Living Dangerously but Independently, or Safely and Contingently?

In the February issue of *TREE*, Stuart Pimm[1] writes: 'This leads to a question for which I genuinely would like an answer. Will a population of mean size *nm* persist longer if it varies in the normal way (say an SDL of 0.5 to 1.0) than one where there are *m* populations of mean size *n* individuals and each varies (independently) at greatest possible rate, but one still smaller than 0.5 to 1.0? In other words, is it better to live dangerously but independently, or less dangerously but contingently?'

Pimm's question is the essence of the SLOSS (single large or several small reserves) debate[2], which has caused much controversy and lately been reviled as a non-issue, a red herring and/or irrelevant to conservation. These viewpoints are troubling, because SLOSS epitomizes the issue of habitat fragmentation, which together with habitat loss is the dominant force in the present global extinction crisis.

Little empirical evidence exists to answer Pimm's question. Forney and Gilpin showed that habitat fragmentation increased the probability of extinction in laboratory populations of *Drosophila pseudoobscura*[3]. I showed the same for a hypothetical organism in a single-species simulation model[4]. Dispersal between fragments alleviated (but did not eliminate) the detrimental effect of fragmentation on extinction probabilities. My result was robust under demographic stochasticity, but could be reversed if environmental stochasticity was large and spatially uncorrelated. The spatial correlation and importance of environmental stochasticity will vary between species and populations, as well as spatially. If environmental stochasticity is criti-

cal and at least partially uncorrelated, then it may be better to live dangerously but independently. If demographic stochasticity is critical, it seems to be best to live less dangerously but contingently. The answer may be scale dependent.

I have investigated the effect of habitat fragmentation on extinction probabilities in laboratory predator–prey systems with *Tetrahymena thermophila* and *Didinium nasutum*. Systems of differing degrees of fragmentation were replicated in three experiments, under different conditions. In fragmented systems, *D. nasutum* became extinct sooner, in some cases much sooner, than in relatively unfragmented systems.

A few data sets exist where one can regress extinction rates against 'island' area. Assuming that extinction rates from an aggregate of species on islands are representative of extinction rates for populations of a single species, and that extinction rates are constant over time, one can calculate the probability of extinction as a function of time and the degree of fragmentation. If the extinction rate is a function of area, $\lambda = f(A)$, the probability that all *m* populations, each of area *A/m*, go extinct by time *t* is $P_\varepsilon(m,t) = \{1\exp[\lambda(A/m)t]\}^m$. In five of the six 'archipelagos' where I have calculated P_ε, fragmentation led to more rapid extinction; one yielded a more ambiguous result. This approach makes several assumptions that are clearly violated, and much biology is averaged out. However, in conjunction with other approaches, it seems to support the notion that fragmentation accelerates extinction.

Some analytical models of extinction under demographic stochasti-

city exist that do not predict any effect of fragmentation[5] (primarily due to the difficulty of incorporating density dependence in stochastic birth and death models). There is, however, a way of thinking about this problem that yields a robust answer. Compare two equivalent tracts of habitat. In one, erect an impermeable barrier, making two equal sized fragments adjacent to each other. In the other, demarcate identical fragments with, say, string. This trick reduces the issue to a simple isolation effect. In each unit of time, the probability of extinction in each fragment is similar, but with the permeable 'barrier' it is reduced by the probability of recolonization from the adjacent fragment. Numerical solutions of simple birth–death processes confirm the conclusions drawn from this theoretical experiment.

To the mechanisms discussed here should be added an assortment of edge effects and practical, epidemiological, autecological, economic, population dynamic and population genetic effects. Most of these, I believe, favor unfragmented systems.

Tormod V. Burkey

Dept of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA

References
1 Pimm, S.L. (1993) *Trends Ecol. Evol.* 8, 45–46
2 Nunney, L. and Campbell, C.A. (1993) *Trends Ecol. Evol.* 8, 234–239
3 Forney, K.A. and Gilpin, M.E. (1989) *Conserv. Biol.* 3, 45–51
4 Burkey, T.V. (1989) *Oikos* 55, 75–81
5 Pielou, E.C. (1977) *Mathematical Ecology*, Wiley

Erratum : $P_\varepsilon(m,t) = \left(1 - e^{-\lambda(A\backslash m)t}\right)^m$

Geometric Morphometrics: An Extension of the Revolution

Rohlf and Marcus in their *TREE* review on the current advances in morphometrics[1], pointed out that a real revolution is occurring with the foundation of 'geometric morphometrics'. This new science really constitutes a framework for the objective description of changes in form – size and shape – during ontogeny or evolution. It is hoped that, in the future, geometric morphometrics will be combined with

genetic and ecological knowledge of organisms – a new synthesis in biology.

Rohlf and Marcus maintained that the revolution in morphometrics became possible as (1) the geometry of the organisms is captured in two or three dimensions (2- or 3-D) by recording coordinates – landmarks – corresponding to homologous anatomical points, and (2) size and shape differences between

organisms are analysed through new techniques allowing one to capture the geometric relations between landmarks by 'fitting an appropriate function to them in 2- or 3-D. The estimates of the parameters of the fitted function can then be used as variables in standard univariate and multivariate statistical analyses'[1]. Their review briefly discusses relative warp analysis, superimposition (Procrustes)