POPULATION PROCESSES AND BIOLOGICAL DIVERSITY

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INTRODUCTION

A major goal of conservation biologists is to preserve biological diversity. The accelerating destruction of habitats by human beings has resulted in fragmented landscapes, which has led to a reduction in biological diversity (Wilson 1988). As fragmentation increases, it leads to a decrease in average habitat patch size and an increase in average distance between patches (Wilcox 1980). Both habitat loss and insularity may reduce population sizes to such low levels that species may go extinct.

The formidable task facing conservation biologists is to develop land management programs to protect species. Successful programs must be based on a thorough understanding of ecological and evolutionary processes of the populations under consideration. The need for information about population processes for the protection of threatened and endangered species is underscored by the continuing debate whether a single large reserve or several small reserves will protect more species (Wilcox and Murphy 1985, Wiens 1989). Reserve design is still a contentious issue after 15 years because not all species respond in the same way to habitat fragmentation (Wilcove et al. 1986).

An interesting question related to the preservation of biological diversity is: What fundamental unit should be preserved? Should the focus be on a local population, a set of interacting local populations (metapopulations), community or ecosystem. As the level

of biological complexity increases from populations to ecosystems, the number of interactions increases making higher levels of biological organization more difficult to study. These higher levels of biological organization have emergent properties resulting from interspecific interactions, thus communities and ecosystems are not simply the sum of their parts. Ideally, we would like to preserve ecosystems but they are not amenable to experimentation. The advantage of a population approach allows for experimental manipulation.

Management decisions about the conservation of biological diversity need to be made quickly because there is neither enough time nor funds to study the population dynamics of all species in a community. Under these difficult circumstances the manager is required to decide which population should be studied. The choice is often based on political forces rather than on sound biological reasons. An understanding of the population biology of certain keystone species (Paine 1966) might be particularly useful in the development of management programs to conserve a large fraction of the entire community (Gilbert 1980, Terborgh 1986, Simberloff 1988).

Population changes in keystone species that provide habitat structure for other species may have profound effects on biological diversity. For example, lichens in some Austrian alpine grasslands required spaces created by the sedge *Carex curvula* (Grabherr 1989). When the sedge disappeared the lichen's productivity decreased, which could lead to a population decline for lichen-dependent species. Keystone species often function as predators that control the numbers of prey species. Their predatory effects can increase the biological diversity of subordinate prey species by reducing densities of a preferred dominant prey species. For instance, in central Chile a rocky intertidal community had a higher diversity index when the major gastropod predator was present than when the predator was absent (Duran 1989). In the absence of predation the dominant competitor could itself be the keystone species if its presence determines the distribution and abundance of subordinate species. For example, the cotton rat

(*Sigmodon hispidus*) was the largest and competitively dominant species that affected the smaller and subordinate species in the small mammal community discussed in the case study below.

We believe that continuous progress will most likely come from conservation efforts focused at the population level (Shaffer 1981). With well-understood organisms, such as small mammals, we can test some of the theories that bear on questions of population persistence for poorly-understood organisms, and supply generalizations for those theories. As we mentioned, there are some problems associated with a reductionist approach, but there are few alternatives given the time and resources available.

In this review we will examine the role of population processes in determining biological diversity. We first briefly discuss how the basic concepts of minimum viable population and metapopulation relate to biological diversity. We then present data from our ongoing study of the effects of habitat fragmentation on population dynamics of small mammals and how this fragmented landscape affects biological diversity. We conclude with recommendations for future research on the effects of habitat fragmentation on population processes.

MINIMUM VIABLE POPULATION CONCEPT

Gilpin and Soulé (1986) considered two kinds of population extinctions, deterministic and stochastic. Deterministic extinctions are due to forces that inexorably result in the disappearance of a population. For example, deforestation in the tropics would be a deterministic force for different species of trees. The outcome is predictable if deforestation continues at its present rate. Stochastic extinctions are those due to random events. Shaffer (1981, 1987) distinguished four sources of variation that could result in the random extinction of a population: 1) demographic stochasticity due to random events in individual survival and reproduction; 2) environmental stochasticity due to unpredictable changes in abiotic factors such as weather, or biotic factors such as

predators, competitors and parasites; 3) natural catastrophes such as fires and floods, which occur at random intervals; and 4) genetic stochasticity due to genetic drift and inbreeding, which may affect individual survival and reproduction.

Several points are worth noting about the distinction between deterministic forces of extinction and stochastic forces. First, the relative effect of stochastic forces increases as populations become smaller. Second, many extinctions are caused by a deterministic event reducing population size to such an extent that stochastic forces will eventually lead to extinction. Third, different stochastic forces operating at low population densities may interact to cause extinctions. For example, an environmental perturbation could reduce population size to a level where a loss of variation in the population would occur as a result of genetic drift. The increase in genetic homozygosity could then reduce individual survival and reproduction.

Population biologists have known for some time that the smaller the population the more susceptible it is to extinction (Shaffer 1981). However, what is required by managers is a precise way to relate population size to the probability of extinction. Attempts to understand and predict the relationship of population size to extinction have spawned a burgeoning literature on the minimum viable population concept. The basic premise of the minimum viable population concept is that a threshold population density must be maintained for a population to persist. Shaffer (1981:132) defined minimum viable population for any given species in any given habitat as "the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental and genetic stochasticity, and natural catastrophes."

Three approaches have been used to estimate minimum viable population sizes and related area requirements: observational, experimental and theoretical. The observational approach examines biogeographic patterns of abundance and distribution across a species' range. If populations occur in habitat patches of different sizes, one can

estimate the smallest patch inhabited by a species and the percent of the patches of a certain size supporting that species. Additional information that is needed to estimate minimum viable population size, but is most difficult to obtain, is species-specific colonization and extinction rates for different-sized habitat patches. There are three critical assumptions in this biogeographic approach: 1) communities are at equilibrium in different patches; 2) population characteristics of a species are solely a function of patch size and do not vary in different parts of its range; and 3) there are no systematic differences in other patch attributes as a function of patch size.

In the experimental approach, minimum viable population size and area requirements are assessed by creating patches of different sizes and monitoring population parameters within them. For instance, Lovejoy et al. (1984, 1985, 1986) have studied the rate of disappearance of populations in 2.4 acre (1 ha) and 24 acre (10 ha) reserves in a Brazilian rain forest. Fragment size determined the persistence rates of different working species. Other researchers have also found that fragmentation affects persistence rates in a variety of species (Quinn et al. 1989, Paine 1989, Bergen 1990) and distributions of various-sized animals (Bennett 1991). We are conducting an experiment on habitat fragmentation on a small mammal community in eastern Kansas, which we discuss below. The major drawback of the experimental approach is that it requires long term monitoring of populations. Unfortunately, the results of these experimental studies often will be too late to be of use due to the high rate of habitat destruction. Furthermore, such studies are impractical for many species and ecosystems.

Theoretical models have been developed to predict the probability that a population of a given size will go extinct and the time to extinction. Goodman (1987) used a classical birth-and-death process model incorporating environmental fluctuations to predict persistence times of different-sized populations. Persistence time strongly depended on the magnitude of the variance in population growth rate. Belovsky (1987) used Goodman's model to calculate the population size needed for mammalian species,

that ranged in body mass from 2 oz. to 99 tons (10^1 to 10^6 g), to persist 100 or 1000 years with a 95% probability. Population sizes ranged from hundreds to millions of individuals with corresponding minimum area requirements of tens to millions of mi^2. As body size increased, the minimum viable populations decreased. The disturbing result was that those small populations of larger bodied species still required larger areas than their smaller bodied counterparts.

The minimum viable population is a useful concept only in that it provides non-biologists who may be in positions of influence, such as politicians, with a single number of individuals needed for a population to persist. As is the case for most oversimplifications there is danger in the misuse of minimum viable population because there is no universal population number for a species. Also, a single number diverts attention from the mechanistic processes accounting for population persistence or extinction, and places the focus on the final outcome or product. It may be more productive to analyze the population processes that result in the minimum viable population rather than estimate this single number. This mechanistic approach has been taken by Gilpin and Soulé (1986), which they refer to as population vulnerability analysis.

METAPOPULATION DYNAMICS AND POPULATION PERSISTENCE

In our discussion of minimum viable population we ignored the effects of spatial structuring on population persistence. Metapopulation dynamics provides a framework for analyzing the persistence of species inhabiting patchy environments and should prove useful in elucidating the conservation implications of fragmentation. Following Levins (1980), Hanski and Gilpin (1991) defined a metapopulation as "a set of local populations which interact via individuals moving among populations." Most models of metapopulations incorporate local extinctions followed by recolonization of individuals dispersing from extant populations (Holt 1985, Pulliam 1988).

Several generalities about metapopulation extinction emerge from simple diffusion models (Harrison and Quinn 1989, Hanski 1989). Metapopulations may go extinct when: 1) habitat patches are small leading to low population density; 2) the number of habitat patches is decreased thereby increasing population isolation, and decreasing dispersal; 3) the population dynamics in different patches are correlated leading to a correlation of extinction probabilities.

Spatial heterogeneity in the environment may cause differences in habitat quality among populations within a metapopulation. Populations in higher quality habitats may contain a surplus of animals that might disperse to neighboring populations. Thus, populations may persist in low quality habitats due to the colonization of individuals from higher quality habitats. Holt (1985) and Pulliam (1988) described populations that produce a surplus of dispersing animals as "sources" and populations in suboptimal habitat maintained by dispersal as "sinks."

Fragmented landscapes containing an array of different patch sizes may lead to source-sink population dynamics. For most species there should be a minimum patch size below which a population cannot persist without immigration. In the following case study, we report on our experiments investigating source-sink population structure in a small mammal community and how this structure affects small mammal biological diversity.

CASE STUDY

In our continuing research in northeastern Kansas we investigate the effects of habitat fragmentation on the rodent species within a 29.6 acre (12 ha) successional old-field (Foster and Gaines 1991). Since 1984 the vegetation has been maintained by mowing to produce archipelagos (Figure 1). Each archipelago consists of one large patch (5,980.0 yd^2 = 50 x 100 m), or 6 medium patches (each 344.5 yd^2 = 12 x 24 m), or 15 small patches (each 38.27 yd^2 = 4 x 8 m). We view the large patches as controls with no

fragmentation. The archipelagos of medium and small patches represent increasing levels of fragmentation. The areas between archipelagos are mowed every two weeks during the growing season and are assumed to be unsuitable habitat. Total area of suitable habitat is 4.7 acres (approximately 1/6 of the original field). The rodent community consists of species that range in body size from large cotton rats (*Sigmodon hispidus*), with adults weighing at least 4.13 oz (118 g) to intermediate prairie voles (*Microtus ochrogaster*), weighing at least 0.87 oz (25 g). Adults of the two smallest species, deer mice (*Peromyscus maniculatus*) and western harvest mice (*Reithrodontomys megalotis*), weigh at least 0.64 oz (18 g) and 0.25 oz (7 g), respectively.

Biological diversity on the small patches is lower than on the large patches because cotton rats are not resident there (Foster and Gaines 1991, Gaines et al. 1992). All species are distributed among habitat types relative to their body sizes such that cotton rats have highest densities on the large patches, prairie voles have highest densities on the medium patches, and deer mice and western harvest mice have highest densities on the small patches. Western harvest mice became rare after 1987 for reasons still unclear. One cause may be due to changes in the plant community. Western harvest mice may prefer early successional grasses over later successional forbs (Birkenholz 1967, Fitch et al. 1984, Johnson and Gaines 1988). The annual and perennial grasses have been gradually replaced by perennial forbs since 1984 (Foster and Gaines 1991). Due to low numbers, western harvest mice are not considered here.

Significant differences in persistence rates between patch sizes indicate that population processes are affected by habitat fragmentation, but these effects vary among species (Foster and Gaines 1991, Gaines et al. 1992). Although sample sizes of cotton rats on medium and small patches are small, persistence rates of cotton rats are highest on large patches and essentially zero on small patches. Persistence rates of prairie voles are lowest on small patches, presumably because small patches have less suitable habitat. That persistence rates of prairie voles are highest on large patches and

intermediate on medium patches lead us to suggest that vole densities should be greatest on large patches, but this is not the case (Foster and Gaines 1991). The lower density of voles inhabiting large patches rather than medium patches could be due to negative competitive interactions with cotton rats (Gaines et al. 1992), although the few voles establishing themselves on large patches are maintaining their territories.

Persistence rates of deer mice are either highest on smaller patches (Foster and Gaines 1991) or equal across all habitat types (Gaines et al. 1992), depending on the season. This contrast between deer mice and the two larger species may be explained by the manner in which deer mice utilize the mowed "interstitial areas" between habitat patches. Based on trapping data deer mice appear to exploit the interstitial areas between habitat patches, whereas the other species do not (Foster and Gaines 1991). This ability to exploit resources in the most unsuitable habitats may explain why deer mice can persist and maintain high densities on small patches. Individuals residing in interstitial areas may move freely onto small patches. Moreover, the small patches and interstitial areas may serve as refuges from larger and more aggressive prairie voles and cotton rats. Competition and competitive refuge effects come from negative correlations in abundances between the deer mice and the two larger species (Gaines et al. 1992). From 1984 to 1987, deer mouse densities increased in the interstitial areas and declined on large and medium patches as prairie vole densities increased (Foster and Gaines 1991). Deer mouse densities remained lowest on large and medium patches from 1987 to 1991, while cotton rat densities increased on large patches and prairie vole densities increased on medium patches (Gaines et al., 1992).

Our system consists of three metapopulations, one for each species, made up of different subpopulations based on patch size. Source habitat patches where individuals persist the longest should contain a high number of dominant individuals who establish territories and are reproductively active. Subordinate individuals born in these source populations should disperse to less suitable sink habitats when carrying capacities in the

source habitats are exceeded. A source-sink structure appears to occur in cotton rats, prairie voles and deer mice (Gaines et al. 1992). In our earlier studies (Foster and Gaines 1991, Gaines et al. 1992), we made no attempt to determine the age structure and reproductive activity of source and sink populations. However, this information is useful for population viability analyses (Mace and Lande 1991).

Habitats in which individuals of a species persist the longest should have the greatest percentage of adults because those older and more experienced individuals aggressively exclude younger inexperienced ones. For instance, most of the cotton rats occurring on the large patches are predicted to be adults, whereas individuals on medium patches will be younger animals. Voles persist longest on large patches, so we predict that large patches will have the highest percentage of adults. Deer mice will have the highest percentage of adults on small patches because they persist longest there.

Due to high variability in the data, we used the Friedman's method for randomized blocks to test for patch effects. Data are separated by patch size and blocked by year for each season. Percentages of adult cotton rats did not differ significantly between medium and large patches. The lack of statistical significance may be due to the small numbers of cotton rats on medium patches. More than 90% of all males, and more than 88% of all females occur on the large patches which represent only 3.7 out of 29.6 acres (1/8 of the original field). Thus, if cotton rats were unable to sustain themselves on large patches then they would probably become extinct from the entire study site.

Percentages of adult male and female prairie voles differed significantly among patches during winter seasons (males: $\chi^2_{[2]} = 7.14$, $p \leq 0.05$; females: $\chi^2_{[2]} = 12.3$, $p \leq 0.05$); and spring seasons (males: $\chi^2_{[2]} = 10.29$, $p \leq 0.01$; females: $\chi^2_{[2]} = 6.0$, $p \leq 0.05$). The pooled data for winter and spring are presented in Figure 2. There tended to be higher percentages of adults on large patches for all seasons. As expected, the deer mouse response was opposite to that of the prairie vole. Percentages of adult male deer

mice were higher on small patches, but not significantly. Except in the summer, percentages of adult female deer mice were also higher on small patches, but not significantly.

Finally, cotton rats, prairie voles, and deer mice should have greater percentages of reproductive adults in source habitats where individuals persist the longest. We calssified adults as reproductively active based on testes position (scrotal), and nipple size (medium or large). Reproductive activity did not differ significantly among patches for any species. However, percentages of reproductively active male and female cotton rats were always higher on large patches. There were no apparent trends for voles and deer mice.

Habitat fragmentation had different effects on the age structure and reproductive activity of small mammals within habitat patches of different sizes. Fragmentation affected biological diversity: there are fewer rodent species on small patches because of the absence of cotton rats. However, the higher densities of small-bodied species on smaller patches may be due to competitive release from the cotton rat. There were no obvious effects of fragmentation on the age structure and reproductive activity of prairie voles and deer mice. However, cotton rats, prairie voles and deer mice were utilizing the landscape differently. We suggest that the demographic consequences of body size are necessary population statistics when considering what area of habitat fragment is needed to sustain populations (Belovsky 1987).

There are several lessons from this study that are germane to understanding the relationship of population processes and biological diversity:

1) It is difficult to generalize about the effects of habitat fragmentation on population processes of different species.
2) Competition may be a factor superimposed on source-sink dynamics. The effect of fragmentation apparent in one species (e.g. a competitive dominant)

may indirectly reflect the impact of fragmentation on another species (e.g. a competitive subordinate).

3) Sink populations may contribute to the total number of individuals in an area and retard species' extinctions from fragmented habitats, but the species' chances of going extinct through stochastic processes are high due to poor-quality habitat. Because fragmentation is likely to produce source-sink structures, the total size of a population may be a poor index of how vulnerable a species is to further habitat degradation.

CONCLUSIONS

Much work needs to be done before a unified approach to conservation biology emerges. Several issues remain unresolved including scale. An anthropocentric bias towards small spatial scale was illustrated by a survey (Karieva and Anderson 1988) in which 80% of experimental community studies were done in areas $\leq 9\ ft^2$ ($1\ m^2$) area. Some ecologists claim that the processes affected by habitat fragmentation on small spatial scales are similarly affected at large spatial scales. Ims (1990) and Stenseth (1990) suggested that small mammals in small-scale fragmented landscapes can serve as "empirical model systems" for larger mammals living in areas fragmented by human activity. Similarly, J. A. Wiens (personal communication 1991) believes that it might be possible to use information obtained at a micro-landscape level (e.g. beetles on a lawn) to make predictions about larger scales (e.g. elephants on the Serengeti). To extrapolate processes that occur at a microscale to a macroscale phenomena is appealing because the smaller the scale the more amenable the system is to experimental manipulation. However, making generalizations about population dynamics from small to large landscapes may be possible only if ecological processes scale monotonically with area. The complexity of biotic and abiotic interactions increases with area so that a

straightforward relationship between small and large scale ecological processes are unlikely.

Another major area of contention is the relative role of genetic and demographic factors in causing population extinctions. The "50/500" rule, which has been disputed (Simberloff 1988), focuses on the relationship between genetic stochasticity and population extinction. An effective population size of 50 results in inbreeding depression (a short term effect), whereas 500 results in genetic drift and a loss of genetic variation (a long term effect). In both cases there would be a high probability of population extinction, particularly in a changing environment. However, Lande (1988:1455) concludes from theoretical and empirical examples "that demography is usually of more immediate importance than population genetics in determining the minimum viable sizes of wild populations." Nevertheless, Lande (1988) suggests that future conservation plans include integration of ecology and population genetics. An understanding of the ecological genetics of threatened and endangered species in fragmented habitats may be the only hope for species' survival.

A fertile area for future research is population persistence in the context of source-sink dynamics. Species live in a heterogenous landscape with subpopulations occurring on patches of varying quality. Habitat fragmentation due to human disturbance has greatly contributed to this heterogeneity. Detailed information on movement between semi-isolated refuges and the manner in which corridors facilitate this movement is needed. Information about the mating success of individuals after they immigrate to a new patch can be obtained with recent advances in radiotelemetry and DNA fingerprinting.

As wildlife conservation increases in scope and sophistication, ecological theory will be needed in conservation planning and management policy. The development of relevant theory has been rapid despite the complexity of the questions addressed. The concepts of minimum viable population and population vulnerability analysis (Gilpin

and Soulé 1986) have provided a valuable heuristic tool: small populations are vulnerable, and very small ones may quickly succumb to stochastic processes. However, a more fundamental issue is how to keep populations and whole species from falling below a critical size. Since nearly all species exist as several populations, and most threatened species are limited to a few disconnected subpopulations, theories of metapopulation dynamics seem promising. Metapopulation models can be further refined within a source-sink structure by determining how individuals are exchanged between subpopulations. Our experimental work with small mammals in fragmented populations lends support to these new theoretical approaches, and that source-sink components incorporated in metapopulation dynamics should be particularly fruitful. As the need for informed conservation management decisions increases, our understanding of the ecology of threatened populations continues to grow.

ACKNOWLEDGEMENTS

We are grateful to Andrea J. Freeman, Michael L. Johnson, John L. Koprowski, Lee McClenaghan, Robert Tamarin, John Wiens, and Frank Wray for their comments on the manuscript. Our work on small mammals was supported by National Science Foundation grant number BSR-8718088.

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