

The importance of time scale in conservation biology and ecology

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The issue of time scaling in conservation biology and ecology is rarely considered, yet has crucial implications. If time scale is inappropriate, it impedes the search for generalities. Data on threatened species are typically limited, so the search for generalities is important in conservation biology where extrapolations from well studied taxa to threatened species are often needed. When time scale is specified in conservation biology and ecology it is typically defined in years. However, theoretical and empirical evidence indicates that extinction risk scales to generations, as do catastrophes, and environmental and genetic stochasticity. Examples are given of important insights achieved by analyses using generations. Conversely, human social and political considerations are more likely to require scaling to years, so the purpose of studies needs to be carefully defined. Progress in conservation biology and ecology will be impeded if the issue of time scale is not addressed carefully.

Introduction

Time scales are rarely discussed explicitly in conservation biology and ecology, but are often tacitly assumed to scale to years rather than generations, or some mixture of these. The World Conservation Union (IUCN) uses a mixture of years and generations in its threatened species categorization system, with both being used for critically endangered and endangered categories, but years alone being used for the vulnerable category (IUCN 2002). By contrast, the genetic factors contributing to extinction risk (inbreeding

depression and loss of genetic diversity) clearly scale to generations (Frankham *et al.* 2002). Does this ambiguity regarding time scale really matter? Here we argue that careful consideration of the units of time scale is crucial for successful interpretation of many ecological processes, especially those related to extinction risk.

The choice of biological time scale is crucial in several contexts in conservation biology and ecology, as follows:

- A major objective of science in general and conservation biology and ecology

in particular is to seek general principles (Belovsky *et al.* 2004). Shared evolutionary history leads us to expect similar principles to apply across related taxa. General principles are extremely important in conservation biology where there is often a lack on data on threatened species, but an urgent need for immediate action. Finding generalities useful for conservation management will be impeded if inappropriate time scales are used in analyses. In analyses of data across taxa there is a need to minimise experimental noise to maximise statistical power. If analyses are carried out using an inappropriate time scale then uncontrolled variation may be excessive and statistical power low. It is notable that there are many generalities across taxa in evolutionary genetics where most processes are modelled and analysed on generation scales (Falconer & Mackay 1996, Futuyma 1998, Frankham *et al.* 2002). By contrast, in conservation biology and ecology the unique characteristics of each species is usually stressed and few generalities have emerged (Primack 1998, Belovsky *et al.* 2004), except for the pervasive allometric scaling of body mass with various demographic and physiological attributes (Peters 1983). Recently there has been an upsurge in interest in searching for generalities in ecology with the establishment of centres such as the National Center for Ecological Analysis and Synthesis (NCEAS) and large data bases such as the Global Population Dynamics Database (NERC 1999) for analyses of long term data sets from different taxa (e.g. Fagan *et al.* 2001, Inchausti & Halley 2001, 2003).

- Data for most threatened taxa are very limited. Since political and administrative decisions are frequently made without the time or data to support detailed case-specific evaluations, there is a need for simple scientifically based rules of thumb for minimum viable population sizes and minimum habitat areas to use in such cases. Even for threatened species with some data, there is a great need for “default” data sets to use from related taxa, especially for variances of life history parameters. Variances have extremely high sampling errors (Sokal & Rohlf 1995)

and are underestimated with short data sets (Pimm & Redfearn 1988, Arino & Pimm 1995, Inchausti & Halley 2001). In particular, reliable information on environmental stochasticity and the frequency and severity of catastrophes (extreme drop in population size due to extreme weather, disease epidemics, etc.) has been very limiting in population viability analyses (Reed *et al.* 2003a). Consequently default values for these parameters are badly needed and must be based on as broad a range of species as possible.

In evolutionary biology, scale must be addressed when data from different sized animals are compared. Size allometry has been known since the classic work of D’Arcy Thompson (1942). For example, the impact of breeding system on testis size was only revealed after the effect of body size was removed (Harcourt *et al.* 1981). Similarly, brain size comparisons must account for differences in body size (e.g. Gittleman 1994). Scaling of extinction risk by generations also has the effect of removing body size effects, as we indicate below (Millar & Zammuto 1983, Peters 1983).

Does extinction risk scale to years or generations?

Contemporary extinctions are caused by the combined effects of systematic human-associated factors (habitat loss, over exploitation, introduced species and pollution), and stochastic factors (demographic, environmental and genetic stochasticity and catastrophes) (Frankham *et al.* 2002, Merilä & Kotze 2003). Theoretical and empirical evidence indicates that extinction risk and its stochastic components scale more closely to generations than years. We argue below that the human-associated systematic risk factors are so variable in impact over time that they often have no clear scale.

Based on analytical models, Leigh (1981) predicted that extinction risk would scale to generations. Armbruster *et al.* (1999) demonstrated the inappropriateness of year-based viability assessments for elephant populations and indicated that generations was the natural time scale for

extinction risk. Belovsky (1987) found that extinction risk scaled with body size, being less for large bodied species when other factors, such as population size, were held constant. Since body size is closely related to generation length (Millar & Zammuto 1983), this indicates that extinction risk scales to generations. Further, Newmark (1995) found that age at maturity, an indicator of generation length, was positively related to species survival in mammals in US national parks when population size effects were controlled for. O'Grady (2002) has shown that extinction risk due to the combined effects of all systematic and stochastic factors scales better to generations than years. He determined, for 30 vertebrate taxa, minimum viable population sizes (MVP) required for a 90% probability of persistence for 100 years and then asked if generation length was a useful predictor of MVP. Extinction risk was significantly related to generation length, being lower on a per year basis for long-lived species, all other factors being similar. However, when the analyses were repeated for the same taxa, but MVPs determined for a 90% probability of persistence over 11 generations (the mean number of generations for 100 years for these taxa), number of years was not a predictor of extinction risk. A related result can be gleaned from Reed *et al.* (2003b). Minimum viable population sizes for 99% persistence for 40 generations across 102 vertebrate taxa were similar across trophic levels (herbivores, omnivores and carnivores), major vertebrate taxa (mammals, birds and poikilotherms) and latitudes, but these similarities would not be apparent on a scale of years (Bessa-Gomes *et al.* 2003). Thus, extinction risk scales better to generations than years in animals.

Most of the stochastic components of extinction risk also scale better to generations than years. As indicated above, there are compelling theoretical reasons and empirical evidence that inbreeding depression and loss of genetic diversity occur on a generational scale (Frankham *et al.* 2002). Recently, we have found that the frequency of catastrophic die-offs (50% or greater decline in population size) scales better to generations than to years, based on analyses of data on 88 vertebrate species with long-term population dynamics data sets (Reed *et al.* 2003a). Environmental stochasticity and maximal rates

of population increase (r_m) may also scale better to generations than to years, at least in mammals. The widely quoted view that small mammals grow faster and fluctuate more in population size than large mammals disappears when they are compared on a per-generation scale (Fowler 1988, Sinclair 1996), indicating that regulatory processes and environmental stochasticity scale better to generations than years. Whilst we are not aware of any explicit consideration of the scaling of demographic stochasticity, natural variations in sex ratios, birth and death rates are associated with greatest risk around reproduction, so they may be more closely associated with generations. Further, deterministic population fluctuations, driven by unstable age- or stage-cohorts (Beckerman *et al.* 2003), will be more strongly related to generational time scales.

The scaling of human impacts on wildlife populations is rather variable and inconsistent. Human impacts do not scale to human population growth (and therefore human generations) alone, but also to per capita consumption of natural resources, especially total energy use (Ehrlich 1994). Habitat loss is generally accelerating in wild areas, but varies for particular species and countries (WCMC 1992). Habitat loss is typically increasing in the developing world, but national parks and other protected areas are now increasing across the globe (Rodrigues *et al.* 2004). The time trend and scale of over-exploitation of populations is very variable. For some species, such as many fish and forest tree species, harvest is increasing with the demographic and economic growth of human population, especially in the third world, but for others such as koalas and whales it has peaked and then declined thanks to legislation and effective protection.

The impact of introduced species on native taxa is very variable and has no obvious scaling unit. Overall, it has tended to get worse over time, but in the developed world the rather free flowing and liberal period of introductions during the 19th and early 20th centuries gave way to more restrictive regulations designed to curb undesirable introductions. More recently, however, the huge increases in human population, travel and trade have probably increased the number of introductions of undesirable spe-

cies (e.g. fire ants into Australia; Henshaw *et al.* 2004).

Pollution is expected, in theory, to increase with human population and per capita consumption. However, in the developed world it has peaked and declined due to legislation and effective controls. In the developing world, pollution is generally increasing with human population size and time. Yet, overall, the lack of clear scaling of systematic human-associated impacts has not affected the general conclusion that extinction risk scales better to generations than to years (Belovsky 1987, O'Grady 2002, Reed *et al.* 2003b).

Clearly, the purpose of a study, whether scientific or social/political, needs to be defined before deciding upon the most appropriate scale. We have been referring to natural biological scales. When we turn to human social and political considerations, time scales are more naturally expressed in years, or some other unit appropriate to human population or economic growth (Hutton & Dickson 2000, IUCN 2002). Consequently, different scales are likely to be best for biological versus human political considerations.

What insights have been achieved by using a generation scale?

Catastrophes are predicted to have a major influence on the probability of extinction. The use of the generation scale has allowed us to reduce noise in the analysis of the frequency and severity of catastrophes in 88 species of vertebrates (Reed *et al.* 2003a). Catastrophes have a frequency of approximately 14% per generation, and there are no significant differences in frequency among major vertebrate taxa. In a similar manner, minimum viable population sizes (MVP) required for long term persistence are generally believed to be highly circumstance and species specific, depending on the environment and life history characteristic of the species (Bessa-Gomes *et al.* 2003). However, MVPs for a 99% probability of persistence for 40 generations for 102 species averaged approximately 7000 and did not differ among major taxa, or with latitude or trophic level (Reed *et al.* 2003b). Length of data set in generations was shown to have a major effect on

minimum viable population size (longer monitoring detected more variation, leading to larger MVPs), but study duration in years did not have a significant effect. Even the widely perceived gulf between small and large mammal population dynamics (Caughley & Krebs 1983) no longer exists when time is considered on a per generation basis (Sinclair 1996).

An evaluation of the relative importance of 16 widely used indicators of extinction risk gave a clear and intuitively satisfying outcome when analysed on the scale of generations. Population size and trend in population size were clearly the best predictors across 45 vertebrate taxa, with most of the other 14 widely promoted variables either having non-significant explanatory powers or entering only in significant interaction terms with the best predictors (O'Grady *et al.* 2004). Population size predicts the impact of stochastic factors, while trend indicates the extent of human impacts. Thus, data collection on threatened species can be concentrated on population size and State of the Environment reporting can usefully concentrate on population size and trend. Revisions of endangered species categorization systems might also give higher weighting to these variables.

In conclusion, it is critical that the appropriate biological time scale be used in conservation biology and ecology if useful generalizations are to be made. Extinction risk scales biologically to generations and analyses on this scale have revealed a range of important insights. Other time scale dependent phenomena such as predator-prey interactions, competition and succession may also yield improved insights if considered on a generational scale.

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References

- Arino, A. & Pimm, S. L. 1995: On the nature of population extremes. — *Evol. Ecol.* 9: 429–443.
- Armbruster, P., Fernando, P. & Lande, R. 1999: Timeframes for population viability analysis of species with long

- generations: an example with Asian elephants. — *Anim. Conserv.* 2: 69–73.
- Beckerman, A. P., Benton, T. G., Lapsley, C. T. & Koesters, N. 2003: Talkin' 'bout my generation: Environmental variability and cohort effects. — *Amer. Nat.* 162: 754–767.
- Belovsky, G. E. 1987: Extinction models and mammalian persistence. — In: Soulé, M. E. (ed.), *Viable populations for conservation*: 35–57. Cambridge University Press, Cambridge, U.K.
- Belovsky, G. E., Botkin, D. B., Crowl, T. A., Cummins, K. W., Franklin, J. F., Hunter, M. L. Jr., Joern, A., Lindemayer, D. B., MacMahon, J. A., Margules, C. R. & Scott, J. M. 2004: Ten suggestions to strengthen the science of ecology. — *BioScience* 54: 345–351.
- Bessa-Gomes, C., Danek-Gontard, M., Cassey, P., Møller, A. P., Legendre, S. & Colbert, J. 2003: Mating behaviour influences extinction risk: insights from demographic modelling and comparative analysis of avian extinction risk. — *Ann. Zool. Fennici* 40: 231–245.
- Caughley, G. & Krebs, C. J. 1983: Are big mammals simply little mammals writ large? — *Oecologia* 59: 7–17.
- Ehrlich, P. R. 1994: Energy use and biodiversity loss. — *Phil. Trans. Roy. Soc. Lond. B* 344: 99–104.
- Fagan, W. F., Meir, E., Prendergast, J., Folarin, A. & Karieva, P. 2001: Characterizing population vulnerability for 758 species. — *Ecol. Lett.* 4: 132–138.
- Falconer, D. S., & Mackay, T. F. C. 1996: *Introduction to quantitative genetics*. — Longman, Harlow.
- Fowler, C. W. 1988: Population dynamics as related to rate of increase per generation. — *Evol. Ecol.* 2: 197–204.
- Frankham, R., Ballou, J. D. & Briscoe, D. A. 2002: *Introduction to conservation genetics*. — Cambridge University Press, Cambridge, U.K.
- Futuyma, D. J. 1998: *Evolutionary biology*. — Sinauer, Sunderland, MA.
- Gittleman, J. L. 1994: Female brain size and parental care in carnivores. — *Proc. Natl. Acad. Sci. USA*, 91: 5495–5497.
- Harcourt, A. H., Harvey, P. H., Larson, S. G. & Short, R. V. 1981: Testis weight, body weight and breeding systems in primates. — *Nature* 293: 55–57.
- Henshaw, M. T., Kunzmann, N., Vanderwoude, C., Sanetra, M. & Crozier, R. H. 2004: Population genetics and history of the introduced fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), in Australia. — *Aust. J. Entomol.* [In press].
- Hutton, J. M. & Dickson, B. 2000: *Endangered species, threatened convention: the past, present, and future of CITES, the convention on international trade in endangered species of wild fauna and flora*. — Earthscan, London.
- Inchausti, P. & Halley, J. 2001: Investigating long-term ecological variability using the global population dynamics database. — *Science* 293: 655–657.
- Inchausti, P. & Halley, J. 2003: On the relation between temporal variability and persistence time in animal populations. — *J. Anim. Ecol.* 72: 899–908.
- IUCN 2002: *IUCN Red List of Threatened Species*. — Available on the web at <http://www.redlist.org/>.
- Leigh, E. G. J. 1981: The average lifetime of a population in a varying environment. — *J. Theor. Biol.* 90: 213–239.
- Merilä, J. & Kotze, J. D. 2003: Extinction thresholds. — *Ann. Zool. Fennici* 40: 69–247.
- Millar, J. S. & Zammuto, R. M. 1983: Life histories of mammals: an analysis of life tables. — *Ecology* 64: 631–635.
- NERC 1999: *The global population dynamics database: NERC & Centre for Population Biology, Imperial College, London*. — Available on the web at <http://www.Sw.ic.ac.uk/cpb/gpdd.html>.
- Newmark, W. D. 1995: Extinction of mammal populations in Western North American national parks. — *Conserv. Biol.* 9: 512–526.
- O'Grady, J. J. 2002: *Evaluating the accuracy of species assessment systems using population viability analysis*. — Ph.D. thesis, Macquarie University, Sydney.
- O'Grady, J. J., Reed, D. H., Brook, B. W. & Frankham, R. 2004: What are the best correlates of predicted extinction risk? — *Biol. Conserv.* 118: 513–520.
- Peters, R. H. 1983: *The ecological implications of body size*. — Cambridge University Press, New York.
- Pimm, S. L. & Redfearn, A. 1988: The variability of population densities. — *Nature* 334: 613–614.
- Primack, R. B. 1998: *Essentials of conservation biology*. — Sinauer, Sunderland, MA.
- Reed, D. H., O'Grady, J. J., Brook, B. W., Ballou, J. D. & Frankham, R. 2003b: Estimates of minimum viable population size for vertebrates and factors affecting those estimates. — *Biol. Conserv.* 113: 23–34.
- Reed, D. H., O'Grady, J. J. & Frankham, R. 2003a: Frequency and severity of catastrophes in vertebrates. — *Anim. Conserv.* 6: 109–114.
- Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., Fishpool, L. D. C., da Fonseca, G. A. B., Gaston, K. J., Hoffman, M., Long, J. S., Marquet, P. A., Pilgrim, J. D., Pressey, R. L., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., Watts, M. E. J. & Yan, X. 2004: Effectiveness of the global protected area network in representing species diversity. — *Nature* 428: 640–643.
- Sinclair, A. R. E. 1996: Mammal populations: Fluctuation, regulation, life history and their implications for conservation. — In: Floyd, R. B., Sheppard, A. W. & De Barro, P. J. (eds.), *Frontiers of population ecology*: 127–154. CSIRO Publishing, Melbourne.
- Sokal, R. R. & Rohlf, F. J. 1995: *Biometry, 3rd edition: the principles and practice of statistics in biological research*. — W. H. Freeman & Co, New York.
- Thompson, D. W. 1942: *On growth and form*, 2nd edition. — Cambridge University Press, Cambridge, U.K.
- WCMC 1992: *Global biodiversity: status of the earth's living resources*. — Chapman & Hall, London.