

Variation in top-down control of avian reproductive success across a fragmentation gradient

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Understanding mechanisms that inhibit population persistence in fragmentation-sensitive species is a key to conservation and management. It has become clear that species vary in their sensitivity to habitat fragmentation caused by urbanization and other land uses. We studied variation in avian reproductive success in coastal sage scrub habitat across a fragmentation gradient (interior of large habitat blocks (> 2300 ha) → edge of large habitat blocks → large habitat fragments (37–80 ha) → small habitat fragments (5–17 ha)) in urban southwestern California. We focused on four species of birds: the shrub-nesting wren (*Chamaea fasciata*) and California towhee (*Pipilo crissalis*) and the ground-nesting spotted towhee (*P. maculatus*) and rufous-crowned sparrow (*Aimophila ruficeps*). Snake abundance was the best predictor of nest failure in the ground-nesting species, whereas abundance of avian predators (Corvidae, Mimidae) was associated with nest failure of the wren and a combination of snake and avian predator abundance was correlated with nest failure of the California towhee. Avian nest predator abundance increased across the fragmentation gradient; by contrast, snake abundance decreased across this gradient. As a result, top-down control of reproductive success in populations of the spotted towhee and rufous-crowned sparrow was largely absent in habitat fragments. These two species enjoyed much higher nest success on fragments yet, paradoxically, both species are sensitive to fragmentation whereas the shrub-nesting species are not. Our findings suggest that another process – perhaps differential survivorship or dispersal – yields reduced abundance of ground-nesting species in habitat fragments. Studies of top-down control and trophic cascades in fragmented landscapes should reflect that the strength of top-down forces across a landscape varies with characteristics of predator and prey and their autecological responses to ecological gradients.

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Habitat fragmentation and attendant edge effects are among the principal threats to persistence of biological diversity (Soulé 1991). Many plant and animal species are sensitive to fragmentation and edges (Wilcove 1985, Soulé et al. 1992, Bolger et al. 1997a, b, Suarez et al. 1998, Burke and Nol 2000); i.e. their abundance declines with fragment size and proximity to an edge. However, ecological mechanisms generating these patterns are often obscure (Hanski 1994, Harrison and Bruna 1999).

Birds have been the focus of numerous studies of fragmentation in the temperate zone. The chief determi-

nant of reproductive success in birds is the rate of nest failure (Ricklefs 1969), and the major cause of nest failure is predation (Lack 1954, Nice 1957, Ricklefs 1969). Consequently, most mechanistic studies of the effect of fragmentation on birds have focused on the top-down effects of nest predation, brood parasitism, and mesopredator release (Robinson et al. 1995, Crooks and Soulé 1999). Research in forests fragmented by agricultural development and timber harvesting in eastern and midwestern North America fueled the “top-down paradigm” in fragmentation studies (Bolger, in

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press). Top-down effects are striking in those regions: nest predation and brood parasitism increase with proximity to forest edge and the degree of fragmentation in the landscape (Robinson et al. 1995, Donovan et al. 1997), perhaps because of increases along edges of avian and mammalian nest predators and of the brown-headed cowbird (*Molothrus ater*), a brood parasite. Increased abundance of nest predators and parasites may be a response to elevated densities of nesting birds – themselves responding to anthropogenic changes in habitat structure (Gates and Gysel 1978) – or to resource subsidies associated with human land use (Wilcove 1985, Andrén 1992, Robinson and Wilcove 1994).

Conservation biology textbooks (Primack 1993, Cox 1997, Meffe and Carroll 1997) have featured these studies prominently, creating the impression that a general relationship exists between nest predator abundance and fragmentation. Nonetheless, the generality of this relationship is questionable (Tewksbury et al. 1998, Morrison and Bolger 2002). Furthermore, whether nest predation increases near habitat edges is contentious (Paton 1994, Lahti 2001). Although numerous studies have reported a significant edge effect, more have failed to detect an effect (Lahti 2001), even in species sensitive to habitat fragmentation (Morrison and Bolger 2002). The degree of fragmentation at the scale of the landscape appears to be important: edge effects are more often detected in regions with high landscape fragmentation (Lahti 2001).

Predation risk varies with position in the landscape (Wiens 1985, Martin 1993, Hunter et al. 1997). For instance, native predators often decrease from undisturbed sites to edges to fragments, but non-native predators and human commensals generally increase across this gradient (Crooks and Soulé 1999, Gering and Blair 1999, Crooks 2002). Conflicting results of studies of edge and fragmentation effects on predation rates (Paton 1994, Lahti 2001) may be the result of heterogeneity among predator and prey. The predation risk experienced by a bird species at a particular point on a fragmentation gradient depends on the vulnerability of that species to the suite of nest predators in the landscape and the responses of predators to the fragmentation gradient. Bird species vary in their vulnerability to different predators depending on nest placement and egg size (Ricklefs 1989, Martin 1993, Schmidt 1999). Shrub nests are more vulnerable to avian predators, whereas ground nests are more vulnerable to snake and mammalian predators (Martin 1987, Yahner and Cypher 1987, Nour et al. 1993, Söderström et al. 1998). Moreover, the three chief predator types – birds, mammals, and snakes – may respond differently to fragmentation. Research on variation in predator abundance along habitat edges and in habitat fragments has focused on avian and mammalian predators. Many studies have shown that avian nest predators, especially

crows and jays (Corvidae), increase along urban habitat edges (Wilcove 1985, Andrén 1992, Danielson et al. 1997). Effects of fragmentation are less clear, though it appears that avian diversity on large fragments is similar to that on edges but is lower on small fragments (McDonnell et al. 1993). Studies on the effects of edges and fragmentation on abundance of small mammals have shown either a strong effect (Bolger et al. 1997a, Schneider 2001) or little to no effect (Heske 1995, Laakkonen et al. 2001). Studies of larger mammals have reported mesopredator release resulting from fragmentation (Crooks and Soulé 1999, Terborgh et al. 1999).

In contrast to work on endothermic vertebrates, comparatively little attention has been devoted to the effects of edges and habitat fragmentation on snake populations, even though there is good evidence that, at least in open habitats, snakes are a principal consumer of bird eggs and nestlings, particularly of species that nest on the ground (Thompson et al. 1999, Morrison and Bolger 2002). The few studies that have been published suggest that snakes are not susceptible to edge effects (Sullivan 2000) but they are to habitat fragmentation (Hager 1998).

Patterns of abundance of many bird species occurring in coastal sage scrub – a Mediterranean habitat of coastal southern California and Baja California – suggest that they are sensitive to fragmentation (Soulé et al. 1988, Bolger et al. 1997b, Bolger, in press). In this system, avian species richness increases with fragment area and decreases with fragment age (Soulé et al. 1988) and local extinctions exceed colonizations across the urban matrix (Crooks et al. 2001). Crooks and Soulé (1999) demonstrated mesopredator release in habitat fragments: the abundance of coyotes (*Canis latrans*) decreases with fragment area, but the abundance and activity of mesocarnivores, particularly the gray fox (*Urocyon cinereoargenteus*), Virginia opossum (*Didelphis virginianus*), and domestic cat (*Felis sylvestriscatus*), increase concomitantly. These authors hypothesized that an increase in the abundance of mesopredators leads to a trophic cascade wherein the abundance of birds (primary consumers in the ecosystem) is depressed. Under this scenario mesopredator release is responsible, at least in part, for the sensitivity of birds to fragmentation. However, Morrison and Bolger (2002) found little evidence for a role of predation in generating the area-sensitive pattern of the rufous-crowned sparrow (*Aimophila ruficeps*). Survival and reproduction of this species did not differ between sites at the interior of large reserves and those at edges of these reserves, presumably because the abundance of the sparrow's chief nest predator, the common kingsnake (*Lampropeltis getulus*), did not differ between interior and edge (Morrison and Bolger 2002).

We present results from a study of ecological mechanisms influencing avian reproductive success across a fragmentation gradient in coastal sage scrub habitat in

and around urbanized San Diego, California. We monitored reproductive success of four species of birds and quantified abundance of potential nest predators, particularly snakes and members of the avian families Corvidae (crows and jays) and Mimidae (thrashers and mockingbirds). We tested predictions that nest predation would increase as fragmentation and edge increased – a prediction of the mesopredator release hypothesis – and that ground-nesting species would be vulnerable to different predators than shrub-nesting ones.

Materials and methods

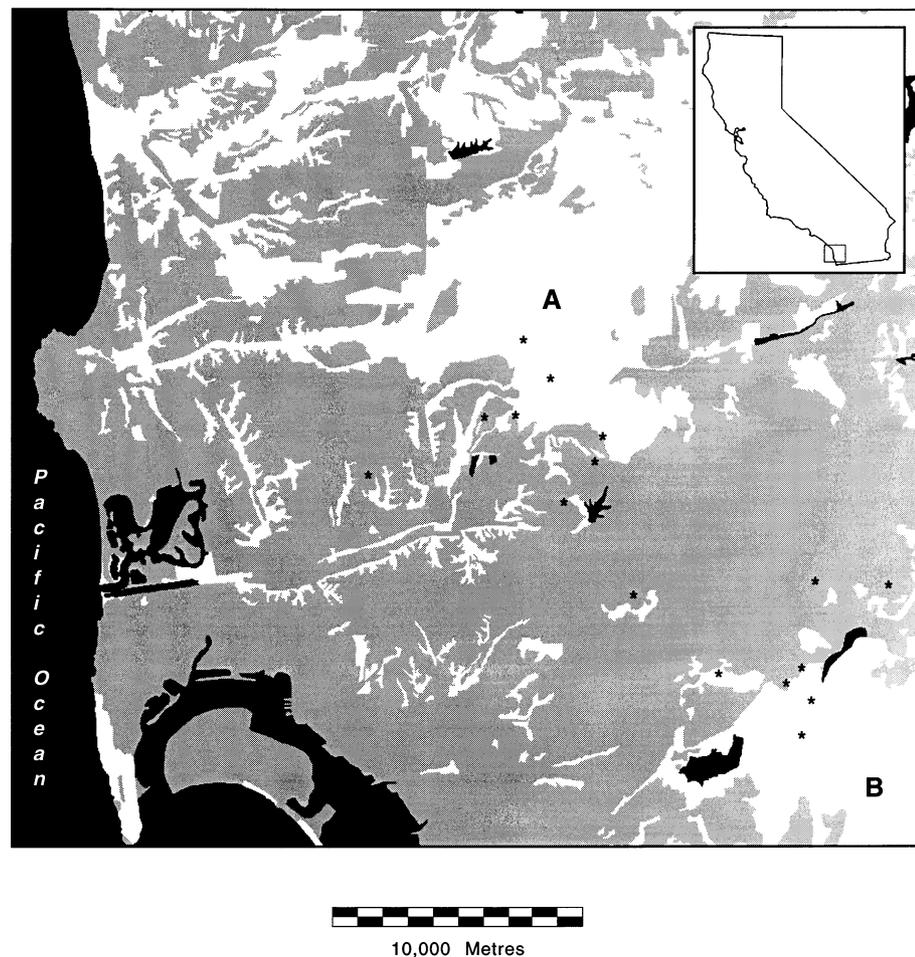
Study area

Plots were located in and around two large (> 2300 ha) reserves in southwestern San Diego County, California: Mission Trails Regional Park and the Otay-Sweetwater Unit of San Diego National Wildlife Refuge. We established four study plots on each reserve, two each in their interior and along their edge. We also established

one plot each on two relatively large (37–80 ha) and two small (5–17 ha) habitat fragments near each reserve. There were thus a total of 16 study plots, four each for interior, edge, large fragment, and small fragment (Fig. 1). Interior plots were located within each reserve, at least 600 m from the nearest urban edge. Edge plots were located along the urban edge of the reserves; plots on large and small fragments were also aligned with the urban edge. All plots were located 12–28 km from the shore of the Pacific Ocean. Along the gradient from interior to edge to large fragment to small fragment a number of measures of fragmentation and urban exposure change. The ratio of urban edge to habitat area increased across the fragmentation gradient, as did the ratio of urban land cover to natural habitat in the immediate vicinity of the plots; the amount of contiguous natural habitat declines along the gradient.

Reserves and surrounding fragments support extensive coastal sage scrub habitat of similar structure and species composition (Morrison and Bolger 2002, Bolger and Patten, unpubl.), dominated by the drought-

Fig. 1. Map of the study area in southwestern San Diego County, California, showing location on in and around Mission Trails Regional Park (A) and the Otay-Sweetwater Unit of San Diego National Wildlife Refuge (B). Shaded areas are urbanized or developed, unshaded areas are undeveloped reserves or fragments.



deciduous California sagebrush (*Artemisia californica*) and California buckwheat (*Eriogonum fasciculatum*) and by the evergreen laurel sumac (*Malosma laurina*). Coastal sage scrub is a drought-deciduous shrub habitat notable for its restricted range and its high diversity of endemic plants and animals (Atwood and Noss 1994). Approximately 85% of this habitat has been converted to other land uses, most often suburban housing; the remainder is highly fragmented and exposed to urban edge. The region's climate is Mediterranean, characterized by winter rain and summer drought (Patten and Rotenberry 1999).

The urban matrix surrounding reserves and fragments was predominantly medium-density (6–18 units/ha), single-family housing; schools or public utility facilities also bordered some plots. Without exception vegetation beyond the plot edge featured a substantial increase in non-native species, especially exotic trees, shrubs, and herbs. Increased watering of yards and gardens created more mesic conditions along the edges, allowing some ornamental plants, particularly *Eucalyptus* and *Carpobrotus*, to invade the margins of the coastal sage scrub.

Field data

We studied four species of birds that are wholly or largely dependent on coastal sage scrub as breeding habitat: the wrentit (*Chamaea fasciata*), spotted towhee (*Pipilo maculatus*), California towhee (*P. crissalis*), and rufous-crowned sparrow (*Aimophila ruficeps*). The wrentit (exclusively) and California towhee (typically) nest in shrubs, whereas the spotted towhee and rufous-crowned sparrow typically nest on the ground. With one exception – a spotted towhee nest 30 cm above the ground in a low shrub – all nests that we located ($n = 266$) fit this pattern.

Our field work focused on locating every nest on one 2–4 ha plot per site. We conducted nest searches daily during the breeding season (22 March to 16 June 2001, 13 March to 4 June 2002) in the morning and late afternoon. We recorded clutch size, hatching success, and fledging success for all nests, each of which was monitored at 2–3 d intervals. Data recorded for each nest included its outcome (success or failure), placement (height above ground [cm]; amount of vegetation above ground [cm]; shortest distance from shrub edge to nest [cm]; approximate distance to urban edge [m]), visibility (% of nest visible at 1 m from above nest; % visible at 1 m from each cardinal direction), and surrounding vegetation (% total shrub cover, in 10% increments).

We recorded every snake encountered during our extensive nest searching efforts ($n = 587$ surveys in 2001, $n = 492$ surveys in 2002). As noted above, habitat is similar on the sixteen plots (Bolger and Patten, unpubl.), so variation in habitat complexity or physiog-

nomomy is unlikely to have influenced detection of snakes. Also, across all sites, Patten's 6–23 surveys/plot yielded counts highly correlated with those of the whole crew ($r = 0.80$), so counts were not biased by plot. Thus, our counts likely underestimated total snake abundance, but in the same way on every plot, allowing us to compare among treatments with a good deal of confidence. Patten quantified avian predators through a series of area-search censuses (Bibby et al. 2000), limited to 30 min and an area of 2 ha/plot. Most studies of avian nest predators have focused solely on corvids (Luginbuhl et al. 2001), but many species in the family Mimidae (mockingbirds and thrashers) are also proficient nest predators (Snyder and Taapken 1978, Sheppard 1996, Spooner et al. 1996, Cavitt and Haas 2000). We therefore recorded numbers of the western scrub-jay (*Aphelocoma californica*), American crow (*Corvus brachyrhynchos*), common raven (*C. corax*), northern mockingbird (*Mimus polyglottos*), and California thrasher (*Toxostoma redivivum*).

We did not quantify mammalian mesopredators although, as reported by Crook and Soulé (1999), we assume that mesocarnivores were most abundant in small fragments. Our fragments were similar in size and location to Crooks and Soulé's (1999), and our observations of coyotes matched theirs: coyote abundance declined across our fragmentation gradient from interior (0.09 ± 0.05 /survey), to edge and large fragment (both 0.05 ± 0.04 /survey) and small fragment (0.03 ± 0.02 /survey).

We also did not quantify another group of potential nest predators, the *Peromyscus* mice, however, evidence suggests that only one of our focal species is vulnerable to these predators. Eggs of the towhees (24×18 mm) and sparrow (20×15 mm) are probably too large for mice (± 10 mm gape) to handle (Roper 1992, DeGraaf and Maier 1996, cf. Blight et al. 1999), but those of the wrentit (18×10 mm) may be small enough. Indeed, two wrentit nests depredated in 2001 retained one egg each with puncture marks that appeared to be from a small rodent (Patten, pers. obs.). Thus, *Peromyscus* mice may contribute to nest failure rates, at least for the wrentit.

Analyses

We calculated daily survivorship probability of eggs and nestlings (Mayfield 1975) and, for as many nests as possible, determined incubation and nestling periods. Fates were uncertain for 12% (31 of 252) of the nests. Accordingly, when calculating Mayfield indices, we employed the Last Active-B method described by Manolis et al. (2000). In essence, this method uses the midpoint between the last date a nest was active and the first date it was inactive for nests with the fate known and the last date a nest was active for nests with the fate

unknown. We avoided problems of autocorrelation – and thus potential pseudoreplication – by (1) using means for each pair of birds across all of their nests rather than using data from individual nests (i.e. n = pairs of birds per plot) and (2) from these means calculating overall plot means per species for all variables (e.g. daily survival probability at the egg stage, clutch size, hatching rate, etc.). Our sample size for most tests, then, was the number of plots ($n = 16$), not the total number of nests ($n = 252$). So that predator data was comparable to nest survivorship, we transformed numbers of snakes and avian predators into encounter probabilities. For the former we calculated an encounter rate as total snakes per 24 hours of surveys. For the latter we calculated the number of days a species was encountered per total survey days. We could not incorporate 2002 nest data because of a major reproductive collapse of the breeding bird community, coincident with the driest year since records began in 1850 (Bolger and Patten, in prep.); we located only nine nests all season.

For analyses of variance, we analyzed data by treatment (interior, edge, large fragment, small fragment). We did not block by “region” (Mission Trails vs Sweetwater) because vegetation was similar across all sites, in pilot analyses there was no effect of region on encounter rates of snakes or avian predators (ANOVAs) and no effect of region on overall survival probability of nests (MANOVA), and the Mission Trails and Sweetwater sites nearest each other are only < 4 km apart. We examined patterns in nest success with correlation analyses (point biserial or ϕ) and logistic regression. We used linear regression to examine relationships between predator abundance and daily nest survivorship probabilities. Degrees of freedom differ, as the spotted towhee and rufous-crowned sparrow are absent from some fragments (see below). To determine which nest predators had the greatest impact, we regressed, in turn, reproductive success of the wren tit, California towhee, and ground nesters against all possible combinations of predator abundances, then compared resultant models using an Akaike Information Criterion (AIC) modified for use with residual sums of squares from linear regression analyses (Hongzhi 1989). We performed statistical analyses either by hand or with the aid of SPSS 9.0.

Results

Nest success

Across all four species, nest success was not related to proximity to an urban edge (“interior” nests excluded; logistic regression: $\chi^2 = 1.53$, n.s., $n = 176$) or correlated with general nest placement (shrub vs ground; $\phi = 0.03$, ns). Similarly, nest success was not associated with

height of the nest above the ground, distance in from the edge of the nest shrub, amount of shrub extending above the nest, or percentage of the nest visible. Success was significantly associated with total shrub cover around the nest (logistic regression: $\chi^2 = 7.45$, $P < 0.01$), although shrub cover accounted for a very low percentage of variance in nest success (Cox-Snell $R^2 = 0.06$).

Daily survival probabilities differed significantly across treatments for the spotted towhee (ANOVA: $F_{3,10} = 4.09$, $P < 0.05$) and California towhee ($F_{3,12} = 3.76$, $P < 0.05$) but did not for the wren tit and rufous-crowned sparrow, the latter perhaps the result of a small sample on habitat fragments ($n = 4$ nests). Considering the two ground-nesting species in concert yields a strong trend across treatments (ANOVA: $F_{3,10} = 11.42$, $P < 0.001$), with the probability of nest success increasing asymptotically from interior plots to small fragments (Fig. 2). Daily nest survival probabilities of the wren tit and California towhee were nearly mirror images of each other, the former peaking on edges and large fragments, the latter on interior sites and small fragments (Fig. 2).

Predator abundance

We encountered 104 snakes on 587 surveys (Table 1). More than half (57) were constrictors in the family Colubridae, the chief ophidian predators of bird nests. Among the colubrids, the vast majority (> 95%) of snakes encountered were of one of three species: the common kingsnake, gopher snake (*Pituophis melanoleucus*), and California whipsnake (*Masticophis lateralis*). Through videotaping and direct observation of active nests, we determined that all three of these species depredate nests of at least the towhees and the sparrow (Morrison and Bolger 2002, Patten, pers. obs., K. J.

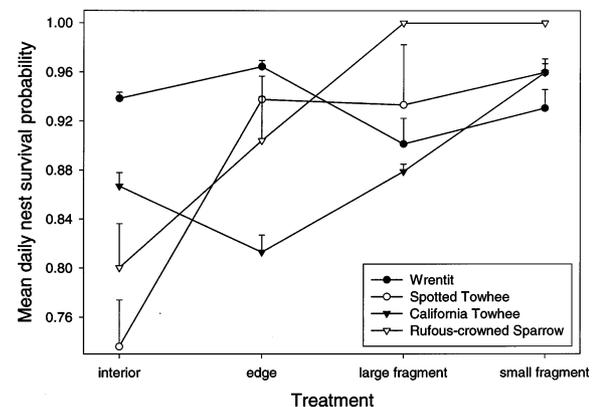


Fig. 2. Mean (\pm SE) daily (Mayfield) probabilities of nest survival for the wren tit (*Chamaea fasciata*), spotted towhee (*Pipilo maculatus*), California towhee (*P. crissalis*), and rufous-crowned sparrow (*Aimophila ruficeps*).

Table 1. Snake encounters in coastal sage scrub habitat across a landscape; see the text for definitions of the four sites types. Snakes/survey is the mean \pm SD of total snakes encountered, averaged across plots.

Site Type	Surveys	Colubridae	<i>Crotalus</i> sp.	Snakes/survey
Interior of reserve	150	25	21	0.27 \pm 0.14
Edge of reserve	143	16	12	0.16 \pm 0.03
Large fragment	148	9	12	0.12 \pm 0.09
Small fragment	146	7	2	0.04 \pm 0.07

Bronson, pers. comm.). Although rattlesnakes (Viperidae; *Crotalus* sp.) do not depredate bird nests, their abundance – as measured by our encounters with them – was significantly correlated with colubrid abundance (Kendall's $\tau = 0.382$, $P < 0.05$). An index of total snake abundance, such as snakes encountered per survey (Table 1), therefore provides an accurate gauge of nest predation risk. Encounter rates of snakes differed significantly across treatments (ANOVA: $F_{3,12} = 3.54$, $P < 0.05$), showing a monotonic and near linear decrease from interior to small fragment (Fig. 3).

Encounter probabilities of avian predators differ across treatments (MANOVA: Wilks' $\Lambda = 0.053$, $P < 0.02$) – they increase markedly from the interior of reserves through edges to large fragments (abundances are fairly equal across these two treatments), then drop slightly on small fragments.

Correspondence between nest success and predator abundance

Snake abundance was a good predictor of average daily survival probabilities for ground-nesting birds (linear regression: $R^2 = 0.42$, $F_{1,12} = 8.82$, $P = 0.02$). Rufous-crowned sparrows were nearly absent on habitat fragments (see below), reducing sample size, so the relationship with that species alone was not significant. However, nearly half of the variation in average daily

survival probabilities of spotted towhee nests was explained by snake abundance (linear regression: $R^2 = 0.45$, $F_{1,12} = 9.97$, $P < 0.005$). For ground-nesting species, snake abundance is strongly negatively associated with probability of fledging (Fig. 4), tracing a path parallel to the daily probability of nest failure (Fig. 5). Snakes accounted for over 90% of predation events of ground nests where the predator was known (Table 2).

By contrast, there was a weak relationship between snake abundance and probability of fledging for shrub-nesting species (Fig. 6). The addition of avian predators clarified the pattern: of five shrub nests with direct evidence of predator type (Table 2), three were depredated by snakes, two by birds (Cooper's hawk, *Accipiter cooperi*, and common raven). Mean daily probabilities of nest failure for the wrentit paralleled avian predator encounters (Fig. 7; $r = -0.79$, $P < 0.01$). The pattern for the California towhee was more complex, but a combination of encounter probabilities of snakes and avian predators fits the pattern ($r = -0.63$, $P < 0.01$); regression models using abundances of snakes (AIC = -0.927) and the western scrub-jay (AIC = -0.936) as predictors provided the best fits for data (all other AIC > -0.92). Underscoring results for the two shrub-nesting species, a model combining all avian nest predators provided a much better fit for data on nest failure for the wrentit (AIC = -0.539) than for the California towhee (AIC = -0.446).

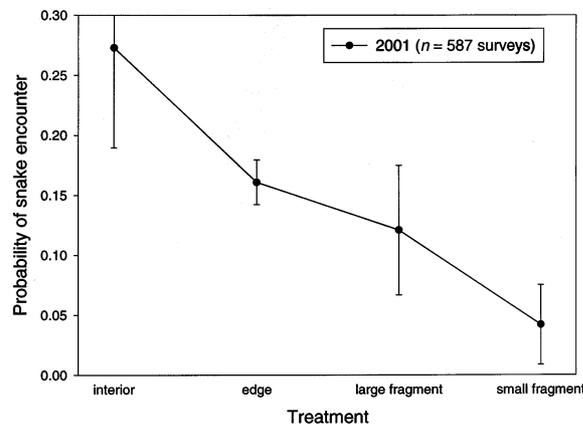


Fig. 3. Snake encounter probability (mean \pm SE) across a fragmented landscape. Potential top-down control varied at the landscape level ($n = 587$ surveys).

Discussion

Effects of fragmentation on nest success and predator abundance

We found no evidence for a general relationship between fragmentation, predator abundance, and avian nest success. Instead, fragmentation affected abundance of predators and success of nests in different ways. For example, avian nest predators tended to increase across the fragmentation gradient, being least common on interior sites and most common on habitat fragments. Snakes, by contrast, decreased steadily across the gradient (Fig. 3). It is unclear whether this decline is the result of increased predation on the snakes, changes in foraging behavior of snakes (Blouin-Demers and Weatherhead 2001), or other factors. In any event, reproductive failure of ground-nesting species, in our

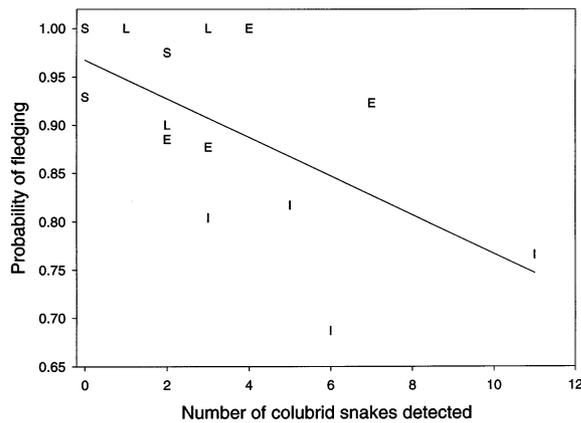


Fig. 4. Colubrid snake abundance and daily nest survivorship for ground-nesting birds, the spotted towhee (*Pipilo maculatus*; $n = 40$ nests) and rufous-crowned sparrow (*Aimophila ruficeps*; $n = 26$). Codes: I = interior, E = edge, L = large fragment, and S = small fragment. The line is from a linear regression ($y = -0.02x + 0.97$; $r = -0.60$, $P < 0.03$); i.e. the probability of fledging decreases by 2% for each additional colubrid snake detected.

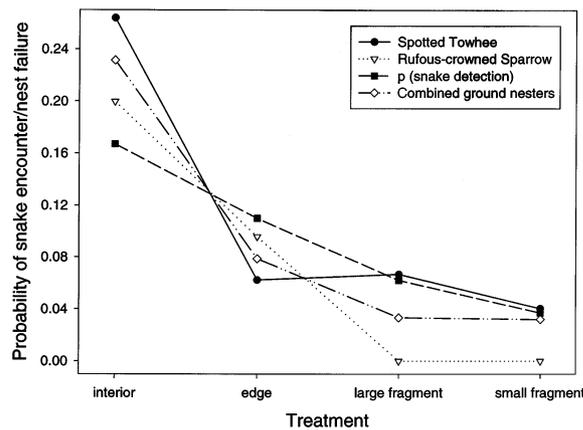


Fig. 5. The probabilities, across a fragmented landscape, of encountering a snake and of a spotted towhee (*Pipilo maculatus*) or rufous-crowned sparrow (*Aimophila ruficeps*) nest failing.

case the spotted towhee and rufous-crowned sparrow, decreased concomitantly, suggesting they are primarily vulnerable to snake predators. This is consistent with our data and published sources that indicate that snakes are the principal predators of nests placed on the ground and also impact nests placed in shrubs (Eichholz and Koenig 1992, Morrison and Bolger 2002, Mullin and Cooper 2002).

Success of shrub nests was relatively uniform across the fragmentation gradient. Although snakes depredate nests placed in shrubs (Table 2), snake abundance alone was not related to success of shrub nests (Fig. 6). For the wrentit, the best fit model of nest failure contained avian abundance only (Fig. 7). Perhaps because this species lays small eggs (see Methods) – too small for

Table 2. Predators of ground and shrub nests, based on either videotaping ($n = 9$; Morrison and Bolger 2002) or direct observation ($n = 7$; Morrison and Bolger 2002, Patten pers. obs., D. C. Bostock, K. J. Bronson, B. D. Smith-Patten, S. B. Sweet pers. comm.). Excluding the mesopredators (for lack of a sufficient sample), the association between snakes and ground nests is significant (χ^2 goodness of fit: $P < 0.03$).

Nest placement	Snake	Bird	Mesopredator
Ground	10	0	1
Shrub	3	2	0

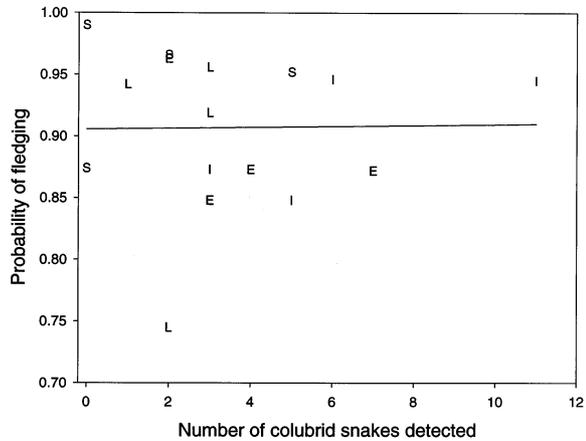


Fig. 6. Snake abundance and daily nest survivorship for shrub-nesting birds, the wrentit (*Chamaea fasciata*; $n = 73$ nests) and the California towhee (*Pipilo crissalis*; $n = 119$ nests). Codes are I = interior, E = edge, L = large fragment, and S = small fragment. A relationship is essentially nonexistent ($r = -0.02$).

most snakes? – and often places its nest on outer portions of shrubs that could not support larger colubrids, it is possible that snakes have little impact on nest success of the wrentit. However, *Peromyscus* mice may contribute to the pattern of wrentit nest failure (see Methods). The relationship between predator abundance and nest failures of the California towhee is less clear, although it appears that a combination of avian predators and snakes accounts for most nest failures (Fig. 7). Opposing patterns of abundance of these predators across the fragmentation gradient may cancel each other enough to yield the relatively constant rate of nest predation on the California towhee across the gradient.

Trophic cascade?

We did not find evidence to support the hypothesis that mammalian mesopredator release causes reduced avian nesting success in habitat fragments. Nest failure rates were not highest in small fragments for either shrub or ground nesters. We hypothesize that a trophic cascade

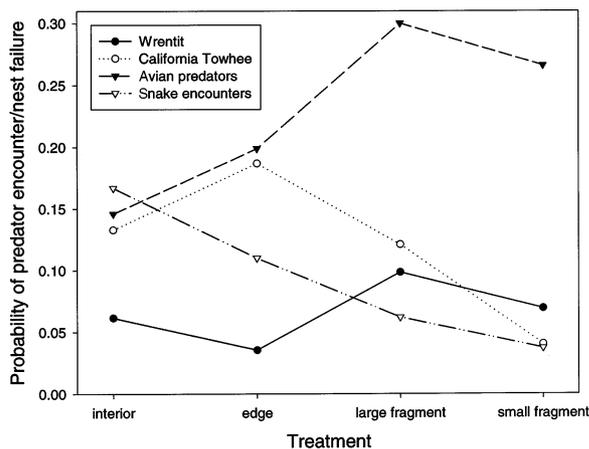


Fig. 7. The probabilities, across a fragmented landscape, of encountering an avian predator or a snake and of a wrenlit (*Chamaea fasciata*) or California towhee (*Pipilo crissalis*) nest failing.

does not occur because of the relative complexity of the nest predator guild (Polis and Strong 1996). The rich predator community in coastal sage scrub has a diversity of responses to habitat edges and fragments and this prevents the linear top-down trophic cascade proposed by Crooks and Soulé (1999). In addition to mesocarnivores, avian predators and snakes are significant predators of nests and of adult and juvenile birds. These predator groups have divergent responses to fragmentation in coastal sage scrub. Also, predatory guilds may interact with each other in complex ways, including intraguild predation (Polis et al. 1989). For example, snakes may consume avian predators, mesopredators may consume snakes, and raptors may consume small mammals.

A cascade could also be prevented if some prey are invulnerable to increased predator abundance (Abrams 1984, Posey and Hines 1991). For example, ground nests are not vulnerable to mesocarnivores during the egg and nestling stages (Table 2; Morrison and Bolger 2002); thus mesocarnivore release should not affect ground-nesting species. Vulnerability of the bird species to particular predators may change ontogenetically; e.g. eggs and nestlings may differ in vulnerability from adults and fledglings of the same species. In our system, snakes appear to be the most potent predator on nests, but raptors and mesocarnivores may be the most potent predators of adults and fledglings. If a cascade does occur it is therefore more likely caused by increases in mortality of fledglings and adults rather than predation of eggs and nestlings.

Paradox of sensitivity to fragmentation of ground nesters

The spotted towhee and the rufous-crowned sparrow

are sensitive to habitat fragmentation (Soulé et al. 1988, Bolger et al. 1997b, Bolger, in press). Both their abundance and occurrence are lower on fragments than on large blocks of habitat, and both decline with proximity to developed edges. Our field work supports this conclusion: we located multiple pairs of wrenlits and California towhees on each of our sixteen plots; however, although we located multiple pairs of spotted towhees and rufous-crowned sparrows on each of our eight interior and edge plots, in both years towhee pairs were absent from one large fragment and one small fragment and sparrow pairs were absent from two large fragments and three small ones.

We are therefore left with a paradox: despite enjoying a substantial decrease in rate of nest predation in fragments, these two ground-nesting species are sensitive to habitat fragmentation. When spotted towhees and rufous-crowned sparrows occupy fragments, their nests are usually successful, suggesting they ought to be able to maintain populations. By contrast, the two shrub-nesting species generally experience increased rates of nest predation across the fragmentation gradient, yet both species persist well even on small fragments (Soulé et al. 1988, Bolger et al. 1997b). Our results suggest that, in this region at least, a solely top-down explanation will not explain patterns of avian abundance across the landscape. Our one caveat to this conclusion is the possibility that mesocarnivore predation of juvenile or adult birds generates the observed patterns of abundance.

Conclusions

Our findings do not support the existence of a general relationship between fragmentation, predator abundance, and avian nesting success. Rather, they underscore the importance of considering both the identity of potential nest predators and the nesting behavior of the bird species when making predictions about the effects of fragmentation on nesting success (Tewksbury et al. 1998). Nest predator guilds respond uniquely to habitat fragmentation, and bird species differ in their vulnerability to different guilds, so patterns of nest predation across fragmentation gradients will vary depending on which predators and which prey are studied. The potential nest predator community varies depending on features of the prey's autecology (Davidson and Knight 2001) including, nest placement, habitat, and egg size. Future studies on top-down control, especially in relation to fragmentation and edges, need to consider a suite of potential nest predators, how each responds to fragmentation, and how they interact.

Regulation of terrestrial ecosystems remains controversial, with nearly equal measures of support for top-down control as for bottom-up control (Power 1992,

Hunter et al. 1997, Hawkins 2001, Terborgh et al. 2001). It seems unlikely to us that control would be exerted from only one direction. Our data show, for example, that top-down control (by snakes) largely determines the fate of ground nests in an average year, but bottom-up control determines the fate of all breeders in a bad year (Patten and Bolger, in prep., Morrison and Bolger 2002). Indeed, because the ground-nesting species we studied do not persist on fragments, where the top-down control is removed, there must be additional control exerted elsewhere. Brooker and Brooker (2001) reported a similar pattern for populations of the blue-breasted fairy-wren (*Malurus pulcherrimus*), for which small fragments “were superior for reproduction but inferior when it came to the survival of the breeding pair.” We infer that population persistence of the spotted towhee and rufous-crowned sparrow is regulated by a combination of top-down and bottom-up mechanisms (Moran and Scheidler 2002), with the principle mortality on habitat fragments occurring at a later life stage (fledgling or adult). Sorting out the relative importance of each regulatory mechanism is one of modern ecology’s primary challenges.

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