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## The effects of habitat fragmentation on chaparral plants and vertebrates

Michael E. Soulé, Allison C. Alberts and Douglas T. Bolger

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The effects of fragmentation in a scrub habitat in California on three taxa (plants, birds, and rodents) are concordant. Extinctions within the habitat remnants occur quickly and the sequence of species disappearances of birds and rodents is predictable based on population density in undisturbed habitat. Distance effects on species diversity are weak to non-existent, and habitat area effects are strong. Edge effects and cumulative habitat loss following isolation of the remnants are correlated with loss of species diversity. Recolonization in these taxa occurs rarely. Rodents appear to be extremely susceptible to extinction. Small, old patches retain a predictable subset of bird and rodent species, reinforcing the principle that larger reserves are generally superior.

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The Equilibrium Theory of Island Biogeography (MacArthur and Wilson 1963, 1967) predicts that remnants of habitat will lose species at predictable rates. If the remnants are virtually isolated (no colonization), and too small for in situ (autochthonous) speciation, then the number of species, overall or in a given taxon, will decline asymptotically to zero, given enough time. The smaller the remnants, the faster the biota should collapse. One of the reasons for this is that population sizes of the contained species should be roughly proportional to habitat area, and it can be shown theoretically (Leigh 1981, Goodman 1987) and empirically (Terborgh and Winter 1980, Diamond 1984, Soulé et al. 1988) that persistence times should be proportional to population sizes, all else being equal. This principle was recognized early by the pioneers in conservation biology (Wilson and Willis 1975, Diamond 1975, Terborgh 1975), who argued that protected areas should be as large as possible.

Diversity of opinion, based partly on the diversity of

organisms, still exists, however, and some believe that small reserves are adequate for certain species (Simberloff and Abele 1976, Quinn and Hastings 1988) and may even be superior, assuming there are enough of them. Hence, the SLOSS (Single Large or Several Small) debate in conservation biology – a controversy that seems impossible to quench (cf. Soulé and Simberloff 1986).

San Diego, a place with a sunny, benign climate and beautiful coastline, has grown by a factor of 10 over the last 50 years, contributing grotesquely to air and marine pollution and habitat destruction in the region. Only about 10% of the native landscape, mostly coastal sage scrub habitat, now remains (Jensen et al. 1990).

We have investigated the effects of habitat fragmentation on three taxa, native birds that are dependent on the indigenous scrub habitats, native rodents, and native flowering plants. Because the results touch on many of the central issues in conservation biology, and because the personal and scholarly stimuli for this research are easily traced to the intellectual and personal influen-

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Table 1. A summary of the results from the studies of native bird, rodent and flowering plant persistence in habitat remnants in coastal San Diego County, California. "No" indicates no significant effect; "yes" indicates a significant effect.

	Birds	Mammals	Plants
A. Distance effects	No	Possible	No
B. Effect of total area in remnant	No	No	No
C. Effect of habitat area in remnant	Yes	Yes	Yes
D. Effect of age of remnant	Yes	Yes	Yes
E. Effect of species interactions	Probable	Possible	Few
F. Differential vulnerability	Yes	Yes	Probable
G. Turnover (recolonization)	Rare	Rare	Rare
H. Hierarchical structure (nestedness)	Yes	Yes	Unanalysed

ces of Paul R. Ehrlich and Edward O. Wilson, we felt that a summary of our results would be especially appropriate here.

### The system: habitat remnants in an urban sea

Coastal San Diego County, California is a series of old marine terraces and hills interspersed with steep-sided canyons. Vegetative cover is mostly woody shrubs (chaparral or coastal sage scrub) adapted to long, dry summers and limited winter rainfall (Soulé et al. 1988). This region has been the site of intensive construction over the past 90 years, and most of the remaining natural habitat is restricted to canyons. The habitat fragments referred to in this review number 36 (for birds, a subset of 25 for mammals and flowering plants) from San Diego to Encinitas, California. Control (unfragmented) habitat is located in the same region (Bolger et al. 1991 and Bolger et al., unpubl.). The species of chaparral-requiring birds, rodents, and plants that were the subject of this study are described in Soulé et al. 1988, Bolger et al., unpubl., and Alberts et al. (unpubl.), respectively.

### Control studies

The fundamental question that we asked of the system was whether native species disappear from isolated habitat remnants, and, if so, how rapidly. One way of establishing the fact and extent of faunal collapse is to determine whether censuses in similar-sized plots that are embedded within large, unfragmented habitat produce significantly different species-area relationships than similar-sized isolated plots. If extinctions have occurred in the remnants, it is expected that the control plots, especially the smaller ones, will have greater spe-

cies richness than do the remnants of similar size. In other words, the y-intercept and slope of the "mainland" or control species-area curves should be higher and less steep, respectively than those of the "island" curve.

Though data are still lacking for the plants, the results for the birds and mammals are revealing. For chaparral-requiring birds, the censuses in the control plots were restricted to the five species for which the data were most accurate (Bolger et al. 1991). Six non-overlapping controls plots (1/8, 1/4, 1/2, 1, 10, and 50 ha) were established in each of three different localities. In all three cases the census plots larger than 1 ha support the full complement of these five species. Our youngest fragment (Montanosa) which was 1 ha in area, also contained all five species. 30 out of the 37 remnants were larger than 1.0 ha, so it is probably safe to assume that the results for birds were not influenced significantly by sampling effects; i.e., it is unlikely that many of the putative extinctions are attributable to the absence of the species when the remnant was isolated. These results, then, lend more credence to the extinction hypothesis.

Similar results obtain for the rodents (Bolger et al. submitted). Control plots  $\geq 1$  ha supported most of the species. Since only 5 of the 25 fragments surveyed for rodents were  $< 1$  ha, it appears that most rodent species absences from the fragments are the result of extinction following fragmentation.

### Canyon remnant studies: results and conclusions

Table 1 presents the results of the three studies in a simplified summary format. The statements in the tables represent conclusions based mostly on multiple regression analyses. Some of the biogeographic variables that we analyzed are reflected in the first five rows of the table. The next three rows represent "meta-results" from more complex, higher level analyses or syntheses.

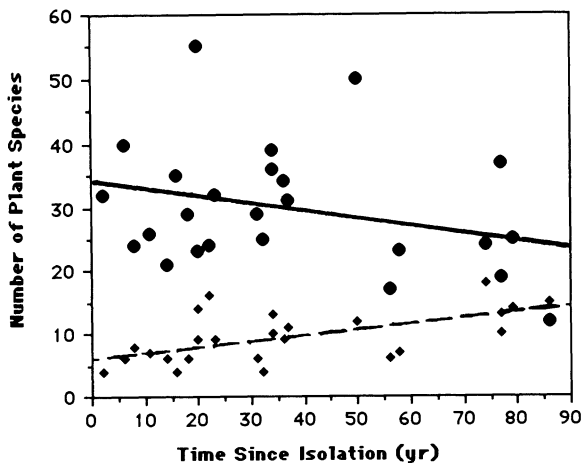


Fig. 1. Trends of species diversity over time for native and ornamental plants in habitat fragments in San Diego County, California. Native species decrease and ornamental species increase as canyons age (see Alberts et al., unpubl. for details). Native species regression line solid, ●;  $y = 34 - 0.117x$ . Ornamental species regression line dashed, ◆;  $y = 6.23 + 0.088x$ . From Alberts et al. (unpubl.).

*Isolation (distance).* With some very minor exceptions, isolation effects were absent. The only possible exceptions are the rodents, for which a slight effect of distance may be present (Bolger et al., unpubl.). The number of native chaparral birds, rodents, and flowering plants that persist in the canyons is not explained, even partially, by the distance between canyons or the distance to the nearest large, unfragmented expanse of scrub habitat. This led us to conclude that the species we studied in the three taxa become virtually isolated once fragmentation has occurred. Apparently, the urban barriers, including highways, streets, and structures impose a very high degree of isolation. This result has profound implications for metapopulation dynamics of species persisting in artificially fragmented landscapes.

*Total area.* Total area refers to the total (original) size of the remnant (canyon) as seen on a map or aerial photo; this includes parts of canyons that are presently highly disturbed, and dominated by alien plant species (Alberts et al., unpubl.) or converted to gardens and recreational uses. The remnants range in total area from 0.4 ha to 103 ha. In some canyons, most of the area is no longer covered by the original vegetation, and hence is not used by many of the animals for breeding, shelter, or foraging. When total area (or its log transform) was included along with habitat area (see below) in multivariate statistical studies, it did not explain a significant amount of the variation in species diversity for any of the taxa. This result suggests that the organisms we studied do not use the disturbed parts of the habitat.

*Habitat area.* Habitat area (CHAP) in the remnants ranges from 0.25 to 68 ha. CHAP is the variable that accounts for most of the variation in species richness for all three taxa. The reasons for this are well understood (e.g., Soulé and Simberloff 1986) and include the positive associations between population size and area and habitat or resource diversity. In other words, the larger the area, the higher the abundances of the species of interest, and the greater the variety of "microhabitats" contained in the remnant. Persistence time is expected to increase in proportion to population size as discussed below.

*Age.* AGE is the number of years since the remnant became isolated. Our studies differ from most other island biogeographic analyses because (1) we were able to determine with about 5% accuracy the date of isolation, and (2) fragment ages spanned almost two orders of magnitude (from 2 to 86 yr). AGE or lnAGE account for a large and significant amount of the variation in the number of surviving species in the canyons for each of the three groups (Fig. 1, Table 2). This is true even after removing statistically the effect of habitat loss since isolation. We interpret this result as additional evidence for the extinction hypothesis, namely that most of the remnants had more species at the moment of isolation than when censused. An alternative hypothesis, namely that many canyons were quite depauperate at the time of isolation, and that the age effect is an artefact, is discounted by results of the control studies in "mainland" habitat discussed above (Bolger et al. 1991). The detection of age effects requires coincident time scales; i.e., the time scale of remnant ages must be similar to the time scale of extinction dynamics, as it is for all three taxa in this study.

*Interspecific interactions.* Extinction is usually the result of interactions between deterministic processes such as predation, and stochastic events: demographic, genetic,

Table 2. Summary of multiple regression results showing the similarity of response to biogeographic factors affecting three taxa of chaparral-inhabiting species. See text for references.

	$\beta$ -coefficient	t-value	Probability
		Native plants	
ln CHAP	.701	5.39	.0001
Age (yr)	-.338	2.51	.0207
Isolation	.103	0.73	.4715
		CR birds	
ln CHAP	1.15	8.69	.0001
Age (yr)	-.23	2.31	.02
Isolation	-.0003	1.24	.22
Fox/Coy	.897	3.66	.0009
		Rodents	
ln CHAP	1.45	7.90	.0001
Age (yr)	-.072	2.36	.036
Isolation	.03	0.09	.929

and environmental (Gilpin and Soulé 1986). Is there any evidence that deterministic interspecific interactions play a role in the disappearance of species from the canyon remnants? As indicated in Table 2, the data hint at some significant interspecific interactions. We hasten to add, however, that our methodology was not designed to study the effects of predation, competition, mutualism or disease.

For birds, the distribution of the large canids in the system (grey fox, *Urocyon cinereoargenteus* and coyote, *Canis latrans*) appears to account for a small but significant amount of the variation in numbers of surviving chaparral-requiring bird species (Soulé et al. 1988), but the effects of these two predators appear to be in opposition. The presence of foxes is associated with less persistence; the presence of coyotes with more. Coyotes are known to vigorously pursue and kill foxes (Katherine Ralls pers. comm., Korschgen 1957). They also prey on other mesopredators, including opossums, raccoons, skunks, and domestic cats, which frequently hunt birds and rodents in canyons. Our results suggest that the persistence of birds is benefitted by the presence of coyotes and the absence of foxes. We speculated (Soulé et al. 1988) that the absence of coyotes could lead to a numerical response in the populations of the carnivores and omnivores that are preyed on by coyotes – a phenomenon we referred to as mesopredator release. The absence of coyotes from a remnant is likely, therefore, to lead indirectly to higher predation rates on smaller prey species, including birds, rodents, insects, reptiles and amphibians.

There is no “coyote effect” evident for small mammals. Coyotes often prey on rabbits and rodents, so a beneficial effect of coyote presence on small mammals is unlikely. However, the number of canyons available for the analysis of these predator effects was smaller for mammals than for birds, so the chance of detection was less.

Preliminary multiple regression results using all remnants for which rodent data were available suggested a negative effect of the introduced murine rodents *Mus musculus* and *Rattus rattus* on the persistence of native rodents. This effect is probably an artefact caused by including too many remnants lacking any native rodents; the apparent interaction disappears statistically when the analysis is restricted to subsets of the remnants which are either younger than 35 years (15 remnants, 10 with at least one species of native rodent) or which still retain at least 49% natural cover (15 remnants, 11 with at least one species of native rodent). Only twelve remnants out of the complete set of 25 had native rodents.

The two introduced species appear to respond in an opposite fashion to patch size: *M. musculus* attains a generally high level of incidence in all fragment size classes, higher than any of the native rodents, and like the natives its incidence increases with increasing area; *R. rattus*, on the other hand, has moderate incidence in the smaller size classes, but its incidence drops to zero in

the largest size class ( $p = 0.043$ , hypergeometric). The trend is opposite to that of the native species.

A few of the invasive, exotic plants could be contributing to the extinction of native plants. The South African ice plant, *Carpobrotus edulis*, for example, overgrows native vegetation in some canyons. The negative effects of iceplant can be especially severe in recently burned areas (Zedler and Scheid 1988) and in sand dunes in central, coastal California. In addition, two genera of introduced trees, *Schinus* and *Eucalyptus*, are likely candidates for competitive effects by shading and allelopathy (Alberts et al., unpubl.).

**Turnover.** It is likely that some of the species that have disappeared in a given canyon may recolonize it at a later time. This could lead to the underestimation of extinction. We have observed apparent recolonizations in one remnant – the appearance of a rufous-sided towhee and the wrentit in El Mac canyon two yr after their recorded absence. Nevertheless, taken together, our results indicate that such events must be rare. If turnovers were frequent, we would have expected a distance effect. In addition, the steepness (high “z” values) of the species area curves for the birds and rodents argues against much recolonization (Bolger et al. submitted). Finally, incidence functions for most of the bird species (Soulé et al. 1988) demonstrate their absence from the smaller and older fragments. This is especially striking in light of the occurrence of most of these species in very small patches in unfragmented habitat, as mentioned above. We concluded that habitat fragmentation virtually precludes recolonization by these obligate chaparral bird species.

**Different vulnerability.** This topic and the next (nested hierarchical structure) are related conceptually, but will be discussed separately. Are the species equally vulnerable to extinction, the differences in persistence between them being due to chance? For the birds and mammals, the answer is no. Most of the variation between species in vulnerability for both taxa is explained by population density. As shown, for example, in Fig. 2, the number of canyons in which a bird species persists is highly correlated with its population density in typical habitat. It would appear, therefore, that rarity increases the risk of extinction.

Some doubt about the cause and effect relationship between density and persistence is justified, however, because the less common species may have been absent at the moment of isolation. Such “original” absences would then be mis-classified as extinctions. It should be noted, though, that control plots of size 1 ha or larger had all five species. In smaller plots, only the California thrasher and rufous-sided towhee were sometimes missing. Based on the expected number of species in each plot, Bolger et al. (1991) have estimated the number of such possible mis-classifications. These results were then used as a basis for correcting downward the num-

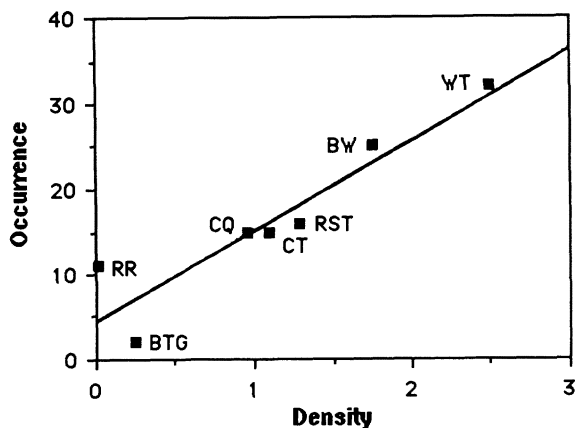


Fig. 2. Persistence of chaparral-requiring birds in habitat remnants in relation to abundance in San Diego County, California. The number of canyons in which a bird species persists is highly correlated with its population density (in pairs per ha) in typical habitat. RR = roadrunner; BTG = black-tailed gnatcatcher; CQ = California quail; CT = California thrasher; RST = rufous-sided towhee; BW = Bewick's wren; WT = wrenit. Regression equation:  $y = 4.71 + 10.5x$ . From Soulé et al. (1988).

ber of species that originally occurred in these remnants. The overall results were changed very little by this correction. Similar results were obtained with the rodent data. Small control plots contain most of the rodent species.

Another factor, body size, contributes to vulnerability as well, at least for the chaparral-requiring birds. Large-bodied birds apparently persist longer than smaller species, after correcting statistically for the variation in population density among species. Together, density and body size explained 95% of the variation in persistence (Soulé et al. 1988).

For plants, no formal analysis of differential extinction vulnerability has been performed, but the more deeply rooted species such as laurel sumac, *Malosma laurina*, lemonade berry, *Rhus integrifolia*, toyon, *Heteromeles arbutifolia*, and chamise, *Adenostoma fasciculatum* apparently persist longer than shallow-rooted species (Alberts et al., unpubl.). The persistence of deep-rooted perennials may be due to their ability to sprout from the root crown after a fire.

*Hierarchically nested subgroups.* The distributions of birds and mammals in canyons (the plant data are as yet unanalyzed) reveals an extreme degree of non-randomness (Bolger et al. 1991, Bolger et al., unpubl.). For example, the presence of the road-runner or California valley quail in a remnant is highly predictive of the presence in the same remnant of all the other CR species. On the other hand, the presence of the California Thrasher only predicts the presence of the rufous-sided towhee, Bewick's wren, and the wrenit, not the road-runner and the quail. This nestedness suggests that ex-

tinctions occur in a predictable sequence. As described in the previous section, we believe that this gradient in extinction vulnerability is explained largely by the effect of population density on the probability of persistence. The implications for conservation of differential vulnerability and the hierarchical distribution of fragment occupation are discussed below.

## Synthesis

*Secondary fragmentation.* Disturbance and fragmentation in the coastal scrub habitats of San Diego County are not singular events; rather they are ongoing processes leading eventually to the complete replacement of the native vegetation and most of the fauna by exotic plants and a combination of generalist native and exotic animals. The primary fragmenting event is the construction of a road, with or without associated housing developments. Later, the habitat remnants may be subdivided by additional development. But these isolated events are just the beginning. Trails soon appear, and homeless people and neighborhood children remove the plant cover during the creation of camping sites for "forts". The edges of the remnant are nibbled by expanding gardens and back yards. These incursions are essentially irreversible in scrub and chaparral-type associations because the vegetation is brittle and very slow to re-establish following removal. The proportion of chaparral habitat in a fragment decreases over time (Fig. 3), and before long no point in the remnant is more than a meter or two from some kind of artificial opening. These internal disturbances represent a form of secondary fragmentation.

These cumulative mechanical insults to the habitat provide visibility and access to predators of all kinds, including scrub jays, owls, hawks, foxes, opossums,

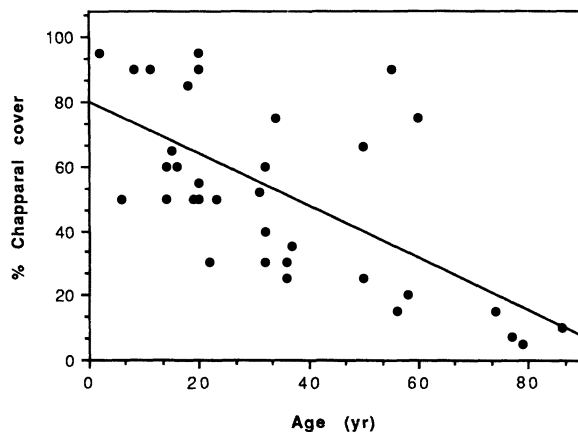


Fig. 3. The change over time in the proportion of native plant cover in isolated habitat remnants in San Diego County, California. Regression equation:  $y = 80.1 - 0.81x$ . From Soulé et al. (1988).

skunks, domestic cats and boys. Domestic cats are particularly effective as predators, we believe, because they are recreational hunters whose numbers are maintained far above carrying capacity by nutritional and other subsidies (Erlinge et al. 1983). Together with the released mesopredators, cats contribute to the inexorable annihilation of much of the small fauna (Erlinge et al. 1983, Ebenhard 1988, Murphy 1988, Usher 1988). There is no evidence, however, that nest predation is proportional to internal habitat fragmentation in this system (Langer et al., in press).

Disturbance dynamics is altered by human beings in other ways. This habitat, like those in other Mediterranean regions, is a fire-climax association. The diversity of plant species depends to some extent on the frequency and intensity of these fires (Forman and Boerner 1981, Westman et al. 1981, Bazzaz 1983, Bond et al. 1988). Humans often change fire frequency and intensity by accident and by active management.

*Deterministic vs stochastic factors in extinction.* Gilpin and Soulé (1986) have emphasized the positive feedback relations between deterministic and stochastic influences on isolated populations, i.e., as populations are reduced in size by deterministic factors such as habitat loss or predation, they become increasingly vulnerable to random environmental, genetic and demographic accidents. Although we are unable to distinguish the deterministic effects (e.g., habitat destruction, presence of particular predators) from random events (births and deaths, variation in sex ratio and weather), it appears that both categories have influenced species persistence in the fragments. Stochastic events may have been important in the small remnants. Canyon remnants in the city of San Diego such as Baja, Juan, 54th St. and El Mac all retain at least 50% chaparral cover and yet do not support populations of native rodents. The populations which these fragments once supported were evidently too small to withstand normal environmental and demographic variability.

*Genetics.* Table 1 does not mention genetic effects because they were not investigated. We therefore have no evidence for the role of inbreeding and genetic drift in these putative extinctions. The deleterious effects of inbreeding cannot be ruled out, however. Some of the bird and mammal populations have persisted for many generations at sizes of less than 25 or so. It is generally assumed (Lande and Barrowclough 1987, Harris and Allendorf 1989) that effective population sizes are much less than census sizes (often 25% or less), and that the loss of heterozygosity and the fixation of deleterious genes will occur much faster than might be expected based on absolute numbers of individuals.

The current fashion in conservation biology is to dismiss the importance of genetics in population viability analysis and to emphasize the roles of demographic and environmental stochasticity (Ehrlich 1983, Schwartz et

al. 1986, Dawson et al. 1987, Lande 1988; see also Pimm et al. 1988, Pimm et al. 1989) on the grounds that their joint effects on population persistence (Belovsky 1987, Goodman 1987) will swamp any impact that inbreeding and loss of genetic fitness might have. Notwithstanding the importance of these non-genetic forces, we favor an approach which looks at the interaction of these phenomena (Gilpin and Soulé 1986, Soulé 1987: chapter 10). We disagree with those who would dismiss genetics (Lande 1988) on the grounds that the life expectancy of small populations is too short to permit inbreeding effects to significantly affect demographic vital rates.

*Some implications of nestedness.* Several factors can account for nestedness. As pointed out by Patterson (1984) and Patterson and Atmar (1986), nestedness within the array of species by locality in a relaxing system is expected where (1) vulnerability is not uniformly distributed among the species, and (2) where colonization of empty sites is relatively rare. Simberloff and Abele (1976) also list (3) differential dispersal ability as a possibility; a fourth factor might be the nested distribution of habitats (Cody 1983). The first three of these conditions apply to most taxa of conservation concern. It is the exception, we think, that species within a taxon or ecological assemblage would all have the same probability of persisting, say, for 200 yr in a given patch or reserve. Differences among species in body size, fecundity, and in susceptibility to predation and weather should produce vast differences in their growth rates and persistence times. The means and variances of intrinsic growth rates can differ by orders of magnitude among species, and these are believed to determine survival times of populations (Leigh 1981, Belovsky 1987, Goodman 1987). The same degree of heterogeneity applies to dispersal capacities and colonization potentials. These manifestations of biological variability will produce systematic and predictable differences in persistence probabilities among species within habitat remnants.

Is nestedness likely to be apparent in relaxing systems that comprise much larger remnants and reserves? Perhaps, but the larger the areas, the smaller the proportion of species that are likely to be below the threshold of long-term viability (e.g., 5000 individuals). Europe and North America, for example, had few if any native species with fewer than 5000 individuals before these continents were invaded by stone age human beings.

The smaller the fragment, the greater the proportion of species that will fall below such a threshold. In our canyons, for instance, only the most common species, such as soil and litter organisms, some insects and the most abundant plants such as black sage, *Salvia mellifera*, California buckwheat, *Eriogonum fasciculatum*, and California sagebrush, *Artemisia californica* normally occur in such large numbers. At the other end of the abundance spectrum are species (such as hawks and

eagles, mountain lion, *Felis concolor*) that we didn't even consider censusing because their home ranges are many times greater than the size of our largest canyon.

*Vagility and metapopulation structure.* Nestedness should increase where species are unable to re-colonize vacant patches. The capacity to re-colonize can be crippled by fragmentation. The plant and animal species in our system are clearly capable of dispersing in undisturbed vegetation. Somewhat paradoxically, though, we noted the virtual inability of these animal taxa to recolonize canyon fragments. Many of them appear to be very reluctant to leave cover.

Ehrlich and his coworkers (Ehrlich 1983) have shown that butterflies like *Euphydryas editha* can persist in a region as a metapopulation, even in the face of extirpation of patch populations. Nevertheless, metapopulation systems may be exquisitely sensitive to changes in rates of immigration and colonization (Gilpin 1987). The sudden collapse of a system can occur when immigration rates fall below a certain threshold. Unless we know, then, how a species responds to barriers such as roads, clearcuts, parking lots, buildings, and the presence of domesticated animals, we cannot safely generalize the dynamics of pre-disturbance to post-disturbance landscape mosaics. *Euphydryas editha*, for example, might be less likely to recolonize a patch that is isolated by 100 m of housing subdivision than 100 m of chaparral. Metapopulation models based on pre-fragmentation dispersal statistics could seriously overestimate persistence times.

*Relative vulnerability of chaparral birds and mammals.* In order to compare the relative vulnerability of chaparral birds and rodents to fragmentation, we must use equivalent species pools. We have selected the five most abundant bird species and the five most abundant rodent species. In the 25 fragments which were surveyed both for birds and rodents there were on average  $2.64 (\pm 1.88)$  bird species and  $1.71 (\pm 1.94)$  rodent species, a significant difference (paired t-test,  $p < 0.001$ ). Apparently the rodent populations are more vulnerable to extinction. This is also indicated by the fact that 30 of 36 fragments supported at least one chaparral bird population, but less than half, 12 of 25, supported rodent populations.

What is the reason for greater vulnerability on the part of the rodents? It is likely that rodent population densities are higher than those of the bird species, so initial populations of the rodents would have been larger (McCloskey 1972, Cody 1973, Meserve 1975). But birds, because of their greater mobility and arboreality might be less vulnerable to predation than rodents. Also, some of our species have been shown to undergo pronounced seasonal fluctuations (McCloskey 1972). These fluctuations may predispose populations to extinction (Krebs et al. 1973).

## Conclusions

Ecological research, particularly the disciplines of island biogeography (MacArthur and Wilson 1963, 1967) and population biology (Ehrlich and Holm 1962), is providing the foundation for the management of wildlife and maintenance of ecosystem values in areas subject to habitat fragmentation. The results of the San Diego case study demonstrate most of the principles established by similar research throughout the world (Brown 1971, Emlen 1974, Diamond 1975, Schoener 1976, Soulé et al. 1979, Terborgh and Winter 1980, Karr 1982, Brittingham and Temple 1983, Blake and Karr 1984, Howe 1984, Lynch and Whigham 1984, Patterson 1984, Lovejoy et al. 1986, Wilcove et al. 1986, Diamond et al. 1987, Newmark 1987, Terborgh 1989). The factors that make the San Diego study particularly illustrative are (1) its urban setting, (2) the availability of information on the "ages" of the fragments, (3) the small size of the habitat isolates which contributed to the rapidity of extinctions, (4) species that are homogeneous with respect to habitat requirements and (5) which appear ineffective in dispersing across artificial gaps.

We have learned that habitat remnants in the 10 to 100 ha range do not retain their complement of native vertebrate species for longer than a few decades, on average, in this arid habitat. Only the most abundant chaparral-dependent animal species survive for very long, and even most of these are doomed within a century. There is evidence that large predators retard the biotic collapse of these remnants by controlling populations of smaller, semi-commensal predators, including domestic cats. Plant species also disappear, in large part because of chronic and cumulative habitat disturbance and perhaps also because of changes in the frequency of fires.

Contrary, therefore, to claims that we already have enough biological knowledge and that conservation biologists should now turn their attention to the social and economic contexts of conservation, it is apparent that much more needs to be learned about managing habitat remnants (Soulé and Kohm 1989). Ecologists should follow the paths blazed by P. R. Ehrlich and E. O. Wilson by dedicating a major fraction of their efforts to mission oriented basic research in conservation biology.

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