HABITAT FRAGMENTATION AND SCRUB-SPECIALIST BIRDS: SAN DIEGO FRAGMENTS REVISITED

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ABSTRACT: We resurveyed six fragments of scrub vegetation near San Diego for eight scrub-specialist bird species sampled in two previous studies (Soulé et al. 1988 and Crooks et al. 2001) to determine if species' distributions are changing over time and whether previously reported patterns of occurrence are persisting. We found that these habitat fragments tended to lose resident populations of scrub-specialist birds over the last 20 years, that the number of species detected was positively related to area, that extirpations were negatively related to area, and that local recolonizations were negatively related to the isolation of the fragment. In addition, sensitivity to fragmentation seems to be related in part to differences in body size and dispersal capability.

Habitat fragmentation is considered one of the most significant threats to biodiversity and a primary cause of extinction (Harris 1984, Wilcox and Murphy 1985). When a habitat is fragmented, deleterious effects on animals occupying that habitat may include reduced population size, genetic isolation, and inbreeding depression (Templeton et al. 1990). These effects can be exacerbated further by the loss of opportunity for immigration if fragments are remote from each other (Wilcox and Murphy 1985). Negative consequences birds can experience from habitat fragmentation include increased nest predation and parasitism (Paton 1994) and reduced overall fecundity (Donovan and Lamberson 2001). The result for many birds is an increasing risk of local extirpation with decreasing fragment size (Temple and Cary 1988, Soulé et al. 1992, Crooks et al. 2004).

The effects of fragmentation can change over time (Debinski and Holt 2000), and long-term effects may be difficult to assess, as the length of time a habitat is fragmented can be short in comparison to evolutionary time (Ewers and Didham 2006). Immediately after initial fragmentation, for example, the abundance of species may increase as a result of the population's being compressed into remaining habitat (Hagan et al. 1996) or faunal release caused by elimination of predators (Adler and Levins 1994). Such effects, however, usually diminish after one year (Debinski and Holt 2000). Therefore, long-term studies are important for understanding the true effects of fragmentation.

Soulé et al. (1988) examined the effects of fragmentation in San Diego County, California, through surveys of eight scrub-specialist bird species (species that require coastal sage scrub and/or chaparral habitat for breeding). For these species, Soulé et al. (1988) surveyed 37 canyons vegetated with coastal sage scrub and/or chaparral and isolated from similar canyons by various forms of urban development. These areas of surviving native vegetation (referred to hereafter as fragments) ranged in size from 0.4 to 102.8 ha. The fragments had been isolated from other areas of native habitat for lengths of time ranging from 2 to 86 years. Soulé et al. (1988) revealed that the number of scrub-specialist bird species in a fragment tended to increase with increasing fragment area and native vegetation cover but decrease with time since fragmentation (fragment age).

Ten to eleven years after the initial surveys, in 1997, Crooks et al. (2001) surveyed these fragments again for the same bird species. Of the 34 fragments they examined, 30 had been covered from 1985 to 1987 by Soulé et al. (1988). Crooks et al. (2001) found more extirpations (21) than recolonizations (12) in the fragments surveyed. The proportions of extirpations and recolonizations were significantly related to the area but not to the age or isolation of the fragments. In addition, the percent cover of native vegetation decreased significantly as a fragment's age increased. Their results supported the finding of Soulé et al. (1988) that the number of species in a fragment is positively correlated with its area and negatively correlated with its age.

In our study, 20 years after the surveys of Soulé et al. (1988), we assessed extirpations and recolonizations within six of the fragments studied by both Soulé et al. (1988) and Crooks et al. (2001). We chose fragments representing a range of sizes that contained five or more of the eight species in 1988. The results of the previous studies showed a negative correlation between the age of a fragment and the number of bird species within that fragment; they found that the number of extirpations exceeded the number of recolonizations. We therefore expected extirpations to exceed recolonizations in the six fragments we studied and to find evidence of lower persistence in smaller and more isolated fragments.

METHODS

We resurveyed six of the fragments surveyed by Soulé et al. (1988) and Crooks et al. (2001) in April and May 2006. These six fragments, vegetated with coastal sage scrub and/or chaparral, range from about 15 to 35 km north of downtown San Diego (Figure 1). Two are in Solana Beach (Mil Cumbres and Solana Drive), two in Encinitas (Oakcrest and Montanosa; Figure 2), one in La Jolla (Alta La Jolla), and one in Pacific Beach (Kate Sessions Park; Figure 3) (Table 1). As of 2006, each fragment had been completely surrounded by development, including homes, golf courses, churches, and businesses, for 20 to 35 years. These six fragments ranged in size from 3 to 34 ha, had been isolated for ≤16 years at the time of the original study 1985–87, and supported at least five of the eight scrub-specialist bird species at that time. None of the six fragments we studied showed signs of recent fire at the time of our surveys.

The eight target species were the California Quail (*Callipepla californica*), Greater Roadrunner (*Geococcyx californianus*), Wrentit (*Chamaea fasciata*), Bewick's Wren (*Thryomanes bewickii*), Cactus Wren (*Camplyorhynchus brunneicapillus*), California Gnatcatcher (*Polioptila californica*), California Thrasher (*Toxostoma redivivum*), and Spotted Towhee (*Pipilo maculatus*).

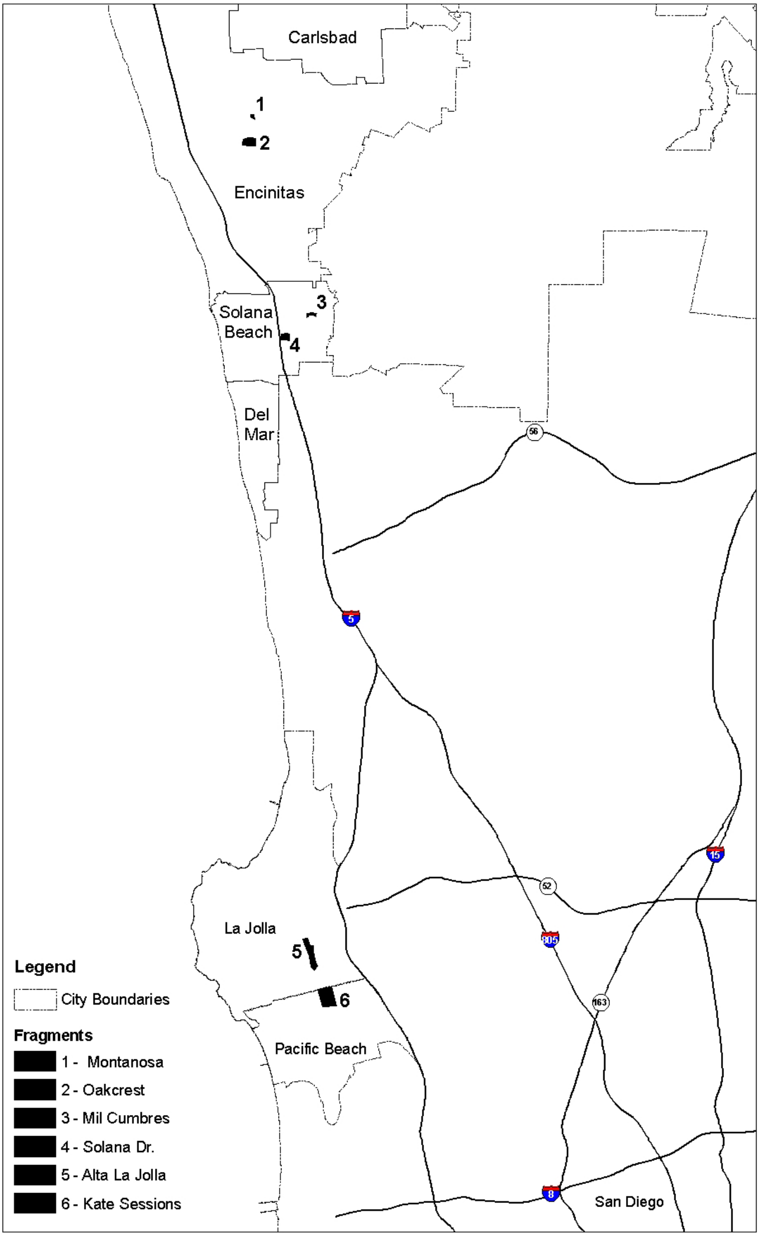

Figure 1. Locations in coastal San Diego County, California, of six fragments of native scrub surveyed for scrub-specialist birds in 2006.

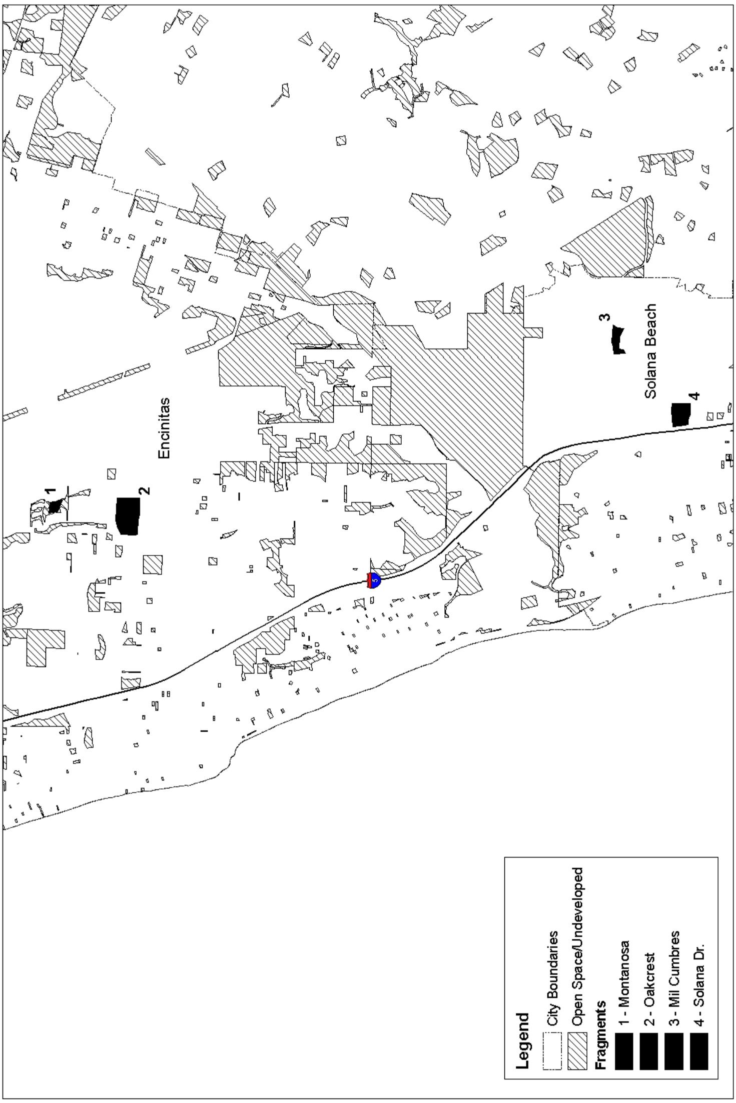

Figure 2. Setting of Montanosa, Oakcrest, Mil Cumbres, and Solana Drive fragments among nearby developed and undeveloped areas.

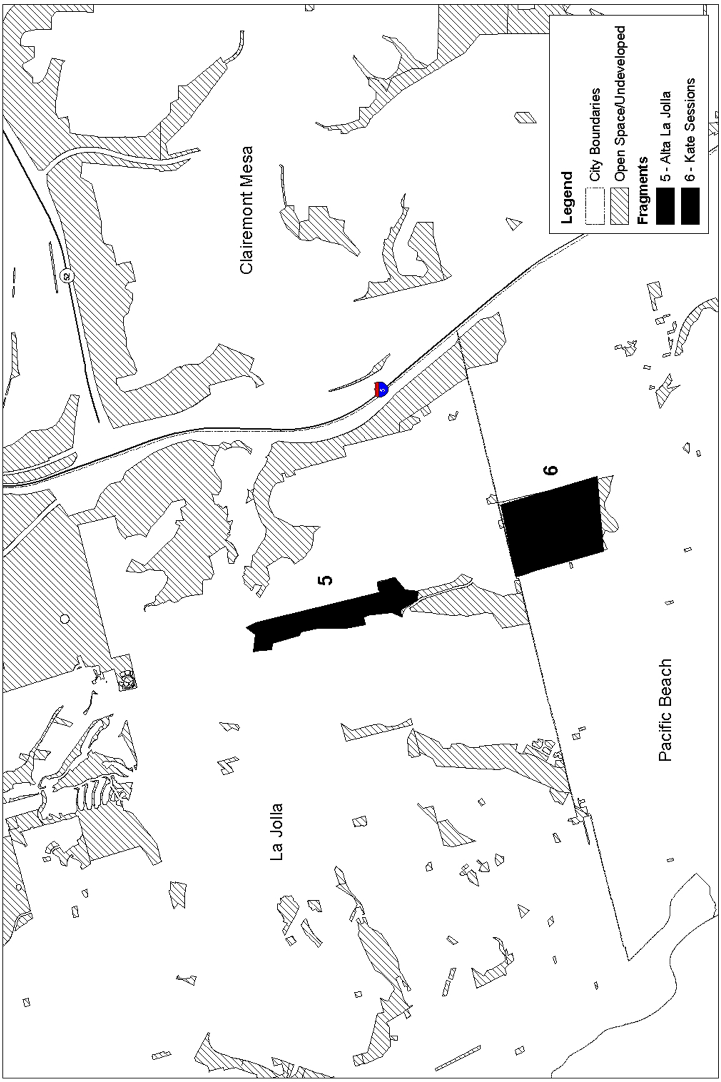

Figure 3. Setting of Alta La Jolla and Kate Sessions Park fragments among nearby developed and undeveloped areas.

Table 1 Fragments of Native Scrub Resurveyed in 2006

	Fragment					
	Alta La Jolla	Kate Sessions	Mil Cumbres	Montanosa	Oakcrest	Solana Dr.
Area (ha)[a]	34	31	6	3	6	8
Isolation distance (m)	121	121	550	91	400	550
1985–87						
Age[b]	14	16	11	2	6	11
Number of species[c]	6	6	6	5	6	7
1997						
Age	23	25	20	11	15	20
Number of species[d]	4	5	4	3	3	4
Extirpations	2	2	2	3	3	3
Recolonizations	0	1	0	1	0	0
2006						
Age	32	34	29	20	24	29
Number of species	5	5	3	4	4	4
Extirpations	0	0	1	0	0	0
Recolonizations	1	0	0	1	1	0

[a]From Crooks et al. (2001).
[b]Number of years since fragment was isolated from other areas of native scrub.
[c]Of eight possible, from Soulé et al. (1988).
[d]Of eight possible, from Crooks et al. (2001).

Our survey methods followed those of Soulé et al. (1988) and Crooks et al. (2001) as closely as possible. To conduct the surveys, Sartain and Cindy Dunn or Erin Reddy walked slowly together along a transect from one end of the fragment, through the interior of the fragment, to the other end. Surveys began at sunrise. Birds were detected by sight and/or sound and recorded regardless of distance from the transect. This same transect was then slowly walked a second time, beginning at the opposite end, and repeated a third and fourth time. On the fourth survey we made 8-minute point counts approximately every 250 meters. Survey time was proportional to the size of the fragment and ranged from half an hour for the smallest fragment to two hours for the largest, averaging one hour per visit per fragment. We surveyed each fragment twice, switching observers so that a total of three people surveyed each fragment. The rotating three-person survey team provided a control for detection bias. The time between the two surveys ranged from 7 to 14 days. Although the 1988 study's methods entailed three visits to each fragment, Crooks et al. (2001) found that the number of times a fragment was surveyed did not significantly influence the number of bird species detected when the effects of variation in the fragments' areas were controlled.

To assess changes in the number of target species in the fragments over time, we performed a one-way ANOVA on the number of species detected in the six fragments by each of the three studies, followed by a post-hoc Holm-Šidák test.

To determine if the presence of the target species was related to fragment size or age, we performed linear regressions with the number of species detected in 2006 as the dependent variable and fragment area (AREA) and fragment age as of 2006 (AGE) as independent variables.

Given small sample sizes, we combined extirpations and recolonizations from 2006 with those from 1997 in order to examine extirpations and recolonizations since the initial Soulé et al. (1988) study. As these combined variables included surveys conducted at different times, we did not use them to examine effects of fragment AGE. However, as area was assumed to remain relatively constant between 1997 and 2006, we performed linear regressions to determine if fragment AREA influenced the number of recolonizations or extirpations.

In addition, we determined how combined 1997 and 2006 recolonizations and extirpations were related to the distance by which the fragments were isolated from similar natural habitat (ISOLATION). Soulé et al. (1988) defined isolation distances in two ways, as the distance to the nearest fragment that contained scrub-specialist species and as the distance to the nearest fragment of equal or greater area. In this study, we used the latter definition. We performed linear regressions to detect the influence of ISOLATION on the number of recolonizations and extirpations.

RESULTS

Our study revealed one extirpation, defined as a species' disappearance in 2006 from a fragment where it was present in 1997: the Wrentit from Mil Cumbres. It revealed three recolonizations, defined as a species' reappearance in 2006 in a fragment where it was absent in 1997 but present in 2006: the California Quail in Alta La Jolla, California Thrasher in Montanosa, and California Gnatcatcher in Oakcrest (Table 2).

Table 2 Distribution of Scrub-Specialist Birds in Fragments Surveyed in 2006[a]

Fragment	Bewick's Wren	Spotted Towhee	Wrentit	Calif. Thrasher	Calif. Quail	Calif. Gnatcatcher	Greater Roadrunner	Cactus Wren
Alta La Jolla	1	1	1	1	**1**[e]	0	0[b]	0
Kate Sessions	1	1	1	1	0[b]	1[c]	0[b]	0
Mil Cumbres	1	1	**0**[b,d]	0[b]	1	0	0[b]	0
Montanosa	1	1[b]	1	**1**[e]	0[b]	0	0[b]	0
Oakcrest	1	1	1	0[b]	0[b]	**1**[c,e]	0[b]	0
Solana Dr.	1	1	1	1	0[b]	0[b]	0[b]	0

[a]Ordered by decreasing frequency. 1, present; 0, absent.

[b]Extirpation since 1985–87 (Soulé et al. 1988).

[c]Recolonization since 1985–1987 (Soulé et al. 1988).

[d]Extirpation since 1997 (Crooks et al. 2001)..

[e]Recolonization since 1997 Crooks et al. (2001).

Our ANOVA results showed that the number of target species in the fragments has decreased significantly over time ($F_{2,15}$ = 15.98, $P < 0.001$, power 0.997). That is, the number of species found in the fragments 1985–87 (6.0 $\pm$ 0.63) was significantly higher than in 1997 (3.8 $\pm$ 0.75) (t = 5.25, $P < 0.001$) and 2006 (4.2 $\pm$ 0.75) (t = 4.44, $P < 0.001$). The difference between 1997 and 2006 was not significant (t = 0.81, P = 0.43).

AREA explained a significant proportion of the variation in the number of target species found in the fragments in 2006, revealing a positive relationship between the two variables (R^2 = 0.71, P = 0.03, power 0.57). That is, more species occurred in larger fragments. AGE did not explain a significant proportion of the variation (R^2 = 0.21, P = 0.36); however, the power of the AGE regression was low (0.14), likely as a result of the small sample size.

AREA also explained a significant proportion of the variation in the number of extirpations, 1997 and 2006 combined, revealing a significant negative relationship (R^2 = 0.98, $P < 0.001$, power 0.997), That is, more extirpations occurred in smaller fragments. AREA did not explain a significant proportion of the variation in the number of recolonizations, 1997 and 2006 combined (R^2 = 0.01, P = 0.90); however, the power of this test was very low (0.03).

ISOLATION explained a significant proportion of the variation in the number of recolonizations, 1997 and 2006 combined (R^2 = 0.72, P = 0.03, power 0.58), revealing a negative relationship. That is, as isolation distance increased, the number of recolonizations decreased. ISOLATION did not explain a significant proportion of the variation in number of extirpations (R^2 = 0.42, P = 0.16), but again the test's power was low (0.27), so the results should be interpreted with caution.

DISCUSSION

Both Soulé et al. (1988) and Crooks et al. (2001) found the number of bird species in fragments to be positively related to fragment area and negatively related to fragment age. In our study, we confirmed that the number of species in a fragment is positively related to its area. We did not find a significant effect of fragment age on the number of bird species; however, we did find a significant decrease in the number of species over the three studies combined (from 1985–87 to 2006). The lack of a direct relationship of species number with fragment age may be partially explained by our limited sample size, as we surveyed only 16% and 18% of the fragments studied by Soulé et al. (1988) and Crooks et al. (2001), respectively. The low power of the regression of species number against fragment age suggests that these negative results should be interpreted with caution. A larger sample size could provide more statistical power for this test and clarify the relationship between the number of species and fragment age. Also, if species richness is negatively related to fragment age in an exponential manner, then the effects of fragment age will become less pronounced over time. We selected fragments to include those with five or more of the target species remaining in 1985–87 study and to cover a range of sizes.

Unfortunately, this resulted in the two largest fragments also being the two oldest. As a result, some patterns may have been obscured because of a lack of variation in the age/size combinations represented. The significant decline in the number of species over the course of the three studies indicates a decreasing ability of these fragments to support scrub-specialist birds over time. Soulé et al. (1988) did not have the ability to compare species gains or losses over time and based their conclusions on the assumption that all species were present at the time of fragmentation. Subsequently, Crooks et al. (2001) confirmed their findings and showed a higher proportion of extirpations relative to recolonizations over the intervening 11 years. When we examined six of the fragments, the number of bird species still showed a significant decline relative to the original 1985–87 study, confirming the observations of Crooks et al. (2001).

We found no significant change in the number of target species from 1997 to 2006, although the change from 1985–87 to 2006 was significant. In addition to calling for study of a larger sample of fragments to elucidate changes in the system, this observation supports the need for long-term habitat-fragmentation studies, especially where sample size is limited.

Species whose persistence rate Crooks et al. (2001) found to be low were similar to those we identified, with the Cactus Wren and Greater Roadrunner absent from all six fragments in both studies. This was expected, as the Cactus Wren has specific habitat requirements and depends exclusively on large stands of cactus for breeding. Crooks et al. (2001) estimated the minimum fragment area in which a species could persist with a 95% chance over the next 100 years, suggesting the Greater Roadrunner needed a minimum of 157 ha. Unitt (2004) estimated it may need at least 400 ha. The absence of the Greater Roadrunner was therefore expected, as the largest fragment we surveyed was only 34 ha.

Crooks et al. (2001) noted high persistence and a net gain in recolonizations among the fragments they studied for the Bewick's Wren, Spotted Towhee, and California Gnatcatcher. In 2006 we observed a similar pattern, with the Bewick's Wren and Spotted Towhee persisting at the highest rate; they were the only two species present in all six fragments. The California Gnatcatcher's persistence rate was also high, given that it was one of only three species to have recolonized a fragment between 1997 and 2006.

The only extirpation we observed was of the Wrentit, one of the smallest of the eight target species. However, the Wrentit was the third most frequent species, present in five of the six fragments. The fragment from which it had been extirpated, Mil Cumbres, was one of the three smallest fragments (6 ha) and was 29 years old. Only two fragments were older, and both of these were much larger (Alta La Jolla at 34 ha and Kate Sessions at 31 ha). The one fragment of a similar age (Solana Dr.) was larger by 2 ha. Because Mil Cumbres was the oldest small fragment, we expected that an extirpation would be more likely there.

The three species for which we found a recolonization were the California Quail, California Thrasher, and California Gnatcatcher. Recolonization by California Quail occurred in the largest fragment (Alta La Jolla, 34 ha), while recolonization by California Thrashers occurred in the least isolated fragment (91 m from suitable habitat). Crooks et al. (2001) found thrashers recolonizing the most isolated fragment they studied (2865 m), suggesting that this bird may be able to travel between fragments separated by large distances.

Crooks et al. (2001) found extirpations and recolonizations to be significantly related to a fragment's area. When we combined the extirpation we recorded with those recorded by Crooks et al. (2001), the pattern of more extirpations in smaller fragments remained. We were unable to detect a significant relationship between recolonization and fragment area; however, these negative results should be considered with caution as the power of statistical test was very low. A larger sample size could improve the statistical power of this test and reveal additional undetected patterns.

Our results show that extirpation from a fragment can be temporary, as we found three recolonizations among the six fragments we surveyed. We found a significant negative relationship between recolonization and isolation distance, however. This relationship suggests that recolonizations may be limited by the isolation of fragments and the ability of a species to reach distant fragments.

The eight species we studied are nonmigratory, and their dispersal is generally thought to be limited. Unitt (2004) assessed the dispersal capabilities of the Greater Roadrunner, California Quail, California Thrasher, Wrentit, and Bewick's Wren as minimal. The Cactus Wren is thought to disperse rarely up to 3 km, the Spotted Towhee has been shown to disperse up to 9.7 km (averaging 6.4 km), and the California Gnatcatcher typically disperses less than 3 km (Unitt 2004). Poor dispersal may explain the decline of these species in fragments over time.

Although these species are thought to be poor dispersers in general, a California Gnatcatcher has moved approximately 20 km, albeit mainly over natural habitats, with the exception of a freeway (K. Fischer pers. comm.). Further studies of other scrub-specialist species could reveal greater dispersal capabilities than previously recorded. The general decline in species diversity in these fragments over time, however, as well as the negative relationship between recolonization rates and isolation distance, suggests the dispersal capabilities of scrub-specialist birds are, on average, not adequate to maintain their populations within an urban matrix.

Crooks et al. (2001) found larger body size to be related to a faster time to extirpation (i.e., low persistence), while Soulé et al. (1988) found larger body size to be related to better persistence. The two recolonizations we observed were by two of the three largest species (California Quail and California Thrasher, mean weights 184 g and 94 g, respectively; Crooks et al. 2001). In addition, the only extirpation we noted was of a small bird (Wrentit, mean weight 14 g). At the same time, one of the two species with the highest persistence (Spotted Towhee, 37 g) and one of the two birds with the lowest persistence (Cactus Wren, 40 g) were of intermediate size. It is likely that body size is only one factor combined with many life-history factors that make a species in this system more or less vulnerable to extirpation.

The amount of suitable habitat within the fragments can affect the presence of these bird species. Soulé et al. (1988) and Crooks et al. (2001) found that the cover of native vegetation was more important than area *per se*, and that this cover decreased with fragment age. Assessing changes in native vegetation cover was not within the scope of our study, but a thorough and accurate longitudinal vegetation analysis that considers the percent cover of both native and nonnative plants would be useful in elucidating the observed patterns of birds' occurrence and persistence.

The area, age, and isolation of the fragments combined to influence the observed pattern of overall decline in the number of scrub-specialist species. It is interesting that no major fluctuations of species occurred in the fragments over the past nine years. There was a fluctuation of only zero to one species in each fragment. Crooks et al. (2001) found two to three extirpations in these same fragments. At the time of the Soulé et al. (1988) study, extirpations ranged from one to three under the assumption that all species were present at the time of fragmentation. The low number of fluctuations we observed may be a reflection of the lower number of species available to be extirpated or they could be due to an initial faunal compression that has now reached a balance. Variation in the sensitivity of each species to fragmentation is likely based on multiple factors, including body size, dispersal capability, dependence on specific microhabitats for breeding, and varying resource requirements.

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Wrentit

Sketch by George C. West