REVIEW ARTICLE

The effects of habitat fragmentation on extinction risk: Mechanisms and synthesis

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Abstract

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Across the globe, much current research reflects concerns over the effect of habitat fragmentation on the viability of species and populations. This is an immediate and important concern for the Kingdom of Thailand, where decisions about land use are at a critical juncture. Thailand is in danger of losing species that play a special role in Thai culture and history such as the Asian elephant (*Elephas maximus*) and the tiger (*Panthera tigris*). We provide a selective review and synthesis of the effects of habitat fragmentation on extinction risk. Our emphasis is on objectives, causal mechanisms, and the validity of some of the arguments that have been made in the debate. Heuristic models are explored to elucidate mechanisms that may affect populations in fragmented landscapes and we point out gaps in our knowledge of this important and complicated question. Our synthesis of the current evidence suggests that fragmenting landscapes usually increases the risk of extinction, especially as the isolation of patches increases or the size of patches decreases. The Kingdom of Thailand, and other countries facing similar circumstances, should seek to connect isolated patches of habitat in order to better protect their remaining biodiversity.

Key words : endangered species, environmental stochasticity, extinction,
habitat fragmentation, genetic stochasticity, metapopulations

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Habitat loss and fragmentation are the most serious threats to biological diversity and the primary cause of the present extinction crisis (Groombridge, 1992; Heywood, 1995). This is especially true for the Kingdom of Thailand (Lynam *et al*., 2001; Pattanavibool and Dearden, 2002). Yet, the effects of habitat fragmentation are difficult to study, requiring observation of many different sites at large spatial scales and long time scales. The process of extinction is particularly difficult to study in the field due to the long time scales often involved before extinction occurs -- and the difficulty of determining when it has in fact occurred. And because studying extinction risk involves the estimation of probabilities, a great number of replicate populations are required. Thus, despite its importance, conservation biologists have developed few general principles regarding the effects of habitat fragmentation on extinction risk and it is hard to gain an overall understanding of the issue from the published literature.

The theory of island biogeography predicts that a loss of area will lead to extinctions and reduced species richness. However, it does *not* follow that because small islands (habitat patches or wildlife reserves) have higher extinction rates, a *set* of small islands with the same aggregate area will be more extinction prone than one large island. Because the effect of area on extinction rates and species richness are important and well known, we need to isolate the effect of habitat loss from the effect of the subdivision of the habitat into separate patches, if we are to understand how habitat fragmentation *per se* affects extinction rates and the probability of extinction for a focal species. In this paper, therefore, we will compare systems that are subject to different degrees of subdivision (patchiness), independent of any area effect. Related studies that confound the effects of habitat loss with the effect of habitat fragmentation are not accorded much attention in our discussion.

It seems to be widely held that habitat fragmentation will increase the risk of extinction in populations subject to demographic stochasticity. This may be partly due to the common practice of using the term habitat fragmentation to encompass both the loss of area and the increased subdivision of the remnants that come with increasing land use by humans. But even when we avoid this commingling of effects, by standardizing the total area across systems of different degrees of subdivision, it seems to be widely held that the increased fragmentation (in the narrow sense) leads to higher extinction rates. Yet, it appears that it is not generally understood why this might be so.

Many hold that this is a trivial question with limited practical relevance. We contend that understanding the effects of habitat fragmentation is critical to managing populations in fragmented landscapes, and making decisions about land use patterns. Protected areas are one of our most powerful conservation tools. Yet who can say, in a given case, whether it is better to enlarge an existing protected area or to establish a new one somewhere else in a similar habitat type? Figure 1 shows three hypothetical "extinction curves": the probability of extinction by a given time, *t*, for a single species as a function of the area of the "habitat island" in which it has become isolated. All three curves decline monotonically with area. Yet, only a species following a type III extinction curve has a higher probability of extinction in a fragmented system of independent habitat patches than in single large habitat remnant, keeping the total area constant. Why populations should follow a type III extinction curve, as opposed to a type I or a type II extinction curve is not a trivial question. A satisfactory answer to this question, as well as elucidation of the mechanisms affecting populations in fragmented habitats and their relative importance to natural populations, is required before the effects of habitat fragmentation on the viability of endangered species or how best to manage populations in fragmented landscapes can be understood.

In this paper, we discuss the biological mechanisms we believe impact the relative persistence of contiguous versus subdivided populations and selectively review research that we feel is useful in determining the effect of fragmentation on extinction risk. We also present new material in the form of simple heuristic models and verbal

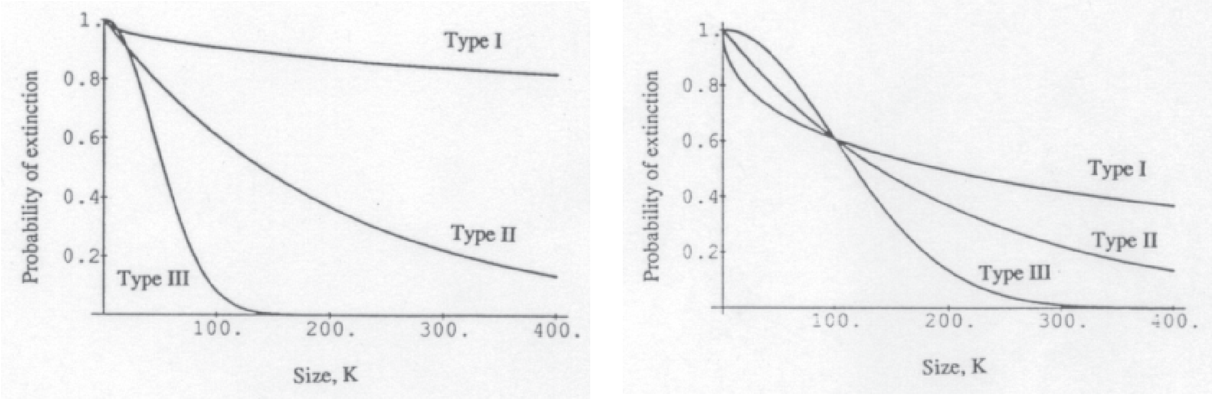

Figure 1. Three types of extinction curves. Assume P_e (A) = exp ($-cK^x$), then a Type I curve is obtained for $x < 1$, a type II curve for $x = 1$, and a Type III curve for $x > 1$. If extinction risk declines with area as in the Type I extinction curve, fragmentation is beneficial. For Type II extinction curves, there is no effect of fragmentation. For Type III extinction curves, fragmentation is detrimental.

arguments that might help us to understand the issues involved and to synthesize what we know concerning the process of extinction in fragmented landscapes.

Mechanisms

Too little effort has been made to elicit the causal mechanisms behind our observations concerning fragmentation effects. Only if we understand the evolutionary, ecological, and behavioral mechanisms that make a population vulnerable to fragmentation, or benefit from fragmentation, will the results be accorded the attention that their urgency warrants (Table 1 and Table 2).

The central problem facing fragmented systems with no migration is the "extinction ratchet". Compare a single large reserve with ten smaller ones that add up to the same total area. Over time one small fragment is more vulnerable to extinction than a large one. Without migration, this fragment will not be recolonized after local extinction. Over the next time interval we now compare the fate of the remaining nine fragments to that of the same single large patch. Again one small fragment may go extinct, and so on in a ratchet-like process until the fragmented system no longer supports the focal species. Whether this ratchet will lead to extinction in a set of small populations, prior to the extinction of a comparable single large population, still remains an empirical question subject to the specifics of density-dependent population growth (Henle *et al.*, 2004), the scale and correlation of environmental disturbances (Reed 2004a), and explicit population trajectories.

Spatial autocorrelation in temporal fluctuations in population size

den Boer (1969, 1981) was the first to point out the importance of asynchronously fluctuating population numbers, in different patches, to increasing the persistence of a metapopulation by spreading the risk of extinction between them. The degree of correlation among temporal fluctuations in population size can greatly influence the relative performance of a contiguous population compared to a metapopulation of equivalent total carrying capacity (Burgman *et al.*, 1993; McCarthy and Lindenmayer 2000; Reed, 2004a).

If the main determinant of extinction is stochastic fluctuations in the environment, it could be better to have spatially separated subpopulations so that individuals remain to colonize patches that have been extirpated. The relative persistence of a

Table 1a. Stochastic mechanisms making species vulnerable to fragmentation.

1) Allee effects
2) Inbreeding depression, loss of rare beneficial mutations in local populations, weakened natural selection
3) Demographic stochasticity: uneven sex ratio or age-structure
4) Fragmentation causing a breakdown of regional density dependence
5) Low carrying capacity in patches
6) "The extinction ratchet". In the absence of recolonization, the extinction within a fragment is an absorption point. Smaller populations go extinct more easily, and are sequentially lost until the species has disappeared from all fragments.
7) Increased susceptibility to invasion from alien species.

Table 1b. Deterministic mechanisms making species vulnerable to fragmentation

1) Migration/dispersal
    a) Old migration routes disrupted
    b) Restricting movement among different required patch types
    c) Fluctuating environments may make some habitat patches temporarily unsuitable (fragmentation would make it difficult to track suitable patches)
2) Inter-species interactions
    a) Loss of predator makes prey explode, then crash (destabilizes system)
    b) Loss of top predator releases other, smaller predators from predation, increasing predation on seeds, eggs, young etc.
    c) Loss of top predator increases inter-species competition
    d) Loss of refugia from predators
    e) A discontinuous prey population is less likely to attain reproductive synchrony, hence suffering higher predation
    f) Patch too small to maintain a population of mutualists (pollinators/dispersal agents)
3) Intraspecific interactions
    a) Cooperative behavior breaks down (too few wolves to form a pack)
    b) Primary social unit needs a large foraging area to persist
    c) Threshold number: minimum breeding colony size (passenger pigeon),
    d) Allee effect: social facilitation, information centers, group defense, mate search, social interaction necessary for reproduction or survival
4) Edge effects
    a) Increased predation/disturbance by humans
    b) Micro habitat changes in edge zones
    c) Increased colonization/interference from species in neighboring habitat
    d) Increased dispersal to uninhabitable areas (or sub optimal habitats)
    e) Edge avoidance
5) Patch smaller than home-range or territory
6) Packing (fewer home-ranges/territories can be packed into a fragmented reserve)
7) Critical resources not protected, or unavailable to the entire metapopulation, within the reserve (e.g. watershed, critical winter grazing grounds, etc.)

metapopulation versus a continuous population of equivalent size depends, however, on the relative importance of demographic, environmental, and genetic stochasticity, and on the spatial correlation of population trajectories in different patches over time.

Much progress has been made, during the past decade, on gathering data concerning the scal-

Table 2. Mechanisms by which species may gain from fragmentation

Stochastic phenomena

1) Bet hedging: disease, spatially uncorrelated environmental variation
2) Could increase genetic diversity on a regional scale (drift, local adaptation)
3) Wright's shifting balance theorem: may allow more rapid evolutionary response to environmental changes if some migration between fragments is possible
4) Greater chance of surviving transients in unstable community interactions

Deterministic phenomena

1) Persistence of predator-prey system
   a) enhanced by prey hiding out in a different patch
   b) overshoot reduced by predator dispersal between patches
2) Refugia from competitors
3) Patches can be selected in high-resource areas or centers of local endemism

ing of spatial synchrony in population dynamics. Spatial synchrony decreases with increasing distance between populations, and eventually asymptotes near zero. However, the rate at which spatial synchrony in population dynamics declines is highly variable. Because the observation times are relatively short, stronger environmental effects ("catastrophes"), which presumably affect populations over a larger area, are rarely witnessed (Reed *et al.*, 2003b) and spatial correlations probably underestimated.

Fluctuations in population size for populations of Stephen's kangaroo rat (Price and Endo, 1989), pool frogs (Gulve, 1994), microtine rodents and shrews (Heikkilä *et al.*, 1994), tetranoids (Ranta *et al.*, 1995), black rat snakes (Weatherhead *et al.*, 2002), and other assorted vertebrates (Lindström *et al.*, 1996) separated by approximately 30 km were all found to be highly and positively correlated. Hanski and Woiwod (1993) found that spatial synchrony between conspecific populations of British moths and aphids remains positive at all distances up to 800 km.

In contrast, significant synchrony occurs only at a limited spatial distance for the rodent *Clethrionomys glareolus* (Steen *et al.*, 1996), for several species of butterfly (Sutcliffe *et al.*, 1996), and for voles and mice (Bj∅rnstad *et al.*, 1999). The largest data sets are for the birds of Britain (Paradis *et al.*, 2000) and North America (Koenig, 2001). Both studies suggest that population synchrony among birds is very weak even at distances of less than 100 km. However, further decline in population synchrony with geographic distance is slight.

Taking a focal species approach to conservation (Lambeck, 1997; Brooker, 2002; Freudenberger and Brooker, 2004), the maximum spacing of reserves will be limited by the range of the species, which in many cases is not great to begin with. Thus, the trade-off between the benefits of partially independent stochastic events and greater connectivity requires further study at relevant spatio-temporal scales. It should also be remembered that within a single large reserve, population distributions may also be textured due to internal patchiness. A certain spreading of risk may therefore occur even within continuous populations. A disturbance that might wipe out an entire subpopulation in a small isolate might only remove a portion of the population in a large, continuous tract of habitat -- which would subsequently be more rapidly repopulated.

Dispersal

Migration among subpopulations can increase metapopulation persistence through demographic and genetic rescue (Brown and Kodrick-Brown, 1977; Richards, 2000). If the populations maintain some independence in environmentally-determined fluctuations in population size, the metapopulation can persist longer than a contiguous population of equivalent size. The introduction of new genetic material into a population through immigration has been shown empirically to boost fitness and retard extinction in laboratory experiments (Spielman and Frankham, 1992; Backus *et al*., 1995; Bryant *et al*., 1999; Richards, 2000; Newman and Tallmon, 2001) and natural populations (Westemeier *et al*., 1998; Madsen *et al*., 1999; Fenster and Galloway, 2000; Comiskey *et al*., 2002; Cooper and Walters, 2002). Immigration has rescued declining populations in the wild even when habitat restoration failed (Westemeier *et al*., 1998) and populations of the blue-breasted fairy wren (*Malurus pulcherrimus*) experienced net population declines in poorly connected patches, as opposed to net population growth in well-connected patches (Brooker and Brooker, 2002). Debinsky and Holt (2000) found that species richness was consistently and positively affected by habitat connectivity.

In addition to its positive effects, immigration can also impact the persistence of populations negatively by introducing diseases or parasites to previously uninfected subpopulations (Hess, 1994; Grenfell and Harwood, 1997; Daszak and Cunningham, 1999; Daszak *et al*., 2000) and by increasing the synchrony of temporal fluctuations among the subpopulations (Allen *et al*., 1993; Ranta *et al*., 1995; Steen *et al*., 1996; Schöps, 1999; Kendall *et al*., 2000; Trenham *et al*., 2001).

Edge effects

Fragments are well-known to be inferior to intact habitat because they are more vulnerable to fire, desiccation, predation from introduced species, as well as other types of ecological stress and the interactions among the different stressors (*e.g*., Lovejoy *et al*., 1986; Noss, 1988; Burkey, 1993a; Robinson *et al*., 1995; Jules and Rathcke, 1999; Eisto *et al*., 2000; Golden and Crist, 2000; Komonen *et al*., 2000; Laurance *et al*., 2002; Pattanavibool and Dearden, 2002; Luck, 2003). Most models assume a linear relationship between patch size and carrying capacity, yet, if edge effects are important, this will not be the case. Kindvall and Ahlen (1992) found an exponentially increasing relationship between the local population size of bush crickets (*Metrioptera bicolor*) and the size of habitat patches. Similar results have been obtained with orb spiders (Toft and Schoener, 1983), checkerspot butterflies (Harrison *et al*., 1988), fruit bats (Wiles *et al*., 1989), pikas (Smith, 1974), and migratory forest birds in Hokkaido (Kurosawa and Askins, 2003). The relationship may or may not be due to edge effects, but the result seems general (Bender *et al*., 1998) and indicates that models which assume a linear relationship may underestimate the risk of extinction in fragmented landscapesc.

In our globalized world with ever-increasing trade and movement, invasive alien species are considered the second biggest cause of biodiversity loss, after habitat loss and fragmentation. But as with many such factors, there are interactions. Edge effects make fragmented systems more disturbed, and disturbed systems are more vulnerable to invasion and increase the arrival of potential invaders. Previous species loss in fragmented systems may also make fragments more prone to invasion. Yet isolated subpopulations may prove a hedge against invasive species, in a manner similar to the way they may protect against epidemics and, therefore, make eradication or control easier.

Although much work has been done on edge effects, much remains. For instance, how do decomposers react to the changes in temperature and humidity experienced in newly delineated habitat edges (Lovejoy *et al*., 1986)? Changes in the community of decomposers might conceivably affect the recycling of nutrients in such a way that it has repercussions in the abundance and diversity of plant species. Changes in the seed predator fauna near introduced edges may alter the dynamics of individual tree species, the outcome of competitive interactions between tree species, and ultimately the diversity and structure of the forest community.

Genetics

Genetic considerations generally favor contiguous over fragmented habitats. Inbreeding depression is greater in smaller (subdivided) populations than larger, and the effects of inbreeding depression can be powerful and are ubiquitous in wild populations (Madsen *et al.*, 1998; Saccheri *et al.*, 1998; Westemeier *et al.*, 1998; Crnokrak and Roff, 1999; Richards, 2000; Keller and Waller, 2002; Reed and Frankham, 2003). The population sizes at which inbreeding depression, and other forms of genetic stochasticity, can have major effects on the persistence of populations are usually underestimated (Brook *et al.*, 2002; Reed, 2005).

Selection is more efficient in large populations than in small (Crow and Kimura, 1970). The occurrence of rare beneficial mutations can have substantial effects on the ability of a population to evolve in the face of a changing environment (Elena *et al.*, 1996; Burch and Chao, 1999; Giraud *et al.*, 2001; Imhoff and Schlötterer, 2001). These beneficial mutations are less likely to be lost through drift in a single large population than in a number of smaller isolated populations (Kimura, 1983). Furthermore, the spread of the beneficial allele among subpopulations is not possible in totally isolated fragments, disrupting evolutionary and adaptive processes (Templeton *et al.*, 2001).

A large number of issues concerning fragmentation and genetics need to be addressed. Interactions between genetics and population dynamics are probably crucial, but are rarely considered. Most models have concentrated on maintaining heterozygosity while ignoring the loss of alleles in the population. Allelic diversity and heterozygosity are not interchangeable entities (Allendorf, 1986). Heritable genetic variation for ecologically important quantitative traits is what is generally most important for population persistence, yet most conservation efforts concentrate on molecular genetic variation (Reed and Frankham, 2003).

Community Level Effects

Much of what we know about the effects of fragmentation on species viability has been elucidated through the use of simple models and simplified model communities. We know little about how multiple species interactions in a complex community will influence the dynamics of subdivided populations. Terborgh (1988) postulated far-reaching community effects of losing the top predator and Burkey (1993) speculated that the uneven distribution of seed predators and egg predators with respect to habitat edges may have severe manifestations on the community level. Komonen *et al.* (2000) demonstrated the truncation of a food chain based on old-growth forest bracket fungus, due to fragmentation.

Consider a mutualistic interaction, say a pollinator-plant system. Make the pollinator, *B*, self-limiting with a factor $\varphi(T)$ that enhances the carrying capacity of the pollinator relative to the number of plants, *T*. Make $\varphi(T)$ a simple multiple of T, $\varphi(T) = cT$ where *c* is a constant. Make the plant, *T*, self-limiting and declining in the absence of pollinators, and increasing in proportion to the visitation by pollinators, specifying some functional response, such as a type 2 functional response (Holling, 1959), on the part of the pollinator. For instance,

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K + cT}\right)$$

$$\frac{dT}{dt} = -aT - eT^2 + \frac{\alpha}{(1 + \alpha\beta B)}BT$$

where *K* is the carrying capacity of the pollinator in the habitat, *r* is the intrinsic growth rate of the pollinator, *a* specifies the rate of decline of the plant in the absence of pollinators, *e* specifies the extent to which the plant is self-limiting, α is the rate at which pollinators encounter plants and β is their handling time.

We find the isoclines for this system

$$\frac{dB}{dt} = 0 \Rightarrow B = cT + K$$

$$\frac{dT}{dt} = 0 \Rightarrow B = \frac{a + eT}{\alpha - \alpha\beta a - \alpha\beta eT}$$

If this system is fragmented, each resulting fragment has a lower *K* and a higher *e*, all other factors should remain the same. Reduced *K* shifts the pollinator isocline downwards. Increased *e* shifts the plant isocline to the right. As fragmentation proceeds an unstable equilibrium point arises,

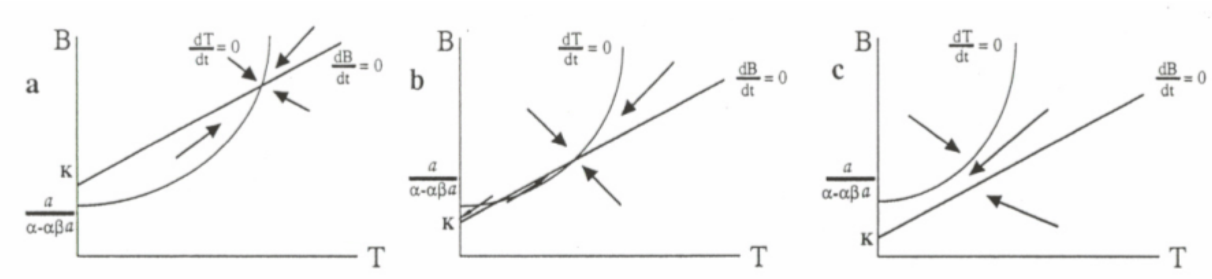

Figure 2. The extinction of a fragmented plant population in a plant/pollinator mutualism. As fragmentation proceeds the system changes from globally stable in a) to having an unstable equilibrium point introduced in b), and the plant population goes to extinction in c).

$K < a/(\alpha - \beta\alpha a)$, creating the possibility of the plant going extinct. As fragmentation proceeds further, the isoclines no longer intersect, leaving a single equilibrium point at $T = 0, B = K$ (Figure 2). Thus, a set of smaller reserves may not support this plant/pollinator interaction at all -- no matter how many of them there are. Similar effects may occur for other kinds of species interactions. However, it may be argued that the encounter rate, α, should be scaled with patch size so that the number of encounters per pollinator remains the same regardless of patch size if the densities of pollinator and plant remain the same. In that case, the threshold effects tend to disappear. The actual scaling of encounter rates in natural populations may be somewhere in-between these extremes.

The existence of thresholds in population dynamics of wild species will have profound effects. At what level of fragmentation such a breakdown will occur is an empirical problem which has been addressed only once to our knowledge. Lennartsson (2002) found pronounced extinction thresholds at certain levels of fragmentation for the grassland herb *Gentianella campestris* due to both pollinator deficit and inbreeding depression. Visitation rates Bowers (1985) has shown that by bumblebees and seed set of plants have been found to be reduced on small and isolated mountain meadows relative to larger ones. Reduced visitation by birds, reduced pollination and reduced fruit and seed set has been documented on a small island compared to a large island (Linhart and Feinsinger, 1980; Feisinger *et al*., 1982; Jennersten, 1988), and on islands compared to mainland and far islands compared to near islands (Spears, 1987). Jennersten (1988) found that the number of flowering plant species and flower-visiting insect species, and flower visitations and seed sets in the caryophyllaceous herb *Dianthus deltoides*, were lower in a set of two habitat fragments (80×40 m and 50×30 m) than in a 1 ha meadow. Telleria *et al*. (1991) found higher densities of wood mice (*Apodemus sylvaticus*) and higher rates of predation on acorns (*Quercus rotundifolia*) in smaller woodlots than in larger ones. More studies of this sort, coupled to mechanistic models, are needed and efforts should be made to equate area across treatments.

In order to get at community level mechanisms we should do large scale studies in natural systems. On a smaller scale, it should be possible to compare experimental populations in simplified communities with that of complete endemic communities. Such experiments should be run in parallel to test if the effects of fragmentation on focal species are different in the two types of communities. Laboratory microcosms, with short-lived organisms, can be used to study the effects of fragmentation on communities of different degree of complexity and species richness.

Behavioral effects

Behavioral mechanisms that make populations vulnerable to habitat fragmentation have not been well studied. Species with long distance migrations, cooperative behavior, or species, such as elephants, that modify their environment are likely candidates. Fragmented populations are also likely to have evolved behaviors that are beneficial in contiguous habitats but detrimental in fragmented habitats. Examples would include long-distance dispersal through a now hostile matrix and choosy females that risk not finding a suitable mate among the limited number of potential mates in that patch. The prevalence of such behaviors should be studied and their effects incorporated into models. Furthermore, the evolutionary outcomes of such altered selection regimes in fragmented landscapes should also be studied.

Little is known about behavioral mechanisms that might cause animals to avoid habitat edges, or seek them out. Narrow clearings like roads and clearcuts have been shown to disrupt dispersal in some large and small animals (*e.g.*, Wegner and Merriam, 1979; Mader, 1984; Powell and Powell, 1987; Klein, 1989; Malcolm, 1994; Offerman *et al.*, 1995; Kalko, 1998; Smith *et al.*, 1998; Gilbert and Setz, 2001; Brooker and Brooker, 2002; Cooper and Walters, 2002; Laurance *et al.*, 2002; Rodriguez and Delibes, 2002). However, other species actively use roads as movement corridors, increasing mortality through collisions with motor vehicles and by making populations vulnerable to poaching (*e.g.*, Young and Beecham, 1986; Ferreras *et al.*, 1992; Beier, 1995; Mladenoff *et al.*, 1995; Mace *et al.*, 1996; Gibbs and Shriver, 2002; Kerley *et al.*, 2002; Tigas *et al.*, 2002).

Relative importance of demographic versus environmental stochasticity

Possibly the major question concerning fragmentation is whether environmental variation in nature is great enough and spatially uncorrelated enough to favor subdivided habitats in the face of demographic stochasticity, genetic stochasticity, edge effects, and a host of potential deterministic effects (Table 2). Models (McCarthy and Lindenmayer, 2000; Reed, 2004a) help to estimate the variance and spatial correlation needed to tip the scales, but ultimately quantitative fieldwork is required to tell us what goes on in nature.

Density Dependence

The strength and form of density dependence in population growth rates is expected by most to strongly influence population persistence (May and Oster, 1976; Ferson *et al.*, 1989; Hanski, 1990; Burgman *et al.*, 1993; Dennis and Taper, 1994; Grant and Benton, 2000; Lande *et al.*, 2002). The use of density dependence in population viability analysis and its importance to fragmented populations has been reviewed by Henle *et al.* (2004) and Heering and Reed (2005). We strongly agree with the conclusions of Melbourne *et al.* (2004) that models of extinction in fragmented populations, in order to accurately reflect extinction risk in fragmented habitats, need to be individual-based and that the incorporation of information concerning density dependence and the spatial arrangement of patches is also important.

Several mechanisms exist by which the birth and death of one individual in a population depends on what others are doing. Most prominent of such mechanisms is density dependence. Other factors have long been recognized, but not always invoked despite their importance. Factors such as sex ratio, age structure, and individual phenotypes might, by pure chance, become unevenly distributed in different reserve fragments. For instance, a fragmented reserve runs the risk of having all females in one patch and all males in the other. Density dependence affects fragmented reserves in the same manner -- making the population growth rate susceptible to uneven population densities between patches.

It can be shown that variance in the abundances of individuals between fragments will always reduce the growth rate of a fragmented population, relative to an unfragmented population, if the growth rate as a function of population size decreases linearly or is concave down; and that the same is true with most cases of concave up growth functions. The types of growth functions we usually consider, and all the growth functions we could find in a survey of the literature, yield concave down phase plots. Hence, a metapopulation will have lower overall population growth than the corresponding continuous population. This is because those subpopulations with relatively high population sizes will be near carrying capacity and not growing very rapidly, and those that are at low population sizes will be growing slowly because their "capital" is small. The lower the overall growth rate, the greater the risk of global extinction, except in the range of growth rates so high that the population dynamics are inherently unstable (May, 1976). Whether overall growth rates of a metapopulation are lower than that of an unfragmented population of the same overall size should be a more readily testable hypothesis than whether the risk of extinction is higher.

A corollary of the density dependence argument is that as long as each subpopulation is far from its carrying capacity, the subdivision has no effect on population viability (as far as demographic stochasticity is concerned). Each subpopulation will be in a phase where it is expected to grow exponentially. Hence, the metapopulation is expected to grow exponentially even if some subpopulations die out, and the per capita expected growth rate is the same irrespective of fragmentation. Experimenters need to keep this in mind when designing their fragmentation experiments; fieldworkers, when interpreting data. When carrying out a field or lab experiment on the demographic effects of population subdivision, make sure the populations are not too far from carrying capacity (where population growth is essentially density independent).

Patchiness can occur at several scales and every single population can be regarded as a metapopulation to some degree with some level of subdivision affecting its viability. This added complexity does not fundamentally alter the nature of the problem. Anthropogenic habitat fragmentation adds an *extra* level of boundedness on populations, regardless of their internal "texture".

In the simplest of systems, an asexual population, with no age structure, edge effects, behavior, deterministic causes of extinction, genetic effects, environmental variance, Allee effects, etc., *only* density dependence with some form of stochasticity in demographic rates -- the population is still negatively affected by habitat fragmentation (Burkey, 1989; Burkey, 1999). In addition, uneven population densities between patches will make it more difficult for the average individual to find a mate, find and defend a territory, avoid inbreeding, and so on.

Consider the simplest logistic model:

$$N_{t+1} = aN_t - bN_t^2 \xrightarrow{N_t \to 0} N_{t+1} = aN_t$$

Denote parameters for continuous and subdivided fragments with a subscript L or S, respectively (*e.g.* a_L and a_S). If areas with small populations all have the same capacity for increase, and as long as a population is far from carrying capacity, the population will be unaffected by moderate fragmentation of its habitat. Ignoring edge effects, Allee effects, etc., we should have $K_L = 2K_S$. Hence, we have $b_S = 2b_L$, and it is clear that we need variation in the distribution of individuals in a set of small reserves to get a difference in expected population size. Such variation is easily brought about by demographic stochasticity or partially spatially uncorrelated environmental variation. Note that spatially uncorrelated environmental variation favors fragmented reserves because of the "don't put all your eggs in the same basket" effect, but also disfavors fragmentation because of the effect of variance in population density between spatially separated patches. Models with weak forms of density dependence, or density dependence that manifests itself at much smaller scales than the habitat patches, will show slight effects of fragmentation. Models with strong density dependence will show more severe effects of habitat fragmentation on extinction risk.

Issues of Scale

Species richness and nestedness

It is possible to aggregate more species into a reserve system by selecting several small reserves with low species overlap (*e.g.*, Simberloff and Abele, 1976; Higgs and Usher, 1980). However, depending on the slope of the species-area curve and the degree of species overlap between reserves,

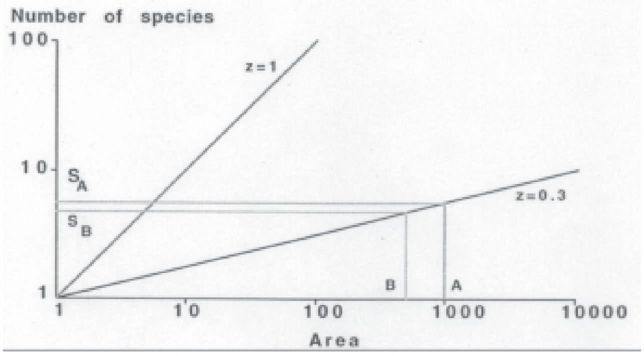

Figure 3. The species-area relationship $S = cA^z$ (*S* = number of species; *A* = area). The small distance between S_A and S_B indicate that two small areas, *B*, may hold more species than area *A* (depending on the slope z). z = 0.3 is thought to be a usual situation in nature. But depending on the amount of species overlap between the two small areas they may also hold fewer species.

a single large reserve may contain a greater or smaller number of species than several smaller reserves (Murphy, 1989) (Figure 3). The argument that overall species richness may be higher in a set of small reserves hinges primarily on a patch heterogeneity that enables different species to exist in different fragments. The degree to which different patches may harbor different species clearly depends on the spatial scale, and on the biogeographic diversity patterning of the biome. The slope of the species-area curve tends to change depending on spatial scale (Martin, 1981; McLellan *et al.*, 1986) and the degree of species overlap and nestedness between patches of similar size is often high (Patterson, 1984, 1987, 1990; Diamond, 1984; Nilsson, 1986; Patterson and Atmar, 1986; Bolger *et al.*, 1991; Cutler, 1991; Boecklen, 1997; Wright *et al.*, 1998; Patterson and Atmar, 2000; Bascompte *et al.*, 2003; Dupont *et al.*, 2003; Watson, 2003). The higher the similarity and hierarchical ordering among a suite of patches, the lower the value of several smaller fragments relative to a single large patch of equivalent size, because these small sites will contain a similar and depauperate sample of the species pool. Larger fragments in the Amazon forest generally contain more species per unit area than smaller fragments (Laurance *et al.*, 2002). The question remains, however, how long any advantage in species number -- provided there is one -- will be retained in a set of smaller patches, given the higher extinction rate in these patches.

Data on the relationship between species richness and area for islands can be used by taking the islands from which the species-area curves were constructed, their species lists and their area measurements, and constructing all possible sets of the islands that together add up approximately to the area of the larger single islands. For all such sets combine the species lists to tally the overall number of species in the set. Then compare the number of combinations in which the "archipelago" of smaller "islands" holds more and less species than the single large "island". When this is done for all the "islands" on which data are currently available, we can compare the results: 1) across landbridge islands and oceanic islands, 2) between terrestrial and oceanic islands (*i.e.*, true islands versus reserves or mountain tops), 3) among taxa, and 4) between complex communities and simple communities. For islands where the pre-fragmentation species compositions are known one should be able to compare extinction rates from single islands with those of archipelagoes. The data most useful are from those communities that are structured by extinction, rather than immigration.

Extinction risk at different scales

The effect of fragmentation, on the number of species maintained, is scale dependent. Clearly, there are spatial scales at which the effects of habitat fragmentation are trivial (*e.g.*, a species cannot persist in isolated patches that are all smaller than the territory size of an individual). Beyond such scales, however, the answer will depend on the relative importance of demographic, environmental, and genetic stochasticity, and the interactions among them; this again depends on, among other things, the exact shape of density dependence in demographic variables, the level of inter-patch dispersal, social interactions, and the spatial synchrony of population fluctuations across patches.

Conceivably, fragmentation could be beneficial at one scale but detrimental at another scale. The critical scale could be species and habitat / biome dependent. Some threshold values are likely. It is important to understand under what circumstances a metapopulation will survive in a set of small patches and when each patch will have to contain a functioning system within itself. For instance, threshold values such as those in some models (Kierstead and Slobodkin, 1953) suggest that there is a scale where even a very large number of small populations will be unable to maintain a particular system. Reserves must be large enough to protect critical watersheds, migration routes, and the entire range of habitat requirements for a focal species.

The importance of threshold values and scale dependence can be illustrated in simple predator prey models. Take for instance the Rosenzweig-MacArthur model of a self-limiting prey species and a predator with a type II functional response (Holling, 1959):

$$\frac{dN}{dt} = rN - \frac{r}{K}N^2 - \frac{aNP}{1+abN}$$

$$\frac{dP}{dt} = -eP + \frac{caNP}{1+abN}$$

where *N* is the number of prey, *P* the number of predators, *r* the instantaneous growth rate of the prey, *K* the carrying capacity of the prey, *a* the encounter rate of predators and prey, *b* the time a predator uses in handling encountered prey, *e* the death rate of predators in the absence of prey, and *c* the efficiency with which the predator converts captured prey into new offspring. The area of a habitat fragment is specified in terms of the number of individuals of a species it can hold. Hence area and density dependence are inherently interwoven. Since the predator is limited by the density of prey, the predator isocline $\left(N = \frac{e}{ca - eab}\right)$ is independent of K.

The magnitude of the equilibrium predator population in two small reserves relative to a single large one is now dependent upon the spatial scale, *K*. For small *K*, a single large reserve has the higher predator equilibrium; for large *K*, two small reserves have the higher predator equilibrium. In this model, the stability of the equilibrium point can change fundamentally with *K*. For reserves so small that *K* is less than $\frac{e}{ca - eab}$, the only predator equilibrium is at zero and predators go extinct. Hence, no number of such small reserves will be adequate to maintain a population of predators (Figure 2).

Of course, this is a simplistic model, and the critical threshold value disappears in some models. For instance if the encounter rate is made a function of the ratio $\frac{N}{K}$, there are no thresholds and no changes in equilibrium population sizes. This kind of phenomenon may occur for some species. For instance, if population densities are lower in small patches than in large patches, as is likely for interior species (see review by Bender *et al*., 1998), similar thresholds should be expected. If we assume that *K* scales linearly with area and scale encounter rates so that each predator (or pollinator) encounters the same number of prey per unit time regardless of patch size then densities will remain the same (except for stochastic effects). In that case, we should not expect any abrupt thresholds in persistence in response to loss of habitat area or fragmentation. We do not really know, however, how encounter rates scale with area. Possibly the most interesting conclusion to be drawn from this kind of exercise is the existence of critical threshold values in simple deterministic models which may cause extinction of the predator even in relatively large patches.

Encounter rates must be scaled to reflect changes in the number of prey and predator individuals in patches of different sizes. Most predator-prey models are deterministic and thus do not allow extinction from demographic stochasticity. In these models the interaction is either deterministically unstable or the populations never go extinct. For instance, the persistence in a metapopulation of otherwise unstable predator-prey or competitor interactions (Huffaker, 1958; Atkinson and Shorrocks, 1981) is well known, but in conservation efforts we are most likely concerned with a situation where the species already coexisted in a continuous landscape prior to fragmentation. Stochastic predator-prey models must solve the problem of how encounter rates scale with the spatial scale of a habitat remnant, if they are to say something about the effects of habitat fragmentation. Metapopulation models tend to describe the state of a subpopulation only as "present" or "absent". To understand the effect of habitat fragmentation on extinction risk the density dependence and population trajectories of individual subpopulations must be modeled explicitly and realistically (Fahrig, 2002; Baguette and Schtickzelle, 2003). It is the highly nonlinear relationship between available area and persistence time that determines the effect of fragmentation on extinction risk.

Detection of differential extinction rates in different landscape mosaics also depends on the temporal scale of observation (Burkey, 1989). Before we apply the design principles obtained from models and small scale experiments we must determine whether or not they can be extrapolated to the large spatial and temporal scales of real landscapes and also determine for what temporal and spatial scales we are going to plan conservation efforts (McCarthy and Lindenmayer, 2000; Reed, 2004a).

Experimental and Theoretical Approaches to Fragmentation

Experiments

The first experiment on the effects of habitat fragmentation on population dynamics (Forney and Gilpin, 1989) used a single species community where population numbers were very low and the effects were likely entirely due to demographic stochasticity. Continuous populations of *Drosophila melanogaster* persisted longer than subdivided populations with the same overall area available to them. Subdivided populations with dispersal corridors between them were intermediate in their persistence.

Burkey (1997) studied the process of extinction in response to habitat fragmentation in simple three trophic level laboratory communities of bacteria and protozoa. Fragmented systems went extinct sooner, and in some cases much sooner, than corresponding continuous systems of the same overall size. Unfragmented populations persisted longer than fragmented metapopulations with and without dispersal corridors between subpopulations. In fact, metapopulations that were linked by dispersal corridors went extinct significantly sooner than those where the subpopulations were completely isolated.

Gonzalez and colleagues (Gonzalez *et al.*, 1998; Gonzalez and Chaneton, 2002) found that experimental fragmentation of landscapes, without habitat loss, of a naturally occurring microecosystem led to widespread declines in abundance and the extinction of many species. When patches were connected by immigration, the declines were arrested.

The Biological Dynamics of Forest Fragments Project is the world's largest and longest-running study of habitat fragmentation. A review of the extensive data collected over the course of this 22-year investigation, into fragmentation of the central Amazonian Forest, was recently published (Laurance *et al.*, 2002). The results paint a mostly grim picture of continued habitat fragmentation, especially in tropical forests. Larger forest fragments contain more species per unit area than do smaller forest fragments and small fragments (1-100 ha) lose forest-interior species to extinction rapidly. Edge effects on forest fragments are generally strong and their most prevalent influence is to increase tree mortality, altering forest structure, composition, and diversity. Further, the dispersal of many species among forest fragments is blocked by even small (30-40 m) swathes of a hostile matrix, precluding natural recolonization of patches where a species has gone extinct, in these cases.

Models

Figure 1a and b show three types of extinction curves that yield different results under fragmentation. In general, if P(K) is log convex, fragmentation increases the risk of extinction. This result can be generalized to *n* patches of any size distribution using Jensen's inequality. If the probability of extinction, *P*, as a function of patch size (*K*) is described by a negative exponential function $P(K) = \exp(-cK)$, then fragmentation does not affect *P*, since $\exp(-cK) = [\exp(-c(K/n))]^n$ (where *n* is the number of fragments into which the area is subdivided). If P(K) declines more rapidly than a negative exponential, then fragmentation is detrimental. If P(K) declines less rapidly, then fragmentation is beneficial. Specifically, if isolated fragments are independent and *x* is a positive constant such that $P(K) = \exp(-cK^x)$, the probability of global extinction is $P_\varepsilon(n,K) = \exp(-c\,K^x\,n^{1-x})$, where *n* is the number of fragments. For $x = 1$ fragmentation is neutral; for $x > 1$ fragmentation accelerates extinction; and for $x < 1$ fragmentation decelerates extinction.

Wright and Hubbell (1983) modified the Markov process studied by MacArthur and Wilson (1967) by including recolonization from outside the system, and by introducing a version of diffuse competition between species. They concluded that for closed systems extinction takes longer in a single large than in two small reserves. For open systems, the difference was usually negligible.

Goodman (1987a,b) introduced environmental variation into a birth and death process model by letting the fates of individuals be correlated. He concluded that mean extinction times go up exponentially with K under demographic stochasticity, but less than linearly under environmental stochasticity. Hence, if environmental variance is high enough and spatially uncorrelated enough, and there is at least some recolonization of extinct patches, subdivision is beneficial. The pivotal issue is whether this scenario is common in nature. More complicated dynamics and more biological realism than has currently been incorporated into theoretical models may yet impose limits on the applicability of this view. Furthermore, the "correct answer" is likely scale dependent, both spatially and temporally (Burgman *et al*., 1993; McCarthy and Lindenmayer, 1999; Reed, 2004a).

Burkey (1989) developed an individual-based simulation model for a single population, that incorporates migration between reserve fragments, spatial and temporal variance in carrying capacity, and "catastrophes" that can be spatially correlated. Simulation runs of relatively small reserve systems show that the probability of extinction in a population subject to demographic stochasticity goes up exponentially with habitat fragmentation. It is possible to reverse this effect if catastrophes are spatially uncorrelated, less likely to hit a smaller area, and kill the same *proportion* of individuals in a patch regardless of its size. That is, however, a rather extreme model in the way that it biases in favor of a fragmented system. In this model, migration between fragments can partially alleviate the effect of fragmentation (Burkey, 1989), but not reverse it.

Burkey (1995) regressed extinction rates against island size for five data sets, and calculated the probability of archipelago-wide extinction as a function of the number of islands. Figure 4 shows the result from one such calculation, using the best fitting logarithmic, exponential, or linear function (data from Diamond, 1984). The estimated probability of extinction increases monotonically with increased "subdivision". Implicit assumptions are: a) all species equal so that extinction probabilities can be obtained from extinction rates estimated from many different species, b) no colonization from outside, and c) independence, so that extinct-

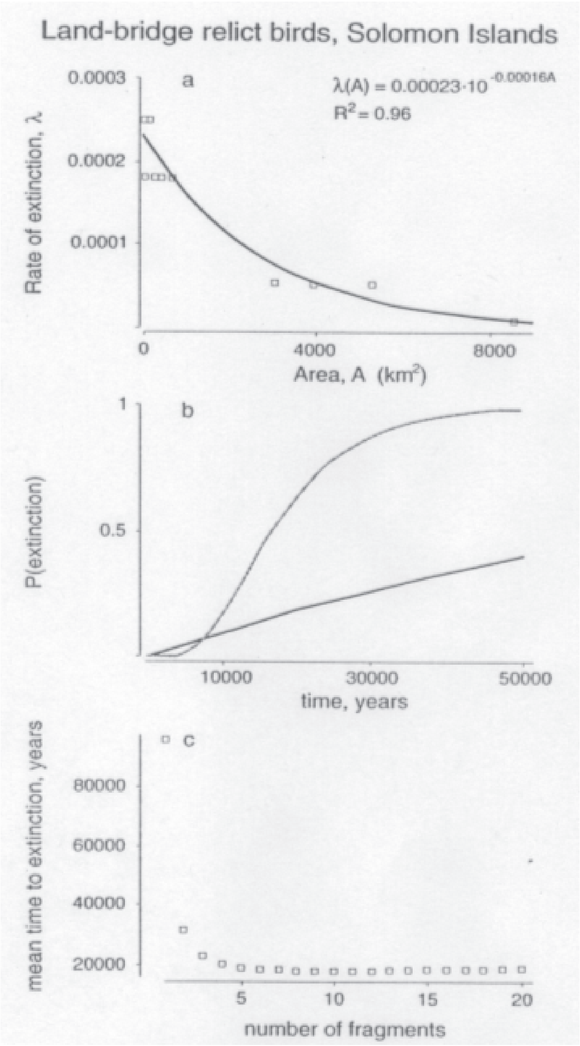

Figure 4. Estimating the effect of fragmentation on land-bridge relict bird species on the Solomon islands (model calibrated from data by Diamond 1984). a) per species rate of extinction, λ, as a function of area, *A*. b) Probability of extinction as a function of time, for a single large population (black line) and for a set of five smaller populations (grey line) occupying the same total area. c) Mean time to extinction for populations on an island as large as the largest island in the data sample, as divided into different numbers of fragments (without any loss in area).

ion on one island is independent of events on the other islands. Since extinction rates are estimated from a common pool of focal species on the island, the extinction probabilities and extinction times estimated apply to some hypothetical "average" species. Extinction prone species will have much lower persistence and much higher rates of extinction than the hypothetical "chimera" species, and will probably be much more negatively affected by habitat fragmentation. For this and other reasons, this analysis yields conservative estimates of fragmentation effects.

It may be possible to extract more data on extinction rates as a function of area from the

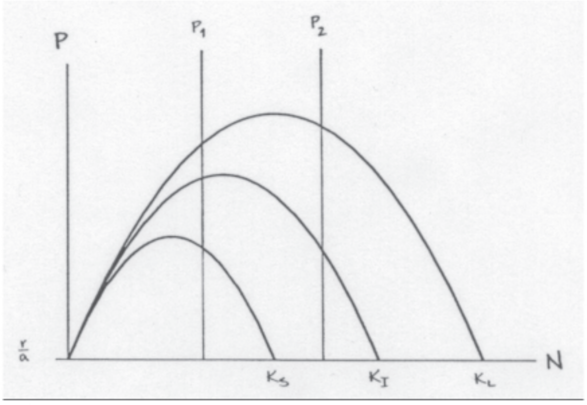

Figure 5. Isoclines for the Rosenzweig-MacArthur model for reserves of three different sizes ($2K_s = K_L$, K_I intermediate) and two different predator isoclines. The predator isoclines are independent of reserve size. For P_1, the small reserve has a non-trivial stable equilibrium, but the larger reserves have locally unstable equilibria. For the smallest reserve, P_2 has dropped below the critical threshold size and the only feasible predator equilibrium is for "P = 0".

literature. If it can be assumed that individual species were at some point present in all the islands of a particular set, or the likelihood of initial presence can be estimated from other data, it may be useful to use a binomial maximum likelihood estimator to fit a logistic regression to the binomial presence/absence data against area. From that one may be able to get estimates of extinction rates against area, which can be used to calculate probabilities of extinction as a function of time, area, and degree of fragmentation.

Extinction probabilities as a function of the degree of subdivision can be reconstructed for different types of extinction curves (Figure 5). In the MacArthur and Wilson model, the mean time to extinction increases approximately exponentially with *K* (see also Richter-Dyn and Goel, 1972; Leigh, 1981; Gabriel and bürger, 1992; Lande, 1993). If the rate of extinction in a single population, λ, remains constant through time, extinction is a Poisson process. The mean time to extinction for a single population, assuming a Poisson distribution is $T_\varepsilon = 1/\lambda$. Gabriel and bürger (1992) report that in their stochastic birth-death models the mean time to extinction is approximately geometrically distributed, but the distribution is not any standard statistical distribution, because the earliest time at which extinction can occur is after N_0 time steps, where N_0 is the initial population size. For the geometric distribution, the rate of extinction can be calculated from $T_\varepsilon = 1/\lambda$. Assuming that K scales linearly with area, *A*, we get

$$\lambda(A) = c\ \mathrm{Exp}[-b\ A] \qquad (1),$$

where *c* and *b* are positive constants. If extinction is a Poisson process with constant rate $\lambda(A)$ determined by the area of the patch, the probability of extinction for a population in a patch of area *A* is

$$P_\varepsilon = 1 - \exp[-\lambda(A)\ t] \qquad (2).$$

The probability that *n* independent populations on *n* islands of individual size *A*/*n* are all extinct by time *t* is

$$P_{\varepsilon,n} = (1 - \exp[-\lambda(A/n)\ t]\ )^n \qquad (3).$$

The corresponding probability density function of time to extinction is

$$p_{\varepsilon,n} = \frac{d\ P_{\varepsilon,n}}{dt} = \lambda(A/n)n\ \exp[-\lambda(A/n)t] \\ (1-\exp[-\lambda(A/n)t])^{n-1} \qquad (4)$$

and the mean time to extinction for a system of n islands of size *A*/*n* is

$$T_{\varepsilon,n} = \int_0^\infty t p_{\varepsilon,n} dt = \sum_{k=0}^{n-1} (-1)^{n-1+k} \binom{n-1}{k} \frac{n}{\lambda(A/n)(n-k)^2} \quad (5).$$

The median time to extinction is the time at which the cumulative distribution function, $P_{\varepsilon,n}$ equals 1/2, namely

$$M_{\varepsilon,n} = \frac{-\ln(1-\sqrt[n]{0.5}}{\lambda(A/n)}, n > 1; M_{\varepsilon,1} = \frac{-\ln(0.5)}{\lambda(A)} \quad (6).$$

This new model predicts either that fragmentation is always detrimental, or that it is beneficial in the short term but detrimental in the long term. Fragmentation usually increases the risk of extinction and often increases it drastically, but there exists a small region of parameter space (very small values of *bA* and *ct*) where fragmentation might reduce the probability of extinction. The median time to extinction also has this property, its derivative with respect to *n* can be positive for very small values of *bA* and small values of *n*. This region may, however, be in biologically unrealistic parameter space or an artifact of the population not being able to go extinct prior to N_0 time steps. Unfortunately, we have no information about the magnitude of *b* or *c*.

With more detailed analysis (Burkey, 1999), the distribution of extinction times under density dependent birth and death rates turns out to be gamma distributed (w. $\beta > 1$) rather than geometric. Gabriel and bürger (1992) seem to have concluded that extinction times were geometrically distributed because they displayed their results in histogram form, pooling across a relatively large interval on the time axis, obscuring the increase phase of the gamma distribution. This means that the analysis above, which assumed a geometric distribution of extinction times greatly overestimates extinction rates in the short term, making the short term comparison of unfragmented and fragmented systems precarious.

None of this scale dependence is evident if the extinction process is solved explicitly, which can be accomplished numerically (Burkey, 1999). For instance, let per capita birth and death rates be linear with respect to population size, births decreasing and deaths increasing. The probability of extinction as a function of time can be found exactly, either by iteration or by finding the eigenvalues and eigenvectors of the matrix of transition probabilities for population sizes one through a maximum population size. The extinction probability as a function of time emerges as the decay of the process described by the characteristic equation. Under the assumption that the viability of populations in a set of fragments is independent of each other we can solve the system for a single large habitat area and for the same area split into different numbers of fragments. In such a system, the effect of fragmentation is always large and detrimental.

If the mean time to extinction increases exponentially with *K* (MacArthur and Wilson, 1967; Gabriel and bürger, 1992), we can write

$$T_\varepsilon = cK^b, \ c > 0, b > 1.$$

If extinction is a Poisson process, $\lambda = 1/T_\varepsilon$, and we can write

$$\lambda = c' A^{-b}, \ c' > 0$$

assuming *K* increases linearly with *A*. If the times to extinction in isolated patches are independent and identically distributed, the probability of extinction in an area *A* subdivided into *n* isolated fragments is

$$P_{\varepsilon,n} = (1 - \exp[-c't(A/n)^{-b}])^n \quad (7).$$

The median time to extinction for n = 1 is

$$M_{\varepsilon,1} = \frac{-\ln(0.5)A^b}{c'}. \quad (8).$$

The median time to extinction for $n \geq 2$ is

$$M_{\varepsilon,n} = \frac{-\ln(1-\sqrt[n]{0.5})(\frac{A}{n})^b}{c'}. \quad (9).$$

Consequently, the ratio of the median to extinction in an unfragmented area and a fragmented area is

$$M_{\varepsilon,1}/M_{\varepsilon,n} = \frac{\ln(0.5)}{\ln(1-\sqrt[n]{0.5})(\frac{1}{n})^b}. \quad (10).$$

This ratio is always greater than one, indicating that the median time to extinction is greater in an unfragmented reserve system than in a fragmented system for all $n \geq 2$, at all spatial scales. For proof see Appendix.

In the models by Shaffer (1987) and Goodman (1987b) the mean time to extinction is shown to increase exponentially with *K* on a log log scale under demographic stochasticity -- ergo the mean time to extinction increases faster than exponentially with *K*. Consequently, the effects of fragmentation demonstrated above are even stronger if these results are used as inputs. Furthermore, these studies indicate that mean time to extinction increases linearly with *K* under environmental stochasticity, also on a log log scale (*i.e.*, exponentially on arithmetic scales). Consequently, the effect of fragmentation demonstrated above should also hold under a regime of environmental stochasticity as used by Shaffer and Goodman. In a rendition of the relationship between *K* and the mean time to extinction by Shaffer, only under the regime of environmental stochasticity they denote as "catastrophes" does the mean time to extinction ever increase with *K* more slowly than exponentially. In that case, the effect of fragmentation on median times to extinction may be dependent on the particular spatial scale in question. However, it should be noted that there was no density dependence in the model on which this relationship between area and persistence time was based.

Simulation models (Possingham *et al*., 1992; Possingham *et al*., 1993) have yielded viability estimates for a variety of Australian marsupials in different sized habitat areas under demographic stochasticity and fire regimes. We use these to calculate the probability of extinction with and without subdivision of such areas, under the assumption that isolated fragments are entirely independent. For instance, Possingham and colleagues estimated extinction risk for Leadbeater's opossum after 300 years in single patches of different sizes, with and without fires (Figure 6a). Assuming independence, we can calculate from these numbers the probability that two populations in 30 ha areas go extinct and compare this with the viability of a single population in a 60 ha area, *etc*. Figure 6b shows the result of such comparisons under demographic stochasticity only (no fires) based on the data in Figure 6a. The fragmented systems go extinct sooner than the unfragmented systems. Even in this implementation the effect of fragmentation is conservative since any correlation between the fate of isolated populations will increase the risk that they both go extinct. In a similar calculation based on the simulations with fires, this concern is even more evident -- since fires may spread from one patch to the other and the assumption of independence is likely to cause an underestimation of the effect of fragmentation if fires are important.

Figure 6c shows the extinction risk of a continuous population versus a fragmented population based on simulation data with fires. Note the spatial scale dependence in the effect of fragmentation that emerges from this treatment of their data. Assuming independence, fragmentation appears to increase overall extinction if the available area is small, but reduce the risk of extinction at larger spatial scales (see also Table 3). The importance of environmental disturbances like fires must be investigated further before this issue is resolved, and the spatial correlation structure is of special concern in such an endeavor.

McCarthy and colleagues (McCarthy and Lindenmayer, 1999; Lindenmayer *et al*., 2000; McCarthy and Lindenmayer, 2000) have continued the work on Australian marsupials. Their major conclusions are: (1) Including spatial correlations in environmental perturbations increases the risk of extinction when compared to totally independent environmental stochasticity. (2) The time frame of the analysis influences optimum patch size. A single patch is optimum when considering longer time frames. (3) Dispersal among patches, and considering the quality of the matrix surrounding habitat patches, is important to making accurate predictions concerning patch occupancy and metapopulation persistence.

Using a stochastic patch occupancy model, Etienne and Heesterbeek (2000) suggested that the expected time to extinction was generally greater

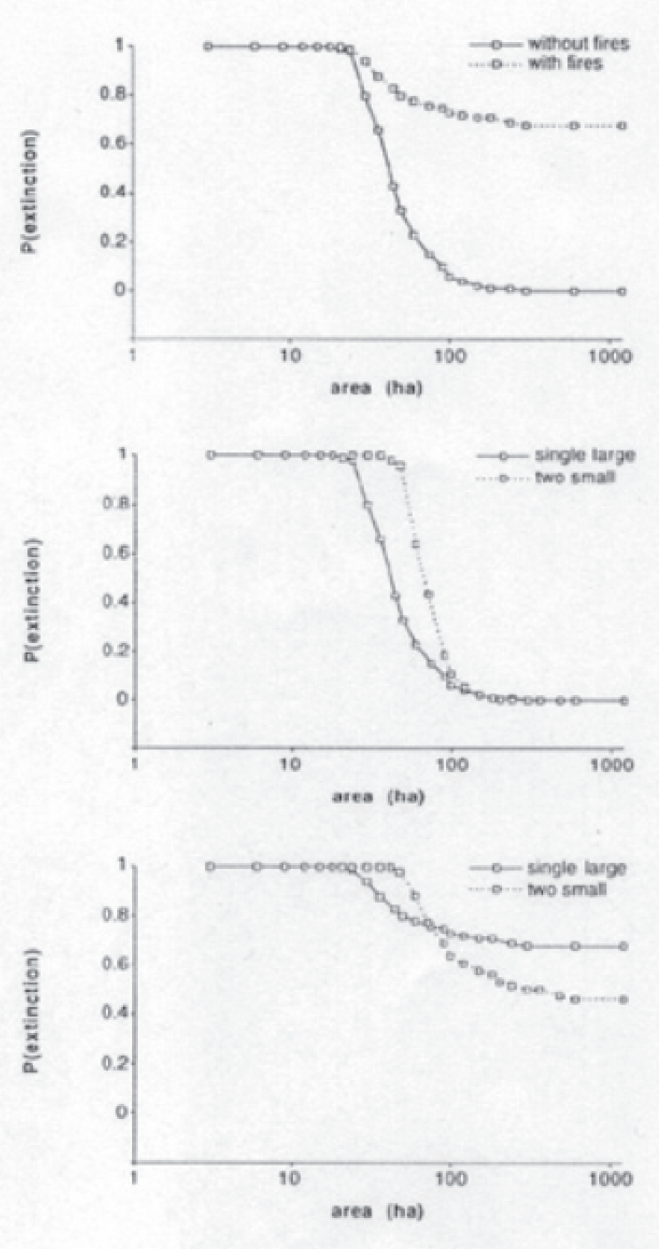

Figure 6. **a) The population viability of Leadbeater's possum, with and without fires, calculated by Lindenmayer and Possingham (1994). Assuming that individual subpopulations in a patchy landscape are independent of each other, we can calculate from (a) the probability of extinction in a single large patch of a given area and in a set of two patches each half that size -- without fires (b) and with fires (c). The annual probability of wildfires used for the simulation was 1%. The calculation with fires is biased in favor of fragmented systems, because it assumes that a fire burns a constant proportion of a forest patch regardless of its size (in this case 75%) and because it assumes that the occurrence of fires is independent in a set of small patches.**

Table 3. The probability of population extinction for *Lycaon pictus* (Reed, 2004a). The models cover a range of total carrying capacities (*K*), degrees of fragmentation (*n* = number of identical sized fragments with a carrying capacity of *K*/*n*), and time spans in generations. The model demonstrates that the relative performance of a metapopulation versus a single population is dependent on the total available area for conservation and the time span of interest.

	40 Generations		
	n = 1	**n = 2**	**n = 3**
K = 200	0.735	0.851	0.972
K = 400	0.499	0.541	0.725
K = 1600	0.171	0.092	0.062
	100 Generations		
K = 400	0.823	0.929	0.993
K = 1600	0.594	0.677	0.864
K = 3200	0.217	0.140	0.124

in a single large rather than several small reserves. However, they mention several caveats regarding variance in patch size and distribution, dispersal among patches, and spatial correlation of local extinction times -- none of which were modeled explicitly. Ovaskainen (2002) also used a patch occupancy model, where population dynamics in each patch are independent of each other, to investigate persistence in fragmented versus unfragmented landscapes. The conclusion was that an intermediate number of patches maximizes the time to extinction. It should be emphasized again that models that do not include explicit dynamics within subpopulations seem to favor population subdivision to a far greater extent than do models that include subpopulation dynamics. As the actual shape of extinction probability as a function of carrying capacity (or area) is critical to the impacts of fragmentation on extinction risk (Figure 1) it would seem that models that do not explicitly model the extinction process within patches are of limited relevance to the question of fragmentation.

Reed (2004a) created models from long-term data on 30 populations of vertebrates. Each model was individual-based and incorporated demographic, environmental (including catastrophes and disease), and genetic stochasticity. The probability of extinction for a single population in a continuous habitat was compared to that of multiple isolated, or semi-isolated, populations occupying a fragmented landscape with an equivalent total carrying capacity. Populations occupying a fragmented landscape were modeled for a range of migration rates and levels of asynchrony in the effects of environmental disturbances. This study had three major findings: (1) The relative probability of extinction for a continuous versus a fragmented population is highly dependent on the total carrying capacity of the available habitat, the time frame over which extinction is to be measured, and the initial fitness of the population. (2) Immigration among subpopulations ameliorates, but does not eliminate, the negative effects of fragmentation. This is despite the fact that disease epidemics, spread via immigration, were included in the models. (3) The relative probability of extinction for a single population in a continuous habitat is usually going to be less than that of multiple isolated populations occupying a fragmented landscape with an equivalent total carrying capacity.

Conclusions

Most experimental and modeling results

favor continuous over fragmented habitats, and the circumstances where this relationship might be reversed seem to be unlikely in a conservation context. Lower fitness and reduced evolutionary potential due to increased genetic stochasticity, increased demographic stochasticity, decreases in density due to edge effects or competition from already common edge species, increased environmental stochasticity due to edge effects, and the lack of dispersal through a hostile matrix in a fragmented habitat are unlikely to be outweighed by benefits gained through added redundancy in the face of spatially uncorrelated environmental stochasticity.

Thus, reserves should be large enough to encompass the natural regime of disturbances and the natural scale of environmental patchiness within them. If our political priorities preclude this, occupied habitat should at least be linked or managed so as to emulate this patch structure and disturbance regime as much as possible within the landscape. Surrounding matrix habitats and corridors are critically important to dispersal (Laurance *et al*., 2002) and should be managed so as to mimic the structure and microclimate of the habitat patch as closely as possible. The special needs of migratory species like wildebeest, monarch butterflies, and caribou must be met. In light of the outlook for future temperature changes, north-south links and altitudinal links may be especially important. At the very least, if the needs of low density, wide ranging, and area sensitive species can be met within such reserve systems we will have significantly simplified the task of managing ecosystems and eliminated the need for continual and expensive rescue operations. It may also preserve the evolutionary and population genetic integrity of the resident species, and their ability to survive and adapt to future environmental changes. Ultimately, we should aim for continuous patches of habitat capable of supporting several thousand individuals of any species we wish to protect (Reed *et al*., 2003a; Reed, 2005).

The situation in Thailand is especially urgent. Thailand's forests are now extremely fragmented and few large habitat patches remain that are capable of supporting large vertebrates (Lyman *et al*., 2001). Populations of species that are representative of Thailand, such as tigers, exist at populations that are much too small to be viable for more than two or three human generations. Lack of sufficient habitat interacts in a negative synergistic fashion with poaching and habitat fragmentation to create an extinction vortex that the people of Thailand must find a solution to if they wish to maintain the fauna that are symbolic of their country.

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APPENDIX

Claim: $\dfrac{\ln(0.5)}{\ln(1-\sqrt[n]{0.5})(\frac{1}{n})^{b}} > 1, \mathrm{n} \geq 2, \mathrm{b} > 1$

Proof: Call the expression on the left hand side *f*.

$$\frac{\partial f}{\partial b} = \frac{\ln(0.5)n^{b}\ln n}{\ln(1-\sqrt[n]{0.5})} > 0$$

Since the partial derivative of *f* with respect to b is always positive, *f* is smallest for b as close to one as possible. Thus we only need to investigate the claim near b = 1.

We will show that

$$\frac{\ln(0.5)}{\ln(1-\sqrt[n]{0.5})\frac{1}{n}} > 1, n \geq 2 \text{ (actually for n > 1)}$$

This requires that

$$\left(\frac{1}{2}\right)^{n} + \left(\frac{1}{2}\right)^{1/n} < 1$$

Call the left hand side S(n). S(1) = 1 and S(∞) = 1. S(2) $\approx$ 0.957<1. Therefore, if $\frac{\mathrm{dS}}{\mathrm{dn}}$ = 0 only has one solution between 1 and infinity, then S(n) <1 for all n >1.

$$\frac{dS}{dn} = \frac{\left(\left(\frac{1}{2}\right)^{n} n^{2} - \left(\frac{1}{2}\right)^{1/n}\right)\ln\left(\frac{1}{2}\right)}{n^{2}}$$

$\frac{\mathrm{dS}}{\mathrm{dn}}$ = 0 requires that

$$n^{2} = 2^{n-\frac{1}{n}}$$

To show that this expression only has one solution we take logs on both sides to obtain $2\ln n-(n-1/n)\ln 2 = 0$.

Call the left hand side F(n). F(1) = 0, F(∞) = -∞.

$$\frac{dF}{dn} = \frac{2}{n} - \left(1 + \frac{1}{n^{2}}\right)\ln 2$$

$$\frac{d^{2}F}{dn^{2}} = \frac{2(\ln 2 - n)}{n^{3}}$$

The latter is equal to zero if and only if n = ln 2 $\approx$ 0.69 (n>0), and negative for all values of n greater than ln 2. Since F is concave down for all n > ln 2, F=0 can only have one solution. F(ln2) $\approx$ -0.11.

Since both partial derivatives of *f* are positive over this domain, the smallest values of the ratio is at the lower boundary of the domain, at n=2, as b tends towards unity.

The value of the ratio at n=2, b=1 is

$$\frac{2\ln(0.5)}{\ln(1-\sqrt{0.5})} \approx 1.13$$