Population viability analyses on a cycling population: a cautionary tale

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Abstract

Population viability analysis (PVA) packages do not always allow realistic simulation of particular life cycle features, so they may produce unrealistic predictions of extinction risk. This was suspected for a cycling Soay sheep population, *Ovis aries* L., that grows, overeats its habitat and then suffers high winter mortality. We compared projections of PVA models for the sheep that incorporated either an unrealistic ceiling carrying capacity using INMAT (the only choice) and VORTEX (the default), or realistic density dependence for survival (VORTEX). At year 50, the ceiling models predicted extinction probabilities of 60.4% (INMAT) and 87.4% (VORTEX), compared to only 4.6% for the density-dependent model. Small populations were equally likely to increase or decrease with the ceiling models, while they had high probabilities of increase with the density-dependent model, as found in reality. PVA cannot be relied upon to produce realistic projections if inappropriate mechanisms of population regulation are used. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Population viability analysis (PVA) is a process that evaluates the probability of population extinction over a specified time (Gilpin and Soulé, 1986; Shaffer, 1990; Boyce, 1992). Most commonly PVAs are conducted through the use of computer simulation models that incorporate the interacting deterministic and stochastic factors threatening small populations (Burgman et al., 1993; Akçakaya et al., 1997). By incorporating elements of uncertainty these models provide a stochastic projection of population fate. PVA has been shown to have good predictive accuracy, given sufficient data (Brook et al., 2000b).

PVA is now a widely used process and is recognised to be a valuable management tool for threatened species conservation and recovery (Clark et al., 1991; Lindenmayer et al., 1993; Possingham et al., 1993; Carroll et al., 1996). Species can be listed or classified as endangered on the basis of a PVAs predicted probability of extinction (IUCN, 1994). Further, PVA is becoming increasingly important in the implementation and formulation of conservation policy and legislation (Lindenmayer et al., 1993; Possingham et al., 1993). The Conservation Breeding Specialist Group of the World Conservation Union has conducted over 150 PVAs with the PVA package VORTEX alone (Seal et al., 1998). Many more have been conducted with other generic PVA packages (Lindenmayer et al., 1993; Lindenmayer and Possingham, 1994).

PVAs that are conducted using complex computer simulation models require detailed knowledge of species demography, ecology and life history (Clark et al., 1990; Ruggiero et al., 1994; Harcourt, 1995; Lacy, 1995). In particular, this requires an understanding of both the density-dependent and independent processes underlying population dynamics. Density dependence occurs when survival or fecundity depend on the absolute size of a

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population and density-independent changes may arise through the uncertainties of environmental stochasticity. The observed dynamics of any real population typically arise from a mixture of both density-dependent and independent processes (Hassell, 1986; Strong, 1986).

Detecting density dependence and distinguishing it from density independence has proven to be difficult in practice (see Hassell, 1986; Gaston and Lawton, 1987; Fox and Ridsdill-Smith, 1996). Further, given the limitations of time, money and species rarity, the data required to formulate functions of density dependence and to make estimations of any associated variation may either be unknown or impossible to collect (Harris et al., 1987; Lindenmayer et al., 1993; Ruggiero et al., 1994; Beissinger and Westphal, 1998). Previous studies (Ginzburg et al., 1990; Mills et al., 1996) have shown that PVA projections can be greatly influenced by the presence/absence or formulation of a particular regulatory mechanism. If the density-dependent and/or independent processes that regulate a population are incorporated in inappropriate manners, then the corresponding results from a given PVA may be unrealistic. This is the first study to compare PVAs which incorporate different mechanisms of population regulation for a cycling population.

Many populations of conservation concern are subject to density-dependent processes (Fowler, 1981; Sinclair, 1996; Capurro et al., 1997). This is particularly important for populations living in limited or decreasing habitats. Island populations, which have elevated probabilities of extinction (World Conservation Monitoring Centre, 1992), have limited habitat. For example, the population of Lord Howe island woodhen is limited by the extent of suitable habitat for breeding territories (Brook et al., 1997). Threatened populations living in protected reserves or in areas where habitat loss continues may also become subject to density-dependent regulation. For example, density dependence affects both African rhinoceros (Rachlow and Berger, 1998) and elephant populations in reserves (Ambruster and Lande, 1993; Whyte et al., 1998), and is seen as being critical to their conservation and management. Further, competition with existing wild animals affects the success of reintroduced orangutans (Price and Gordon, 1989).

In general the differences between different PVA packages has been shown to be relatively minor (Brook et al., 2000a, Brook et al., 2000b). In particular, standardised comparisons yielded no meaningful differences among packages (Brook et al. 2000a). However, some PVA packages cannot accurately reflect the density dependence of particular species and so may lead to inaccurate projections. For example, the PVA package INMAT can only regulate population numbers through the application of a ceiling carrying capacity. Further, the majority of PVAs that have been performed using VORTEX were conducted using a ceiling carrying capacity (as this was the only option until version 8). In some cases, this assumption may have been unrealistic. Unrealistic or not, the question to be addressed is: does this matter?

The Soay sheep, *Ovis aries* L., display overcompensatory density-dependent mortality, resulting in an irregular cycle of about 3–4 years duration, where the population grows, over eats its habitat and then suffers high winter mortality. While it has been shown that PVA packages generally produce accurate projections in retrospective analyses (Brook et al., 2000b), projections for the Soay sheep using INMAT were notably poor. As other packages which could incorporate more appropriate models of density dependence gave better predictions, this finding suggests that models using inappropriate density dependence may produce poor predictions. The impact of different mechanisms of density dependence on extinction risk can be evaluated using a package, such as VORTEX, that allows different mechanisms of density dependence to be used.

The objective of this study was to compare projections of the PVA packages INMAT (Mills and Smouse, 1994) and VORTEX (Lacy, 1993; Lacy et al., 1995) for the cycling Soay sheep population using models with different mechanisms of population regulation. Comparisons were based on (i) a ceiling model (applied in both INMAT and VORTEX) and (ii) a density dependent survival model (applied in VORTEX). We ask the questions: (1) What differences arise between the projections of a ceiling model and a density-dependent model? (2) Do these differences matter?

2. Methods

2.1. The Soay sheep

The Soay sheep are the most primitive domestic sheep in Europe (Boyd and Jewell, 1974; Campbell, 1974). They have lived on the St Kilda archipelago (57°49′N, 08°34′W) for over 1000 years and until quite recently they were restricted to the Isle of Soay (Boyd and Jewell, 1974). However, following the human evacuation of St Kilda in 1930, 107 sheep were transported from Soay to the main island of the archipelago, Hirta (Boyd, 1974). The sheep population on Hirta has been monitored in detail between 1959 and 1968 (Jewell et al., 1974), and from 1985 to 1993 (Clutton-Brock et al., 1991, 1997). These studies have focussed on a sub-population of sheep living in the Village Bay area of Hirta (Jewell et al., 1974; Clutton-Brock et al., 1991). Over these study periods the sheep have displayed a level of overcompensatory density-dependent mortality that yields a recurrent 3–4 year cycle of population growth and decline (Grubb, 1974; Clutton-Brock et al., 1991; Clutton-Brock et al., 1992; Clutton-Brock et al., 1997;

Grenfell et al., 1992; Fig. 1). The observed fluctuations arise as the sheep increase in numbers, overeat their food supply, and suffer high mortality (where up to 70% of all animals may die) due to over-winter starvation (Grubb, 1974; Clutton-Brock et al., 1991).

2.2. Population viability analysis packages

The PVA packages used in this investigation were INMAT (v6) and VORTEX (v8.03). These packages were designed from different starting points and for slightly different intentions, but both are suitable for generic application and have been used in the management and conservation of threatened species (Lacy and Clark, 1990; Clark et al., 1991; Mills and Smouse, 1994). INMAT was developed to investigate the short term effects of inbreeding depression. VORTEX is the more flexible of the two and the most widely used package (Seal et al., 1998). It was developed to model species with low fecundity and long lifespan (Lacy, 1993). INMAT is a 'cohort' based package that uses, projection matrices (Leslie, 1945; Lefkovitch, 1965), whilst VORTEX is an 'individual based' package that tracks the fate of each animal independently.

Both packages incorporate age specific survival and reproduction, and demographic and environmental stochasticity. Values for survival and reproduction are not deterministically fixed in either package, but are varied at each point in time according to the user's input estimates of annual environmental variation. The packages thus project the fate of a population through a process that is stochastic. As no two simulation trajectories will be the same, 500 replicate runs were conducted to ensure statistical reliability (Harris et al., 1987). Both packages modelled the population through a pre-breeding census.

Population regulation in VORTEX can be achieved with the implementation of (i) a ceiling carrying capacity (K), (ii) a user specified or package designated density-dependent function of reproduction, (iii) user specified density-dependent functions of survival or (iv) a combination of the former three alternatives. With the implementation of a ceiling carrying capacity (K) the population is regulated by a proportional truncation back to the value of K whenever a simulation trajectory exceeds this level. For density-dependent functions of survival or reproduction, VORTEX reads in the independent variable (e.g. total population size) and then calculates the value the rate will take (from the specified function). Until quite recently (v8.0 and later) the only options available for regulating population size in VORTEX were by way of either (i) a ceiling K alone or (ii) a ceiling K combined with the package designated density-dependent function of reproduction. Almost all of the PVAs that have been done using VORTEX have been done using a ceiling K. In INMAT, population size can only be regulated with the implementation of a ceiling K.

INMAT and VORTEX can also model the effects of inbreeding depression, but this was not incorporated, as studies by Bancroft et al. (1995a, 1995b) have suggested that the sheep's frequent population crashes result in the selection of more heterozygous individuals.

2.3. Model parameterisation

Models in INMAT and VORTEX were parameterised from the demographic data for the Soay sheep described in Grubb (1974) and Clutton-Brock et al. (1991, 1992). Annual counts on the numbers of male and female lambs, yearlings and those animals aged two years old and over were collected for the years 1960–1967 and 1985–1990. These data were used to calculate year to year values for survival and reproduction.

In all, three PVA models were built, one with INMAT and two with VORTEX. The INMAT model and the first of the VORTEX models used a ceiling K. For these two models, means (with their corresponding yearly variation) were calculated for sex and age specific survival and % number of breeding females (VORTEX; Table 1) and age specific survival and fecundity (INMAT; Table 1). The environmental variation for these rates was estimated as the calculated standard deviation minus the variation that was expected from demographic stochasticity alone (estimated from the annual binomial variances; see Lacy et al., 1995, p. 28; Table 1). K was set at 20% greater than the observed maximum population size (311), yielding $K = 373$.

In the second VORTEX model, population size was regulated by implementing density-dependent functions for survival. Survival (S) was modelled as a function of population size (N) according to the following equation (Maynard-Smith and Slatkin, 1973; Bellows, 1981; Grenfell et al., 1992; Clutton-Brock et al., 1997):
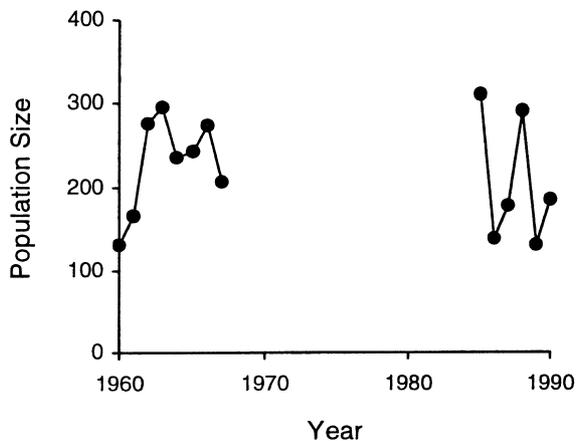

Fig. 1. Total population numbers of adult Soay sheep in the Village Bay area of Hirta in 1960–1967 and 1985–1990.

Table 1
Reproductive and survival measures used in the PVA models for Soay sheep

Model	Rate	Value	EV[b]	Survival function parameters[a]		
				d	a	b
INMAT ceiling	Fecundity[c]	0.515	0.45[d]	–	–	–
	Lamb survival	55%		–	–	–
	Adult survival	77%		–	–	–
VORTEX ceiling	Breeding females[e]	59%	14%	–	–	–
	Survival female lambs[f]	61%	30%	–	–	–
	Survival male lambs	51%	41%	–	–	–
	Survival female adults	84%	13%	–	–	–
	Survival male adults	64%	27%	–	–	–
Density-dependent	Breeding females	59%	14%	–	–	–
	Survival female lambs	–	6%	0.921	0.00380	7.74
	Survival male lambs	–	12%	0.990	0.00455	7.42
	Survival female adults	–	0%	0.952	0.00318	12.74
	Survival male adults	–	6%	0.872	0.00359	10.45

[a] For survival function: $S = d/(1 + (aN)^b)$.

[b] EV = environmental variation. This was estimated by subtracting the expected binomial variation from (i) the S.D. of the mean of the yearly values for the % number of breeding females (for both the VORTEX ceiling model and density-dependent model) and survival (for the VORTEX ceiling model) or (ii) the average deviation of the regression on survival (for the density-dependent model).

[c] Fecundity in INMAT was calculated as the number of lambs per adult.

[d] EV in INMAT is input as one combined figure which effects all rates equally. It is entered as a coefficient of variance.

[e] The % number of breeding females was calculated from the data of Clutton-Brock et al. (1991) where it was estimated that of all breeding females, 85% would produce a single lamb and 15% would produce twins.

[f] As Soay lambs become reproductively mature within their first year of life (Clutton-Brock et al., 1991; Stevenson and Bancroft, 1995), and because VORTEX assumes all reproductively mature animals are adults, values for survival were calculated for (i) male and female lambs and (ii) those male and female animals aged 1 year old and over (i.e. VORTEX adults).

$$S = d/(1 + (aN)^b) \qquad (1)$$

where d represents the level of survival in the absence of density-dependence (i.e. at small population sizes $S \approx d$), a reflects the population size ($1/a$) above which $S < d/2$ (i.e. for values of $N > 1/a$), and b controls the strength of density dependence, from undercompensation ($0 < b < 1$) through perfect compensation ($b = 1$) to overcompensation ($b > 1$). This equation has been used to successfully model the Soay sheep's population dynamics (Grenfell et al., 1992; Clutton-Brock et al., 1997). Parameter estimates were determined through iterative non-linear regression and the resulting equations were used as the functions describing the sheep's density-dependent survival (Fig. 2; Table 1).

For the density-dependent model, environmental variation in survival was taken as the variation around the fitted survival curves (Fig. 2) less that expected from demographic sources. Variation was calculated from the following standard equation:

$$\text{variation} = \sqrt{\left(\sum (y_i - f(x_i))^2 / (n-1) \right)} \qquad (2)$$

where, y_i is the actual value for a given value of (the independent variable) x_i, $f(x_i)$ is the fitted value for y from value x_i, and n is the number of observations.

All three models were run for a simulation period of 50 years with an initial population size of 130 animals (i.e. the actual population size in 1960) set at stable age distribution (van Groenendael et al., 1988; Ferson and Akçakaya, 1990).

2.4. Data analysis

Model comparisons were based on their reported (i) probabilities of extinction and (ii) mean population sizes over persisting replicates (i.e. only those replicates which persisted for the full 50 years). By excluding those replicates going extinct, this measure is independent of the reported probabilities of extinction. These output metrics were collected at simulation intervals of 10 years. Differences between models were analysed using t-tests (for mean population sizes), and contingency χ^2 and Kolmogorov–Smirnov tests (for probabilities of extinction). Based on the Kolmogorov–Smirnov test, with 500 iterations, the predicted probabilities of extinction are bounded by a 95% confidence interval of approximately ±6% (Sokal and Rholf, 1995).

3. Results

The two ceiling models and the density-dependent model gave widely differing predictions for probabilities

of extinction (Table 2). For all models the probabilities of extinction increased with time. However, with simulation length the reported probabilities of extinction for the density-dependent model became increasingly
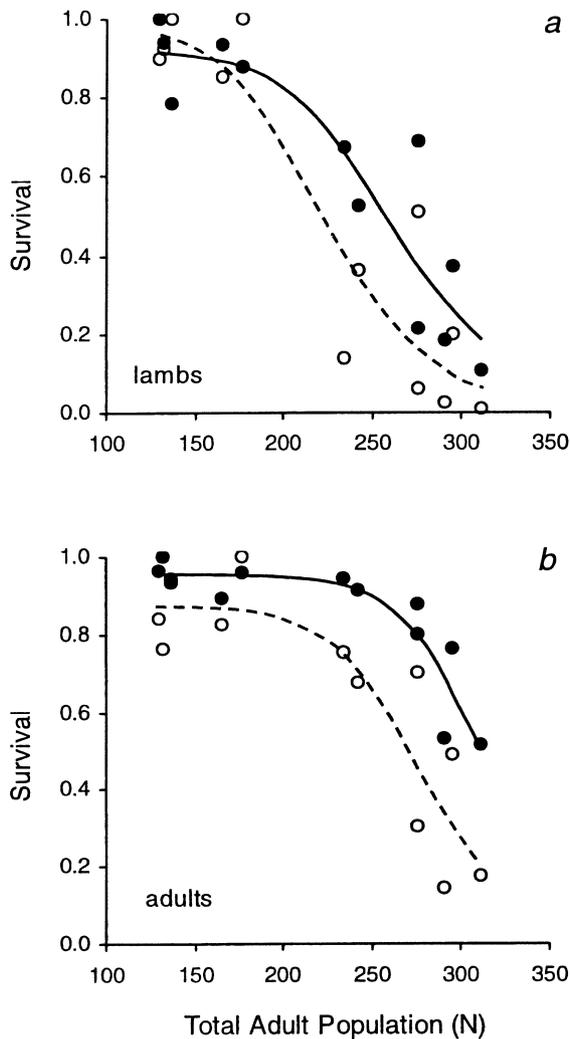

Fig. 2. Relationship between survival and total adult population size for Soay sheep on Hirta, for lambs (a) and adults (b). Male (open circles). Female (closed circles).

divergent from those of either of the ceiling models. The INMAT ceiling model yielded a probability of extinction of 60.4% for simulations of 50 years, while the corresponding probability for the VORTEX ceiling model was 87.4%, and that for the density-dependent model 4.6%. The probabilities of extinction produced by the density-dependent model were significantly lower than either of those produced by the VORTEX or INMAT ceiling models according to chi-squared tests (e.g. at 50 years: for VORTEX $\chi^2 = 690$, d.f. $= 1, P < 0.001$; for INMAT $\chi^2 = 355$, d.f. $= 1, P < 0.001$). Further, the differences between extinction probabilities need only be greater than 7.3% with the Kolmogorov–Smirnov test for a P-value < 0.01. Differences between the reported probabilities of extinction of the density-dependent model with either of the ceiling models are thus highly significant for all simulation lengths greater than 10 years (Table 2).

Model differences were also apparent when comparing mean persisting population sizes (Table 2). The INMAT ceiling model yielded significantly smaller population sizes than the density-dependent model over all simulation durations (e.g. at 30 years: $t = 4.7$, d.f. $= 215$, $P < 0.001$) and the VORTEX ceiling model for simulation durations of 10–40 years (e.g. at 30 years: $t = 2.9$, d.f. $= 171, P < 0.01$). At 50 years the mean population size from the VORTEX ceiling model was significantly smaller than the corresponding mean population size from the INMAT ceiling model ($t = 2.5$, d.f. $= 117, P < 0.05$) and the density-dependent model ($t = 5.6$, d.f. $= 65, P < 0.001$). No other differences were found to be significant.

Underlying these differences in extinction risk were the natures of the trajectories produced by each model (Fig. 3). The ceiling models produced trajectories that were highly variable (Fig. 3a and b), where this variability is echoed in the standard deviations about the mean population sizes (Table 2). Conversely, the density-dependent model produced trajectories that were much more concordant and more realistic than those of either ceiling model (compare Fig. 3a and b to c). As a result of this

Table 2
Simulation results for the ceiling models and the density-dependent model using INMAT and VORTEX. Mean N is the mean population size for persisting replicates and P(ext) is the probability of extinction

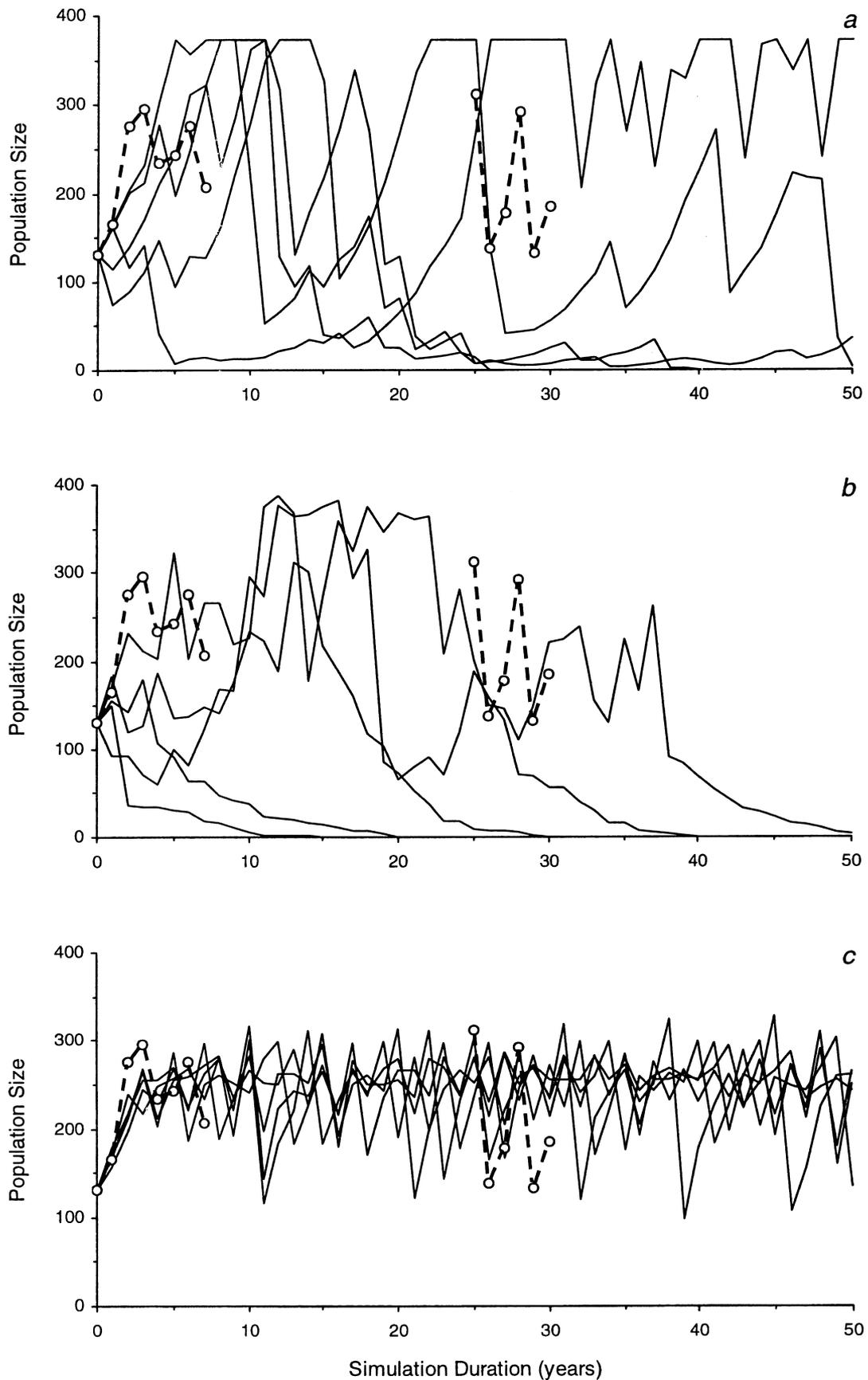| Model		Simulation duration (years)				
		10	20	30	40	50
INMAT ceiling	Mean N (S.D.)	178 (182)	182 (143)	192 (147)	206 (152)	196 (154)
	P(ext)	5.8%	23.4%	38.8%	51.8%	60.4%
VORTEX ceiling	Mean N (S.D.)	240 (98)	253 (98)	237 (91)	243 (109)	146 (136)
	P(ext)	0.2%	33.0%	62.4%	78.2%	87.4%
Density-dependent	Mean N (S.D.)	247 (45)	246 (48)	242 (49)	240 (48)	243 (53)
	P(ext)	0.0%	0.0%	2.0%	3.4%	4.6%

Fig. 3. Plots showing five representative trajectories produced by the INMAT ceiling model (a), the VORTEX ceiling model (b) and the VORTEX density-dependent model (c) over a 50 year simulation period. Actual sheep population numbers (open circles) are shown for comparison.

trajectory concordance, variability was small (as seen in the standard deviations about mean population sizes) and the reported population sizes remained stable over all reporting intervals (Table 2). The density-dependent model also captured some of the sheep's underlying population dynamics. Individual trajectories followed a 2–4 year cycle of growth and decline (Fig. 3c), as observed for the Hirta population.

4. Discussion

The ceiling and density-dependent PVA models gave widely differing predictions of extinction risk; after 50 year projections, the risks of extinction were 60.4 and 87.4% for the INMAT and VORTEX ceiling models and 4.6% for the density-dependent model. The density-dependent model also produced trajectories that were both more concordant and comparable to the actual sheep population.

Differences in model output arose not only because the models incorporated a different mechanism of population regulation, but also because this model difference led to widely different estimates of environmental variation in survival. Estimations of environmental variation can be based on (i) a standard deviation (i.e. the variation across years; as in the ceiling models), or from (ii) the spread around a specific fitted function (as in the density-dependent model). For the ceiling models, this led to very large estimates of environmental variation in survival. Values for survival in the VORTEX ceiling model will on average be > 50% for all sex and age classes (Table 1), but as the estimated environmental variation in survival is large (especially for female lambs, male lambs and adult males), there is about a 1 in 10 chance of female lamb and adult male survival being less than 25% and male lamb survival being zero at any population size or point in time. Likewise, a similar situation arose for the INMAT ceiling model, where the combined coefficient of variance was 0.45. For the Soay sheep, the implementation of a ceiling K results in population trajectories that will on average be growing, but populations cannot grow above K. With such large estimates of environmental variation and long simulations, the chances of decline are high, so any run will eventually fall to extinction. Conversely, by regulating population size with density-dependent functions of survival, the density-dependent model incorporated much smaller estimates of environmental variation in this parameter. Further, as values for survival were dependent on population size, small populations had much higher chances of survival, a situation similar to that found in reality. With low environmental variation and strict regulation of population numbers, the density-dependent model yielded much smaller probabilities of extinction than either of the ceiling models.

The Soay sheep have been living on Hirta for almost 70 years and on the St. Kilda archipelago as a whole for at least the past 1000 years. Consequently, estimated extinction probabilities of 60.4 and 87.4% over 50 years, as given by the ceiling models, are highly questionable. The high probability of extinction for the ceiling models was not due to an unrealistically low value of K, as setting K at +50% or even +100% of the observed maximum population size results in comparable extinction risks (87.3 and 87.0%, respectively, for the VORTEX ceiling model). It is not a factor of K being too small, but rather by modelling the population with a ceiling K, environmental variation was estimated at an inappropriate level. The ceiling models failed, because they unrealistically treated the sheep's population cycle as stochastic variation. Unlike the ceiling models, the density-dependent model produced much smaller estimates of extinction probabilities and produced trajectories that were both more concordant and typical of the actual sheep population numbers, where these trajectories also captured some of the sheep's underlying dynamics, in that they followed a 2–4 year cycle of growth and decline. Further, recent work by Grenfell et al. (1998) has shown that although the sheep's dynamics are inherently irregular, most of the uncertainty is concentrated at high population densities, and that this uneven pattern of noise actually promotes persistence of the population. All information points to the density-dependent model as being the most realistic.

These findings have serious implications in conservation biology. PVAs that incorporate inappropriate mechanisms of population regulation may lead to (i) incorrectly classifying species as endangered, (ii) the incorrect prioritisation of endangered species, and (iii) the implementation of inappropriate management options. Thus, scarce conservation resources may be wasted, species that require the greatest attention may be overlooked, and endangered populations may become even more threatened. Consequently the PVAs that have been run using VORTEX, with the implementation of a ceiling carrying capacity must be interpreted with caution, especially for species where other forms of population regulation may apply.

In practice it will be necessary to (i) carefully check for evidence of density dependence, so the appropriate mechanisms of population regulation are incorporated into a PVA, and (ii) choose a PVA package that will allow the "correct" form of density dependence to be used. Over the past few decades various tests have been put forth for the detection of density dependence, but as yet no one optimal test has been found, and is unlikely to be found (Fox and Ridsill-Smith, 1996). It would seem that one must either have detailed knowledge of the underlying processes governing a population's dynamics or carry out experimental manipulations upon it (Gaston and Lawton, 1987). Explicit knowledge of a

population's regulatory mechanisms is a luxury not afforded for most populations considered for PVA. Often data are so scarce that determining any density-dependent process is virtually impossible, let alone sufficient to make reasonable estimates of environmental variation. Further, even knowing the density-dependent processes for a closely aligned species may not be useful, as there may be large differences in the way density dependence operates in similar species (Eberhardt, 1987). An understanding of the ecological processes governing a species' population dynamics is most important if we are to attain reliable predictions from PVA. In reality however, this understanding may be unachievable, given the limitations of time and money.

In this study VORTEX was chosen because of its wide application and flexibility of model construction. However, some packages can only regulate population size with the implementation of a ceiling K (as in the case of INMAT), while others may be limited to a set of 3 or 4 package designated functions of density dependence (e.g. RAMAS® Age, Ferson and Akçakaya, 1990; and RAMAS® Metapop, Akçakaya, 1994). In those instances where a specific form of density dependence regulates a population but this cannot or is not incorporated reasonably, then the projections need to be viewed with scepticism. As this study shows, the implementation of a ceiling model is unrealistic for the Soay sheep. However, when parameterised properly, VORTEX gave projections and results that were appreciably more realistic.

In conclusion, the ceiling and density-dependent PVA models gave widely differing risks of extinction for a cycling Soay sheep population. In order for PVA simulations to yield realistic predictions of population persistence, it is essential that the correct mechanisms of population regulation be used. In general, we recommend the use of PVA packages that realistically encompass the biology of a particular species.

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