



Modelling differential extinctions to understand big cat distribution on Indonesian islands

DAVID M. WILKINSON and HANNAH J. O'REGAN

Biological and Earth Sciences, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, U.K. E-mail: D.M.Wilkinson@livjm.ac.uk

ABSTRACT

Aims To model differential extinction rates for island populations of tigers *Panthera tigris* and leopards *P. pardus*.

Location Indonesia.

Methods We built VORTEX population models of tiger and leopard populations on an island the size of Bali (3632 km²), using data from the literature.

Results The tiger populations were less extinction prone than the leopard populations. This was unexpected as tigers had the smaller population sizes and, as such, might be assumed to be more extinction prone. We identified

several aspects of tiger breeding biology that explain the result.

Main conclusions Sea level reconstructions suggest that both tiger and leopard would have been present in Java, Sumatra and Bali at the end of the last glacial. Our model provides a plausible mechanism based on population ecology to explain why these leopard populations were more extinction prone than the tiger populations. In addition it illustrates the potential utility of population ecology models in understanding historical patterns in biogeography.

Key words Biogeography, extinction, Indonesia, leopard, *Panthera pardus*, PVA, tiger, *Panthera tigris*, VORTEX.

'Distributions, on modern island fragments, of species unable to disperse across water constitute a study in differential extinctions.' (Mayr & Diamond, 2001).

INTRODUCTION

Historically, until recent human-caused extinctions, the tiger *Panthera tigris* (L.) was found on Sumatra, Java and Bali (but not Borneo) while the leopard *Panthera pardus* (L.) was restricted to Java (Sunquist & Sunquist, 2002). During low sea levels associated with Quaternary glaciations all these islands are thought to have formed a single land mass connected to mainland Asia (van den Bergh *et al.*, 2001), so the two big cat species should have been able to reach all of these islands. It is of note that the islands of Wallacea (Sulawesi and the Lesser Sunda Islands), which have always been geographically isolated from the mainland, lack large carnivores (van den Bergh *et al.*, 2001). We find it hard to envisage how the leopard could reach Java without also occupying Sumatra and Bali. This raises the question of how to explain the recent distribution

of these two cats; why has the leopard apparently experienced more population extinctions than the tiger during the approximately 10 000 years since the end of the last glacial?

In biogeography, explanations of distribution patterns frequently rely on ideas of dispersal, vicariance or sometimes interspecific competition, often expressed as verbal 'just so stories'. Here we take a different approach using a population model to illustrate why island populations of the leopard should be more vulnerable to extinction than the tiger. This result is counter-intuitive as conventional wisdom would expect the tiger (the larger cat with the smaller population density) to be more extinction prone.

We modelled tiger and leopard populations on an island the size of Bali using the VORTEX population viability analysis (PVA) model (Lacy, 1999). Such models have been designed as conservation management tools for investigating the probability of population persistence under various assumptions about population ecology, genetics and environmental variation. However, they can also be informative in studying extinct populations (such as the tiger in Bali) or even imaginary populations (such as the leopard in Bali, for which there is currently no historical or fossil evidence). We are aware of two previous studies that have used PVA models to study extinct populations: Holdaway & Jacomb (2000) used a Leslie

Correspondence: Dave Wilkinson, Biological and Earth Sciences, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, UK. E-mail: d.m.wilkinson@livjm.ac.uk

matrix population model to study the extinction of the New Zealand Moas (*Dinornithiformes*), while we have previously used VORTEX to study the survival of large carnivores in glacial refugia in Europe (O'Regan *et al.*, 2002).

THE VORTEX MODEL

VORTEX is a Monte Carlo simulation model that follows each individual in a population in an independent manner. The probability of an individual either dying or reproducing is randomly drawn from a binomial distribution with a mean set by the inputted life history data, while variation in the carrying capacity (K) is modelled as a normal distribution (Miller & Lacy, 1999). The model was originally designed for vertebrate populations of low fecundity and long life span so it is highly suitable for modelling big cat populations. Even critics of PVA models such as VORTEX seem happy that they are suitable for 'exploring theoretically the implications of model assumptions on extinction probabilities' (Coulson *et al.*, 2001). We have used VORTEX in such an exploratory manner in this study. We consider the qualitative differences in behaviour between the tiger and leopard populations as the important outcome, not the quantitative detail, which is unlikely to be accurate in such a simple model. A similar point has been made in relation to conservation related PVAs by Lindenmayer *et al.* (2003). Beissinger & McCullough (2002) provide a recent review of PVA models.

We took an island the size of Bali (3632 km²) as the base of our models. We started all our models at the carrying capacity. This was determined by the area of the island divided by the median female home range size given in the literature (see Table 1 for the literature used) multiplied by two; so all our

Table 1 Life history data used in our models, based on Bailey (1993), Mazak (1981) and Sunquist & Sunquist (2002). Figures marked * are based on plausible estimates for a big cat species rather than values in the literature

	Tiger	Leopard
Litter size (%)		
1	10	30
2	38	60
3	38	10
4	10	—
5	3	—
6	1	—
Cub mortality (%)	50*	50
Adult mortality (%)	10*	10*
K (10% standard deviation allowed)	376	938
Maximum breeding age	15	12
Start of breeding		
Males	4	3
Females	3	3

models start with a 50 : 50 sex ratio. Inbreeding is often considered important in conservation biology due to problems caused by recessive lethal alleles and other aspects such as increased disease susceptibility (e.g. Acevedo-Whitehouse *et al.*, 2003). In the absence of appropriate data we used the default values in VORTEX for inbreeding (i.e. 3.14 lethal equivalents per individual, which comprises 1.57 recessive lethal alleles and 1.57 lethal equivalents not subject to removal by selection: Miller & Lacy, 1999). We assumed 50% of adult males were in the breeding pool and that 50% ($\pm 12\%$ Standard Deviation) of females breed each year. Cub mortality was taken from the literature. In the absence of good data we assumed a steady rate of adult mortality up to the maximum breeding age. Life history data used in our models are summarized in Table 1. Note that we have been forced to use data from a range of studies rather than using statistics from a single tiger or leopard population. Lack of suitable data prevented us from modelling density dependence at population sizes below the carrying capacity. Prior to the version of VORTEX used in our model (version 8), this has not been an option, and therefore most published VORTEX simulations have used a ceiling carrying capacity to regulate the population (Chapman *et al.*, 2001). We followed this approach. Adding additional density dependence will often increase the survival of a population (McCallum *et al.*, 2000; Chapman *et al.*, 2001). Our approach in this study has been to keep the models as simple as possible. Therefore we did not use VORTEX's capacity to model periodic environmental catastrophes, although on the long time scales (thousands of years) of interest in this study, such catastrophes may be important (Whittaker, 1995). An example of such an event in Indonesia is the eruption of the island of Krakatau in 1883, one of many volcanoes in the region (Thornton, 1996). Apart from our lack of density dependence all our other assumptions are conservative, tending to increase the survival probability of the population. For example, it is unlikely that all of Bali was good tiger and leopard habitat, indeed by the early decades of the twentieth century the Bali tiger appears to have been restricted to the west of the island by human activity (van den Brink, 1980).

We ran 500 replicate populations of each species over 1000 years ('short' time scale), the maximum time span allowed by VORTEX. The time span of 1000 years is very long by the standards of most conservation focused PVAs [see Karanth & Stith (1999) for a 100-year PVA for a small tiger population], however, for the biogeographical questions of interest in the current study longer time spans are clearly relevant. To address this we ran a limited number of populations over a 5000-year time period. To do this we ran a single population for 1000 years (the maximum the program allows) then ran a new model using the output data from the first run, repeating the procedure five times to give a run of 5000 years. As this was a time consuming process we limited ourselves to small sample sizes (five replicate populations for each species).

RESULTS

Short time scale, one thousand years of big cats on Bali

Our optimistic method of calculating K (which assumes all of Bali was suitable habitat) gave values of 376 for tigers and 938 for leopards (Table 1). After running 500 populations for 1000 years all the tiger populations survived while 10% of the leopard populations had gone extinct (Fig. 1). Numerical experiments with the model showed that the main factors increasing the survival probability of the tiger was the larger litter size and the slightly older maximum breeding age for tigers. Adjusting these variables in the leopard model to make them more like those for the tigers reduced leopard extinction probabilities (data not shown).

Long time scale, survival over 5000 years

Over 5000 years all the tiger populations survived while two of the five leopard populations went extinct. Inspection of Fig. 2 shows that the leopard populations tended to show greater fluctuations in size than the tigers, hence increasing their chance of extinction. Indeed two populations went extinct between 500 and 1500 years.

DISCUSSION

VORTEX takes a stochastic approach to modelling population extinction. Causes of stochasticity can be divided into demographic and environmental (May, 1974; Lande, 1993). In addition, there are more unusual 'random catastrophes'

(Lande, 1993), such as the previously described eruption of Krakatau. It is not clear if such catastrophes should really be considered unusual events (Weatherhead, 1986) and treated separately from the more 'normal' year-to-year variation described as environmental stochasticity. Our model essentially only considers demographic stochasticity. While VORTEX models often describe the standard deviation of K as 'environmental variation', in effect this is only equivalent to setting K at a slightly smaller value. Therefore our model is one based on demographic stochasticity as catastrophes were not included for reasons of simplicity (and difficulties in parameterization). This leads to the apparently unrealistic assumption of no environmental variation between years. This may, however, be a reasonable simplifying assumption for large carnivores, for example Saether *et al.* (1998) found that brown bears *Ursus arcos* in Scandinavia appeared to experience environmental stochasticity close to zero although living in an environment which showed year to year fluctuations.

Prior to running the models we would have predicted that the leopard would survive better than the tiger on islands because of its potentially higher population size and the common assumption that smaller animals tend to have higher population growth rates (r). However, according to our model the reverse is true, due to the larger litter size and longer reproductive life of the tiger. Within our model chance plays a larger role in the persistence of leopard populations than it does for the tiger. We have previously stressed the role of chance in the survival of a jaguar-like cat in European glacial refugia using a VORTEX model (O'Regan *et al.*, 2002).

Assuming that the main Indonesian islands were all occupied by both tigers and leopards at low sea level during the

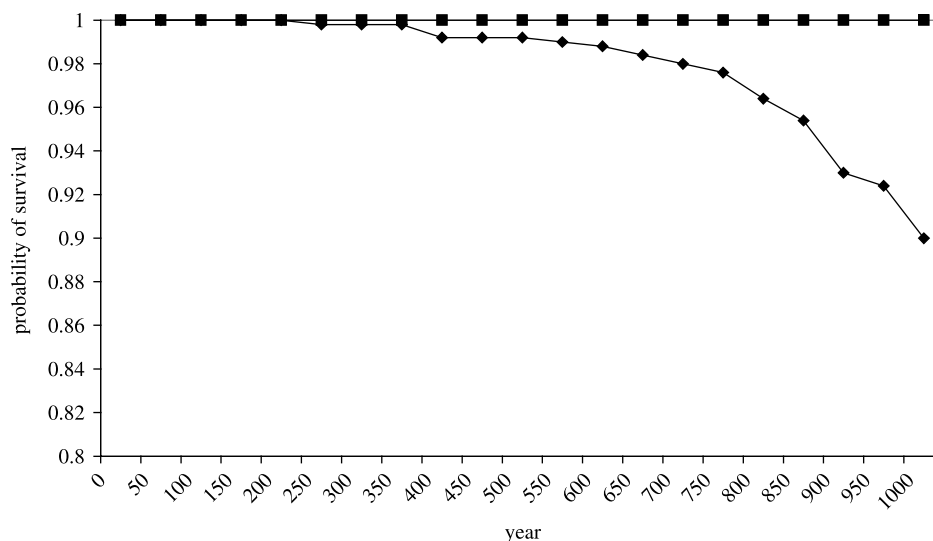


Fig. 1 Probability of survival for 500 replicate model populations of tigers (■) and leopards (◆) run using VORTEX over a period of 1000 years.

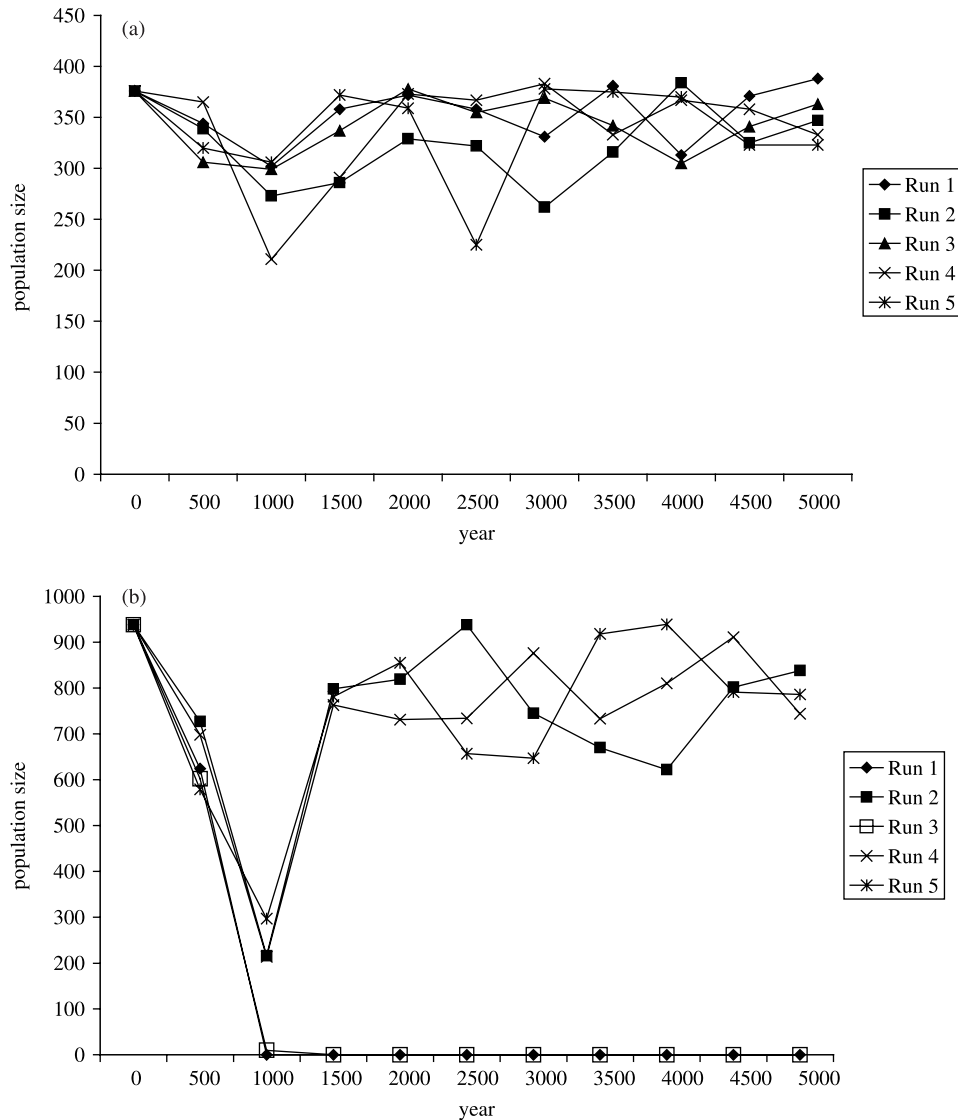


Fig. 2 Comparison of five tiger (a) and five leopard (b) model population sizes over a period of 5000 years. Note that in Fig. 2 (b) two leopard populations become extinct either side of the 1000-year point on the graph.

last glaciation, then this pattern of increased extinction probability for leopards matches the historical distribution of these animals, with leopards absent from all islands except Java. The tiger survived on the relatively small island of Bali and apparently only became extinct on Borneo (Sunquist & Sunquist, 2002). However, the only fossil evidence for tigers on Borneo comes from teeth (Kitchener, 1999), which may have been traded by people from Sumatra or Java. Our model suggests that the tiger could easily have survived on Borneo if present, so supporting this archaeological interpretation of the sub-fossil teeth as the product of trade.

Extinction has been ascribed an important role in island biogeography (MacArthur & Wilson, 1967). Our model suggests a possible mechanism for differential extinction in tigers and leopards based on differences in their breeding biology. While in our model these differences are sufficient to explain the historical distribution of these cats *it is clearly possible that other processes may have been involved*. Our study illustrates how PVA models can be used to experiment with the ecology of extinct populations, potentially adding rigour to the historical explanations common in biogeography. It is in the nature of such explanations that they are often based on

limited data and apply to a particular case (so $n = 1$, with no possibility of replication). This creates problems both for more traditional verbal explanations and our modelling approach. However, our approach at least has the advantage of making explicit the assumptions on which the models are based and allows other workers to experiment with their preferred assumptions by modifying the variables. As Midgley (1989; p. 102) suggested, outside mathematics 'most of the premises of an argument are unstated, and many of them have never even been made explicit' — constructing a mathematical model at least forces one to make the assumptions explicit. Our modelling approach can also produce counter-intuitive hypotheses that may not have been identified by verbal reasoning unsupported by mathematics. This makes the cautious use of such models a useful biogeographical method even though such historical models present great difficulties in terms of parameterization and formal testing. We stress that it is the qualitative differences in behaviour of the populations that are important; we treat the quantitative detail with some scepticism.

Our model also has some relevance to tiger taxonomy. The Bali tiger has been described as a distinct sub species (Schwarz, 1912; Mazak *et al.*, 1978), although this is controversial (Kitchener, 1999; Kitchener & Dugmore, 2000). As Bali is very close to Java, tigers could swim from one to the other (Matthiessen, 2000); such gene flow would tend to rule out a separate subspecies on Bali. Our model, by showing that a self-supporting tiger population is possible on Bali, is consistent with (but does not prove) the subspecies idea. The alternative result, that the model could only support tigers on Bali with regular immigration from Java, would have made the subspecies idea less likely.

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REFERENCES

- Acevedo-Whitehouse, K., Gulland, F., Greig, D. & Amos, W. (2003) Disease susceptibility in California sea lions. *Nature*, **422**, 35.
- Bailey, T.N. (1993) *The African leopard — ecology and behaviour of a solitary felid*. Columbia University Press, New York.
- Beissinger, S.R. & McCullough, D.R. (2002) *Population viability analysis*. Chicago University Press, Chicago.
- van den Brink, J. (1980) The former distribution of the Bali Tiger *Panthera tigris balica* (Schwarz, 1912). *Saugertierkundliche Mitteilungen*, **28**, 286–289.
- van den Bergh, G.D., de Vos, J. & Sondaar, P.Y. (2001) The late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **171**, 385–408.
- Chapman, A.P., Brook, B.W., Clutton-Brock, T.H., Grenfell, B.T. & Frankham, R. (2001) Population viability analysis on a cycling population: a cautionary tale. *Biological Conservation*, **97**, 61–69.
- Coulson, T., Mace, G.M., Hudson, E. & Possingham, H. (2001) The use and abuse of population viability analysis. *Trends in Ecology and Evolution*, **16**, 219–221.
- Holdaway, R.N. & Jacomb, C. (2000) Rapid extinction of the Moas (Aves: Dinornithiformes): model, test and implications. *Science*, **287**, 2250–2254.
- Karanth, K.U. & Stith, B.M. (1999) Prey depletion as a critical determinant of tiger population viability. *Riding the tiger: tiger conservation in human-dominated landscapes* (ed. by J. Seidensticker, S. Christie and P. Jackson), pp. 100–113. Cambridge University Press, Cambridge.
- Kitchener, A.C. (1999) Tiger distribution, phenotypic variation and conservation issues. *Riding the tiger: tiger conservation in human-dominated landscapes* (ed. by J. Seidensticker, S. Christie and P. Jackson), pp. 19–39. Cambridge University Press, Cambridge.
- Kitchener, A.C. & Dugmore, A.J. (2000) Biogeographical change in the tiger, *Panthera tigris*. *Animal Conservation*, **3**, 113–124.
- Lacy, R.C. (1999) VORTEX [WWW document]. <http://pw1.netcom.com/~rlacy/vortex.html>.
- Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, **142**, 911–927.
- Lindenmayer, D.B., Possingham, H.P., Lacy, R.C., McCarthy, M.A. & Pope, M.L. (2003) How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecology Letters*, **6**, 41–47.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Matthiessen, P. (2000) *Tigers in the snow*. Harvill, London.
- May, R.M. (1974) *Stability and complexity in model ecosystems*, 2nd edn. Princeton University Press, Princeton.
- Mayr, E. & Diamond, J.M. (2001) *The birds of northern Melanesia*. Oxford University Press, Oxford.
- Mazak, V. (1981) *Panthera tigris*. *Mammalian Species*, **152**, 1–8.
- Mazak, V., Groves, C.P. & Van Bree, P.J.H. (1978) On a skin and skull of the Bali tiger and a list of preserved specimens of *Panthera tigris balica* (Schwarz, 1912). *Zeitschrift für Säugetierkunde*, **43**, 108–113.
- McCallum, H., Kikkawa, J. & Catterall, C. (2000) Density dependence in an island population of Silver Eyes. *Ecology Letters*, **3**, 95–100.
- Midgley, M. (1989) *Wisdom, information and wonder, what is knowledge for?* Routledge, London.
- Miller, P.S. & Lacy, R.C. (1999) VORTEX: a stochastic simulation of the extinction process, Version 8. Users manual. Conservation Breeding Specialist Group. (SSC/IUCN): Apple Valley, MN.
- O'Regan, H.J., Turner, A. & Wilkinson, D.M. (2002) European Quaternary refugia: a factor in large carnivore extinction? *Journal of Quaternary Science*, **17**, 789–795.
- Saether, B.-E., Engen, S., Swenson, J.E., Bakke, O. & Sandegren, F. (1998) Assessing the viability of Scandinavian brown bear, *Ursus arctos* populations: the effects of uncertain parameter estimates. *Oikos*, **83**, 403–416.

- Schwarz, E. (1912) Notes on Malay tigers, with a description of a new form from Bali. *Annals and Magazine Natural History (London) Series*, 8(10), 324–326.
- Sunquist, M. & Sunquist, F. (2002) *Wild cats of the world*. University of Chicago Press, Chicago.
- Thornton, I. (1996) *Krakatau*. Harvard University Press, Cambridge, Mass.
- Weatherhead, P.J. (1986) How unusual are unusual events? *American Naturalist*, 128, 150–154.
- Whittaker, R.J. (1995) Disturbed island ecology. *Trends in Ecology and Evolution*, 10, 421–425.

BIOSKETCHES

Dave Wilkinson has wide interests in biology, environmental science and the history of science. His theoretical work has concentrated on evolutionary ecology, biogeography and Earth systems science. His more empirical studies have included work on Quaternary palaeoecology, environmental archaeology (especially around the English Lake District) and the ecology of protozoa.

Hannah O'Regan is an archaeologist and vertebrate palaeontologist. Her research interests include big cats (extant and fossil), early human dispersal from Africa and the history of zoos.

