size were the number of lethal recessive alleles and its interaction with both the initial population size and the baiting program. Importantly, the additive effect of predation and inbreeding resulted in dramatic consequences. In fact, while no population went extinct when the simulations were conducted without predation and both of the inbreeding depression models, the probability of extinction in simulations with presence of introduced animal predation increased to approximately 5-20% for mid-high values of lethal alleles (depending on whether a baiting program was also modelled). When both inbreeding depression components (the lethal allele and heterozygosity advantage) were modelled with high severity in the presence of introduced animal predation, the probability of extinction increased to >90% (Fig. 2).

[INSERT TABLE 5 & FIG. 2 ABOUT HERE]

The initial heterozygosity was a significant predictor for both the zero and the count components of the model. This was mostly because of its interaction with other terms. For example, the probability of extinction decreased from an approximate 99% when the simulations were initialised with a low initial heterozygosity (64%) to as low as 10% when a high (83.5%) initial heterozygosity was used (Fig 3).

The beta regression analysis, with H_t as a dependent variable, was in line with the regression model for population size. In both approaches the most important predictors were inbreeding depression, initial heterozygosity and the implementation of the fox- baiting program (Appendix G).

[INSERT FIG. 3 ABOUT HERE]

When examining the predicted $P_{(Ext)}$ as a function of the initial population size in the logistic regression model, our results indicated that populations of around 450 individuals have $P_{(Ext)} =$ 50%. Only when a populations was larger than 1 000 individuals, was $P_{(Ext)} <$ 5% in presence of a baiting program (Fig 4). We also found an almost linear relationship between $P_{(Ext)}$ and H_t, with $P_{(Ext)} <$ 10% only when $H_t >$ 78% (Fig 5).

[INSERT FIG. 4 & 5 ABOUT HERE]

Discussion

The PVA modelling in this study showed that fox-baiting was critically important in reducing the probability of extinction ($P_{(Ext)}$) and increasing the final population size (N) of woylie populations. There are numerous field studies that support this conclusion. For example, a review identified predation from introduced animals as the major cause for the failure of macropod translocations in Australia (Short *et al.* 1992), and fox-baiting has demonstrably resulted in dramatic population increases of woylies (e.g. Burrows and Christensen 2002; Orell 2004; Wayne *et al.* 2016). Introduced predators also are identified as one of the greatest threats to wildlife conservation in Australia (Woinarski 1999). When predation was modelled as not density dependent (as it would be expected in habitats with sparse or open vegetation), the woylie population would go extinct in most simulations, including scenarios that included fox baiting. However, when predation was density dependent, $P_{(Ext)}$ was highly dependent on the implementation of a fox-baiting program.

The interaction between predation and inbreeding depression was particularly detrimental to the persistence of woylie populations, whereas inbreeding depression taken on its own, was not. The potency of the synergistic effects between predation and inbreeding is probably our most important finding. By extension, we argue that any element that may result in a reduction of fitness similar to that modelled for inbreeding depression, for example a disease with mild clinical consequences, could pose a serious threat to the viability of populations of woylies, and probably other Australian native fauna, that are exposed to introduced predators.

Woylie populations between 300 and 500 individuals are considered to be at high risk (~50% probability) of extinction. This is especially so considering that the impacts of catastrophic events or significant changes in the environmental conditions (e.g. bush fires, climate change) were not considered. Our estimates suggest that populations with more than 1 000 individuals have a low probability of extinction ($P_{(Ext)} < 5\%$) in the presence of a fox-baiting program and should therefore be regarded as the absolute minimum size for viable populations. A minimum population size of 8 000 woylies (i.e. the minimum population size multiplied by a factor of eight) would incorporate the recommendations of Caughley and Gunn (1996, p. 206) to take into account the effects of unknown variables, measurement and encoding errors and possible inconsistencies between management recommendations and their practical execution *"before one would be satisfied that an adequate buffer against misfortune had been built in"*. In a recent review of the 50/500 rule, Frankham *et al* (2014) recommended an *effective* population size of

100 for short term and 1000 for long term conservation . This would indicate that *census* population sizes should be above 500 for short term and 5 000 for long term conservation assuming a *Ne*/*N* ratio of 0.2. These expectations are broadly supported by our work as well as theoretical simulations and empirical data on other vertebrates (Thomas 1990; Nunney and Campbell 1993) including macropod species such as euros (*Macropus robustus isabellinus*) (Short and Turner 1991). Additionally, a genetic assessment of outcomes from woylie translocation, empirically established that ~3 000 or more individuals are needed to maintain adequate levels of genetic diversity in the medium-long term (Pacioni *et al.* 2013).

A strong relationship was also evident between the initial heterozygosity and $P_{(Ext)}$. The relationship depicted in Fig 5 could be viewed as the potential returns of the effort made in conservation programs to maintain high genetic diversity in wild populations. The extinction risk of small woylie populations is exemplified by Tutanning Nature Reserve, which supported around 300 individuals (Sampson 1971; Groom 2010) with a mean heterozygosity of ~64% (Pacioni *et al.* 2011). Model projections indicated that at low heterozygosity, inbreeding depression, together with predation, would be detrimental or catastrophic if not otherwise mitigated. Recent reports suggest that this population has subsequently been reduced to undetectable levels (DPaW unpublished data) and may be considered functionally, if not ecologically, extinct.

In this study, the limited information on mortality rates, especially with regards to juvenile and subadult groups, was one of the major challenges. While it is recognised that the initial mortality rates for the juvenile and subadult groups are, in absolute terms, higher than for other age classes, our PVA demonstrated that increased juvenile and subadult mortality rates could explain the recent steep decline in the Western Australian woylie populations. This highlighted the importance of improving knowledge of their rates and factors of mortality (e.g. predation), although it is acknowledged that the lack of information on juvenile and subadult age groups is due largely to the difficulty of studying them in the wild (A. Wayne, personal observation). The identification of knowledge gaps and biological and ecological features that may influence population dynamics is considered one of the main achievements of PVA and alone it may make the process of developing a model worthwhile (Lacy 1993; Lindenmayer *et al.* 1993; Starfield 1997; Morris and Doak 2002).

The results we obtained are directly relevant to extant woylie populations given that the population sizes and starting values of genetic diversity (64 and 83,5%) were based on that found in wild woylie populations (Groom 2010; Pacioni *et al.* 2011; Wayne *et al.* 2013) and strong life history parameter similarity between woylie populations in Western Australia. Nevertheless, this model should be adjusted whenever there is evidence of different environmental conditions.

In conclusion, the model developed in this study highlights the importance of considering the interactions between factors that might influence populations of interest. In the case of the woylie the impact of the interactions of predation with factors that might compromise individual fitness (e.g. inbreeding depression or diseases) were found to be much greater than the effect of these factors in isolation. Population viability also was found to be especially sensitive to the mortality rates of juveniles and subadults and may be sufficient to account for the remarkable declines observed since 1999 (Wayne *et al.* 2013). As such this paper provides important guidance as to where to direct future efforts that should help identify the causes of the recent declines and how populations should be managed to improve the conservation prospects for populations and the species as a whole, for the longer term.

By extension, these findings are also relevant to other endangered species with a similar ecology and living in similar ecosystems, particularly those for which there is currently less information than the woylie. In particular, we argue that based on our results the following points can be generalised to, and should be considered for the management of, populations of woylies, Tasmanian bettongs and Northern bettongs:

- Population size targets should be at the very least 1-2 000, optimally >8 000, individuals. This implies that priority for conservation efforts should be given to sites that can support these population sizes. Similarly, selection of sites for the establishment of new (translocated) populations should have an expected carrying capacity >8 000. A potentially useful management alternative can be to enhance natural or assisted connectivity between smaller populations to obtain an overall meta-population above this size.
- Conservation efforts should aim to maintain H_t to 80% or more to minimise $P_{(Ext)}$. It should be noted that here we considered H_t as an index of genetic diversity, however theory predicts that allelic diversity declines more rapidly than H_t and biological consequences of the lack of allelic diversity should not be underestimated and our estimate of minimum genetic diversity should be considered conservative.

Lastly, we encourage managers and researchers involved in conservation programs for these species to use this PVA model (with the possible necessary adjustments) to plan management actions and refine research priorities.

Acknowledgements

We would like to thank P. Miller for clarifying technical details of VORTEX and all the staff of the Department of Parks and Wildlife (DPaW) and Australian Wildlife Conservancy that contributed to the collection of trapping data over the years. Special thanks go to M. Maxwell and F. Kirkpatrick (DPaW). We are grateful to C. Rafferty, S. Stevenson and K. Morley

(Whiteman Park) for useful comments on this manuscript. This project was financially supported by the Australian Academy of Science, South Coast Natural Resource Management Inc, Woylie Conservation and Research Project (a DPaW ‘Save Our Species’ project) and DPaW (PhD Student Stipend to CP). This study was approved by the Murdoch and DPaW Animal Ethics committees.

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Tables

Table 1. List of woylie PVA scenarios and relative parameters altered with respect to the baseline scenario.

K = Carrying capacity; Ad = adult; Juv = Juvenile; PY = Pouch Young; SD = Standard deviation; N = population size; DD = density dependent; H_t = heterozygosity

Table 2. Summary of final population parameters (with SD between brackets) and statistical comparisons to the baseline scenario (SSMD values and associate p-values between brackets) for scenarios with input parameters altered.

$r_{(ts)}$ = yearly growth rate; N = population size; H_t = heterozygosity; TE = time of extinction; $r_{(\mathrm{Rec})}$ = recovery rate; $P_{(Ext)}$ = Probability of extinction.

Table 3. Regression coefficient estimates with standard errors and related statistics of zero-inflated model fitted to the data from the sensitivity testing simulations carried out with the Latin Hypercube Sampling (N as dependent variable). Coefficients are sorted based on the absolute z-values.

K = carrying capacity; Ad_Mor = adult mortality; Juv_Mor = Juvenile mortality; PY_Mor = Pouch Young mortality; SD = standard deviation; Male_Breed = % male in the breeding pool; Init_N = initial population size.

Table 4. Regression coefficient estimates with standard errors and related statistics of the beta regression fitted to the data from sensitivity testing simulations carried out with Latin Hypercube Sampling (H_t as dependent variable). Coefficients are sorted based on the absolute z-values. Abbreviations are reported in Table 3.

Table 5. Regression coefficient estimates with standard errors and related statistics of zero-inflated model fitted to data from the simulations of additional scenarios carried out with the Latin Hypercube Sampling (*N* as dependent variable). Coefficients are sorted based on the absolute z-values.

Init_N = Initial population size; LEq = Lethal equivalents; LAl = Lethal alleles; Bait = baiting program; DD_Pred = density dependent predation; NDD_Pred = non-density dependent predation.

Figure Captions

Fig. 1. Dot plot of mean $r_{(ts)}$ (growth rate calculated on time-step basis) from sensitivity testing of the population model of *Bettongia penicillata* at year 50 (left panel) and year 100 (right panel). Descriptions of scenarios and abbreviation in the legend are in Table 1.

Fig. 2. Interaction effect plots demonstrating the interaction between the number of lethal equivalent and lethal recessive alleles on the zero component of the zero-inflated model fitted to data from simulations that include density dependent introduced animal predation with (right panel) and without (left panel) a baiting program.

Fig. 3. Interaction effect plots demonstrating the interaction between the initial heterozygosity and the presence (1) or absence (0) of a baiting program on the zero component of the zero-inflated model fitted to data from simulations that include density dependent introduced animal predation, four lethal equivalent, three recessive lethal alleles with a carrying capacity of 500.

Fig. 4. Predicted probability of extinction (with 95% confidence interval) as a function of initial population size obtained by fitting a logistic regression model to simulations with density dependent predation and a baiting program (red line) or without a baiting program (blue line).

Fig. 5. Predicted probability of extinction (with 95% confidence interval) as a function of initial heterozygosity obtained by fitting a logistic regression model to simulations with density dependent predation and a baiting program (red line) or without a baiting program (blue line).