
Extinction and Colonization of Birds on Habitat Islands

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Abstract: *We used point-count and transect surveys to estimate the distribution and abundance of eight scrub-breeding bird species in 34 habitat fragments and the urban matrix in southern California. We then calculated local extinction and colonization rates by comparing our data with surveys conducted in 1987. We classified factors that influence extinction and colonization rates into two types: (1) extrinsic factors, which are characteristics of the habitat fragments such as area, age, and isolation and (2) intrinsic factors, which are characteristics of the species that inhabit fragments, such as body size and population density. Over the past decade, at least one species went locally extinct in over 50% of the fragments, and local extinctions were almost twice as common as colonizations. Fragment size and, to a lesser extent, fragment age were the most important extrinsic factors determining extinction and colonization. Density indices of scrub birds were the most important intrinsic factors determining extinction rates, predicting the number of sites occupied, the probability of local extinction, relative area requirements, and time to local extinction.*

Extinciones y Colonizaciones de Aves en Hábitats Insulares

Resumen: *Utilizamos conteos puntuales e inspecciones en transectos para estimar la distribución y abundancia de ocho especies de aves con reproducción en maleza, en 34 fragmentos de hábitat y en la matriz urbana del sur de California. Posteriormente calculamos las extinciones locales y las tasas de colonización comparando nuestros datos con inspecciones realizadas en 1987. Clasificamos factores que influyen las tasas de extinción y colonización en dos tipos: (1) factores extrínsecos, características de los fragmentos de hábitat (área, edad y aislamiento) y (2) factores intrínsecos, características de las especies que habitan los fragmentos (tamaño del cuerpo y densidad poblacional). Durante la última década, al menos una especie se extinguió localmente en casi el 50% de los fragmentos y las extinciones locales fueron casi dos veces más comunes que las colonizaciones. El tamaño del fragmento y en menor medida la edad del fragmento fueron los factores extrínsecos más importantes que determinaron las extinciones y las colonizaciones. Los índices de densidad de aves de maleza fueron los factores intrínsecos más importantes determinando las tasas de extinción, prediciendo el número de sitios ocupados, las probabilidades de extinción local, los requerimientos de área relativa y el tiempo para la extinción local.*

Introduction

Habitat fragmentation has been implicated widely as a primary threat to natural populations (Wilcove et al.

1998). Many empirical studies have tried to infer species sensitivities to fragmentation from a single snapshot of patch occupancy (Soulé et al. 1988; Bolger et al. 1991), often assuming that all species are present in each fragment at creation. Thus, the absence of a species from a patch is interpreted as evidence of extinction, and the presence of a species in a patch is viewed as persistence since isolation. This approach can overestimate extinction, however, because all species are not necessarily

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present in each fragment initially (Bolger et al. 1991). Further, a static approach does not estimate recolonization, so this important process is often ignored or assumed to be low. Indeed, estimating colonization rates may be as important as documenting extinctions in the evaluation of species-specific sensitivities to fragmentation. Surveys from multiple time points are required to gain a more complete understanding of extinction-colonization dynamics.

Although most research on the effects of habitat fragmentation on birds has focused on forest habitats, other habitats in North America are rapidly disappearing, and the bird populations they support may be particularly sensitive to fragmentation (Herkert 1994). Mediterranean scrub habitats are particularly threatened, and remnant scrub patches may experience avifaunal collapse more quickly than temperate forest fragments (Soulé et al. 1988). Intensive development in coastal southern California over the past century has destroyed all but 10% of the native coastal sage scrub habitat (Jensen et al. 1990), creating a "hotspot" of endangerment and extinction for the highly endemic biota in the region (Dobson et al. 1997).

Previous studies in this system have focused on how island biogeographic variables correlate with the presence or absence of eight species of chaparral and sage-scrub breeding birds in urban habitat fragments (Soulé et al. 1988; Bolger et al. 1991; Soulé et al. 1992). We revisited these fragments to estimate local extinctions and colonizations and to evaluate the factors that drive these processes. We expanded previous surveys by documenting not just the distribution of scrub birds among habitat fragments, but also estimating the density of populations within each fragment. Further, we also surveyed an urban development bordering a large natural area to investigate the degree to which the scrub species in our study are using the urban matrix within which the fragments are nested.

We classified factors that may influence local extinctions and colonizations as either extrinsic or intrinsic. Extrinsic factors are characteristics of the habitat fragments and the surrounding matrix. Soulé et al. (1988) found fragment size and age to be good extrinsic predictors of the distribution of scrub birds in the urban fragments. We therefore expected small fragments to have lost more species than large ones, and we expected fragments that had been recently isolated at the time of the first survey to have lost additional species over the past decade. In addition, the previous studies concluded that scrub bird dispersal was limited, with the habitat fragments functioning as isolated "islands" immersed in a matrix of inhospitable urban habitat (Soulé et al. 1988; Bolger et al. 1991). Therefore, we expected fragments that lacked birds 10 years ago to still lack these species, with few colonizations of previously unoccupied fragments. Overall, we expected the suite of scrub birds to

show a net loss from this system due to further extinctions and limited colonizations.

We classified intrinsic factors as characteristics of the species that inhabit the fragments. Soulé et al. (1988) predicted that two intrinsic factors, abundance and body size, would be important determinants of the order of disappearance of scrub-breeding bird species in this system. First, species with naturally low population densities should be more vulnerable to extinction from a variety of deterministic and stochastic forces (Gilpin & Soulé 1986). Second, larger-bodied birds in insular populations might persist longer than small-bodied birds of equal abundance because larger animals live longer, have lower temporal variability in population size, and are better buffered against short-term environmental stochasticity (Pimm et al. 1988; Tracy & George 1992). We tested these predictions, evaluating how intrinsic factors interact with extrinsic factors to influence extinction and colonization rates.

Methods

Surveys

We surveyed 34 remnant fragments of chaparral and coastal sage scrub habitat in San Diego County, California, isolated at different times over the last century of urban development (for a map of the study area and exact location of the fragments, see Soulé et al. [1988] and Suarez et al. [1998]). Thirty of these fragments were the same as those used in prior studies of birds conducted in 1987 (Soulé et al. 1988; Bolger et al. 1991; Soulé et al. 1992); four recently isolated fragments were added to complement those in the original study (Suarez et al. 1998). Most of the sites are fragments of dendritic canyons dissecting coastal mesas, although a few also contain mesa-top habitat. These canyons, typically ranging from 15 to 60 m in depth, are completely surrounded by human-modified landscapes. The fragments support a mosaic of shrub habitat, including maritime succulent shrub, mixed chaparral, chamise chaparral, and coastal sage scrub, the dominant assemblage in most sites (Alberts et al. 1993).

We focused our surveys on eight scrub-specialist birds in the fragments; we defined a scrub bird as a species that requires coastal sage scrub and/or chaparral habitat for breeding (Soulé et al. 1988). These eight species, also surveyed by Soulé et al. (1988), were the California Quail (*Callipepla californica*), Greater Roadrunner (*Geococcyx californianus*), Cactus Wren (*Campylorhynchus brunneicapillus*), Bewick's Wren (*Thryomanes bewickii*), California Gnatcatcher (*Poliophtila californica*), Wrentit (*Chamaea fasciata*), California Thrasher (*Toxostoma redvium*), and Spotted Towhee (*Pipilo maculatus*).

Species occurrences in each fragment were assessed through transect and point-count surveys. For transect surveys, we walked slowly along the long axis of the entire fragment a minimum of three times and recorded all species detected (mean time spent per transect survey in each fragment = 107 minutes, SD = 82.34). In addition, three 8-minute point counts (following Bolger et al. 1997a) were conducted at stations established in native habitat at approximately 250-m intervals along the long axis of each fragment. The species lists generated from the point counts were combined with the species detected during transect surveys to generate species occurrences for each habitat fragment.

Transect and point-count surveys likely detected most, if not all, scrub species present in each fragment. The first visit to all 34 fragments yielded 76 detections of the eight scrub species (mean number of species detected per fragment during first visit = 2.23, SD = 1.69), the second visit resulted in only 14 new detections of the eight species across all fragments (mean per fragment = 0.41, SD = 0.66), and the third visit yielded only 5 new detections of the eight species across all fragments (mean per fragment = 0.14, SD = 0.36). In addition, multiple regression analyses indicated that the total time a fragment was surveyed was not significantly related to the number of species detected in a fragment ($\beta = 0.095$, $p = 0.640$) after fragment size was controlled ($\beta = 0.642$, $p = 0.003$).

We also used the point-count data to estimate a relative density index, averaged among fragments, for each scrub species. During point counts, we recorded all individuals detected, method of detection (e.g., call, song, visual, fly-over), distance to observer, and whether the bird was in the habitat fragment or the adjacent urban matrix. To estimate density indices for each species, we excluded all fly-overs, detections >100 m from the observer, and detections within the adjacent urban matrix. For each species, we calculated the average number of detections per 8-minute point count per station in each fragment. We then calculated a single density index for each species by averaging the density indices among fragments; to calculate this index we included only fragments in which the species was detected.

To complement fragment surveys and to evaluate the habitat suitability of the urban matrix, we established four parallel transects 250, 500, 750, and 1000 m from the boundary of a large area of continuous habitat, Mission Trails Regional Park, that supported the entire pool of scrub bird species. We conducted point counts at approximately 250-m intervals along each distance transect and calculated density indices for each species at each distance class.

Fragments and the urban matrix were surveyed at least three times by at least two different teams of observers. Surveys were conducted from 4 April to 9 June 1997 between sunrise and 1030 hours.

Local Extinction and Colonization

We defined a local extinction event operationally when a species detected in a given fragment in 1987 was not detected in 1997. We defined a colonization event operationally when a species absent in a given fragment in 1987 was detected in 1997. Because our estimates of extinction and colonization are based on two sample points, multiple extinctions and colonizations would be undetected. Further, our operational definitions of extinction and colonization assume that both studies detected all species actually present in each fragment and did not mistakenly list species that were not present (Hinsley et al. 1995). To ensure consistency between surveys, sampling methods and intensity were similar in both 1987 and 1997, and several researchers who collected data in 1987 also helped conduct surveys in 1997. In the case of the Greater Roadrunner, however, the 1987 surveys used questionnaires distributed to residents bordering fragments to augment field data (Soulé et al. 1988). Because questionnaire surveys likely increased estimated Greater Roadrunner occupancy in 1987 relative to 1997 field surveys, we excluded that species from all statistical analyses comparing 1997 data to 1987 results, including local extinction and colonization analyses.

The absolute number of local extinctions is dependent on the number of species originally present in the previous survey. For example, younger or larger fragments may have experienced more local extinctions because these fragments had more species to lose. To account for the number of species present in each fragment in the 1987 surveys, we calculated the proportion of local extinctions that had occurred since 1987: E/S , where E is the number of local extinctions in a given fragment and S is the number of scrub species detected in that fragment in 1987 (Diamond 1969; Hinsley et al. 1995). We omitted from the analyses fragments that had no scrub species in 1987 because these sites could experience no detectable extinctions.

Likewise, the number of colonizations is dependent on the number of species absent in the original survey. For example, younger or larger fragments may have experienced lower absolute colonization rates because they had more species and hence less opportunity for colonization. We therefore calculated the proportion of colonizations that had occurred since 1987: $R/(7 - S)$, where R is the number of colonizations in a given fragment and $(7 - S)$ is the number of the seven scrub species (excluding Greater Roadrunners) not detected in that fragment in 1987.

Extrinsic Factors

We used fragment area, age, and isolation (Table 1) to assess the effects of extrinsic factors on local extinction

and colonization rates in each fragment. We selected these three measures as the independent variables because they have been identified as important predictors of the occurrence of scrub birds (Soulé et al. 1988; Bolger et al. 1991) and other animals (Bolger et al. 1997b, Suarez et al. 1998; Bolger et al. 2000) in this system. Extrinsic variable data were log-transformed to meet normality assumptions in the statistical analyses. Total area of each habitat fragment was measured from digitized images of scaled aerial photographs taken in 1995. Fragment age, defined as the number of years since isolation of the habitat fragment by urban development, was obtained from San Diego County records (Soulé et al. 1988). Fragment isolation was measured as the distance to the closest fragment that was equal to or larger in size than the given fragment (Soulé et al. 1988). Of the three extrinsic factors, only fragment age and isolation were positively correlated ($r = 0.342$, $p = 0.048$).

In addition to the three extrinsic variables (area, age, isolation) we used in our statistical analyses, we also visually estimated percent native shrub cover remaining in

fragments from aerial photographs and from ground surveys in each habitat fragment (Suarez et al. 1998). Percent shrub cover remaining in a fragment was highly negatively correlated with fragment age ($r = -0.719$, $p < 0.001$); native vegetative cover declined as time since isolation increased. To minimize multicollinearity between independent variables (Tabachnick & Fidell 1996), we included only fragment age in all statistical analyses. We therefore used age not only to measure a time effect in the fragments, but also to represent the cumulative loss of habitat since isolation.

We used logistic regression to evaluate the effects of fragment area, age, and isolation on the probability of occurrence for each species in 1997. The logistic regression models were parameterized with presence-absence data for each scrub species across all 34 fragments surveyed in 1997. For each species, we first entered size, age, and isolation as independent variables into the logistic model in a backwards sequential-elimination procedure (Knick & Rotenberry 1995; Tabachnick & Fidell 1996). At successive steps, the least significant independent variable was removed from the model. If deletion of the variable did not decrease the whole-model chi-square log-likelihood statistic ($p > 0.10$), then the variable was permanently removed from the model and the elimination procedure continued. If deletion of the variable decreased the model's fit to the data ($p \leq 0.10$), the variable was retained in the model. The significance of the final model was then tested by comparing the whole-model log-likelihood chi-square statistic against the log-likelihood statistic of an intercept-only model.

For species with significant area effects, we plotted logistic regression curves of the probability of occurrence of each species as a function of area, after holding fragment age and isolation constant by substituting their median values into the three-way logistic model. Likewise, for species with significant age or isolation effects, we constructed age or isolation curves after holding the other two independent variables constant. From these curves, we calculated the fragment area, age, and isolation at which the probability of occurrence of the species equaled 50% and used these estimates to represent the relative area requirements for each species (following Robbins et al. 1989; Vickery et al. 1994), the relative time to local extinction for each species, and the relative isolation thresholds for each species, respectively.

We also used multiple logistic regression models to evaluate graphically the combined effect of age and area on probability of occurrence for each species. Using these multiple logistic models, we estimated for each species the area requirement for a 95% probability of detection after 100 years of isolation. Relative area, isolation, and age thresholds from the logistic models, however, are not intended to represent the absolute fragment size, age, or isolation necessary to ensure the long-term persistence of populations (Hinsley et al. 1996). Rather, they

Table 1. Extrinsic factors for the 34 habitat fragments surveyed for scrub-breeding birds in 1997.

<i>Fragment</i>	<i>Area (ha)</i>	<i>Age (yrs)</i>	<i>Isolation (m)</i>
32nd Street	10	65	304
34th Street	64	43	853
54th Street	4	29	609
60th Street	4	46	335
Acuna	7	31	110
Alta La Jolla	34	23	121
Baja	8	40	670
Bonita Long	44	8	682
Balboa Terrace	56	43	121
Canon	12	67	1219
Chateau	6	29	110
Chollas	6	45	1005
Del Mar	18	8	1023
El Mac	2	41	883
Florida	102	59	2100
Juan	7	32	228
Kate Sessions	31	25	121
Laurel	10	88	1554
Mil Cumbres	6	20	550
Montanosa	3	11	91
Oak Crest	6	15	400
Paseo Del Rey	8	20	91
Poinsettia	2	59	350
Pottery	10	23	45
Raffee	8	28	61
Sageview	13	19	227
Sandmark	72	29	914
Solana Drive	8	20	550
Spruce	4	95	1767
Syracuse	9	27	40
Talbot	2	64	1219
Titus	3	86	280
Washington	9	83	365
Zena	15	45	2865

are intended to function only as relative indices of sensitivity to fragmentation.

Finally, we used sequential backward-elimination logistic regression analysis to determine how fragment size, age, and isolation predicted the probability of extinction and probability of colonization for each species since 1987. For each species, we included in the extinction models only those fragments occupied in 1987 and included in the colonization models only those fragments unoccupied in 1987. We conducted logistic regressions for extinction probability of the California Quail, Bewick's Wren, Wrentit, and California Thrasher. We omitted the Spotted Towhee because it had experienced no extinctions since 1987; the Greater Roadrunner was omitted for reasons described above, and the Cactus Wren and California Gnatcatcher were omitted because they occurred in only one (Bonita Long) and two (Sandmark, Bonita Long) fragments, respectively, in 1987. We conducted logistic regressions for colonization probability for those species that had experienced colonization over the last decade: Bewick's Wren, California Gnatcatcher, California Thrasher, and Spotted Towhee.

Intrinsic Factors

We used average body weight (Soulé et al. 1988) and average density indices as intrinsic factors characteristic of each species. We used multiple regression analyses to evaluate the effect of the density index and body size of each species on the relative area requirements, or the fragment area at which probability of occurrence equaled 50% from logistic models; the relative time to local extinction, or the fragment age at which probability of occurrence equaled 50% from logistic models; the number of fragments occupied (occupancy); the proportion of population extinctions; and the proportion of colonizations.

Results

Local Extinctions and Colonizations

Twenty-one local extinctions (30 extinctions including Greater Roadrunner) and 12 colonizations occurred across the 30 original habitat fragments resurveyed in 1997 (Table 2), yielding a 1.75 ratio of extinction to colonization. Local extinctions could occur only in previously occupied fragments, and colonizations could occur only in previously vacant fragments. In the 1987 surveys, the eight scrub birds exhibited 94 occurrences and 146 vacancies across the 30 fragments (Soulé et al. 1988). If an equal probability of extinction and colonization is assumed, the expected extinction:colonization ratio is 0.64, significantly lower than the observed 1.75 extinction:colonization ratio ($\chi^2 = 8.42, p = 0.004$).

The mean number of species lost per fragment was 1.00 ± 0.20 (range, 0–3), and the mean number of species gained per fragment was 0.40 ± 0.09 (range, 0–1). Five species exhibited more local extinctions than colonizations (in order of decreasing number of extinctions): California Quail, Greater Roadrunner, Wrentit, California Thrasher, and Cactus Wren (Cactus Wren, found in only one fragment in 1987, was not detected in any of these original fragments in 1997). Three scrub species exhibited more colonizations than local extinctions (in order of decreasing number of colonizations): Bewick's Wren, California Gnatcatcher, and Spotted Towhee. Colonizations of Bewick's Wren and local extinctions of California Quail contributed most to turnover rates (Table 2).

The proportion of local extinctions in a given habitat fragment was higher in smaller fragments ($r = -0.436, p = 0.033$) but was not significantly related to fragment age ($r = 0.070, p = 0.745$) or isolation ($r = -0.003, p = 0.988$). The relative number of colonizations increased with fragment size ($r = 0.382, p = 0.037$) but was not significantly related to fragment age ($r = -0.110, p = 0.562$) or isolation ($r = -0.118, p = 0.536$).

We recorded seven Bewick's Wren and two Spotted Towhee detections within the urban matrix bordering Mission Trails Regional Park (Table 3). Bewick's Wren was detected at each of the 250-, 500-, 750-, and 1000-m transects, and the Spotted Towhee was detected at the 250- and 750-m transects. No other scrub species were detected in developed areas.

Extrinsic Factors

PROBABILITY OF OCCURRENCE

Logistic regression models incorporating fragment area predicted the probability of occurrence of the California Quail, Greater Roadrunner, Bewick's Wren, California Gnatcatcher, Wrentit, California Thrasher, and Spotted Towhee (Table 4). Although the one fragment in which Cactus Wren was detected was relatively large (Bonita Long, 44 ha), logistic regression parameters and their significance could not be calculated for this species due to multicollinearity, ill-conditioning of the correlation matrix, and a resulting instability of estimates (Tabachnick & Fidell 1996). California Quail, Greater Roadrunners, and California Gnatcatchers were likely to occur in only the largest fragments (Fig. 1a). California Thrashers were often found in the largest patches, with probability of occurrence rapidly declining in patches smaller than about 10 ha. Bewick's Wrens, Wrentits, and Spotted Towhees were highly likely to occur in all but the smallest habitat patches. The estimated area at which probability of occurrence was 50% was 63 ha for the Greater Roadrunner, 48 for the California Gnatcatcher, 37 for the California Quail, 10 for the California Thrasher, 4 for the Spotted Towhee, 4 for the Wrentit, and 3 for the Bewick's Wren (calculated from Fig. 1a).

Table 2. Present distribution of eight scrub-specialist bird species in 30 southern Californian habitat fragments originally surveyed by Soulé et al. 1988.^a

Fragment	<i>Bewick's Spotted California California</i>				<i>California Cactus</i>		Total extinctions	Total recolonizations		
	<i>Wrentit</i>	<i>Wren</i>	<i>Towhee</i>	<i>Thrasher</i>	<i>Quail</i>	<i>Roadrunner Gnatcatcher</i>				
Florida	1	1	1	1	1	0	1	0	0	
Sandmark	1	1	1	1	1	1	1 ^b	0	0	1
34th Street	1	1	1	1	0 ^c	0 ^c	0	0	2	0
Balboa Terrace	1	1	1	1	1	0	1 ^b	0	0	1
Alta La Jolla	1	1	1	1	0 ^c	0 ^c	0	0	2	0
Kate Ses.	1	1	1	1	0 ^c	0 ^c	1 ^b	0	2	1
Pottery	1	1 ^b	1	0 ^c	0 ^c	0 ^c	0	0	3	1
Laurel	0	1 ^b	0	0	0	0	0	0	0	1
Canon	0	0	0	0	0	0	0	0	0	0
Zena	1	1	0	1 ^b	0 ^c	0	0	0	1	1
Baja	0 ^c	1	1	0	0	0	0	0	1	0
Washington	0 ^c	1 ^b	0	0	0	0	0	0 ^c	2	1
Solana Drive	1	1	1	1	0 ^c	0 ^c	0 ^c	0	3	0
Syracuse	1	1	1	1	0 ^c	0 ^c	0	0	2	0
32nd Street										
South	1	1 ^b	0	0	0	0	0	0	0	1
Mil Cumbres	1	1	1	0 ^c	1	0 ^c	0	0	2	0
Chollas	1	1 ^b	0	0	0	0	0	0	0	1
60th Street	0 ^c	1	0	0	0	0	0	0	1	0
Juan	0 ^c	1	0	0	0	0	0	0	1	0
Acuna	1	1	1	0	0	0	0	0	0	0
Raffee	1	1	1	0	0	0	0	0	0	0
Spruce	0	1 ^b	0	0	0	0	0	0	0	1
Oak Crest	1	1	1	0 ^c	0 ^c	0 ^c	0	0	3	0
54th Street	1	0 ^c	0	0	0	0	0	0	1	0
Titus	0 ^c	1	0	0	0	0	0	0	1	0
Chateau	1	1	1	0	0	0	0	0	0	0
Talbot	0	0	0	0	0	0	0	0	0	0
Montanosa	1	1	1 ^b	0 ^c	0 ^c	0 ^c	0	0	3	1
Poinsettia	0	0	0	0	0	0	0	0	0	0
El Mac	0	0	1 ^b	0	0	0	0	0	0	1
Extinctions	5	1	0	4	9	9	1	1	30	
Recolonizations	0	6	2	1	0	0	3	0		12

^aFragments are listed in decreasing order of fragment size.^bRecolonizations from 1987 surveys.^cExtinctions from 1987 surveys.

Fragment age predicted the probability of occurrence of California Quail, Cactus Wren, Wrentit, California Thrasher, and Spotted Towhee (Table 4). Probability of occurrence for the Cactus Wren was high in only the youngest fragments (Fig. 1b); the one fragment in which this species was detected was recently isolated (Bonita Long, 8 years). Probability of occurrence of the California Quail and California Thrasher was high in younger fragments but declined rapidly in fragments older than about 10 years. Probability of occurrence of the Wrentit and Spotted Towhee was high in all but the oldest fragments. The estimated age at which probability of occurrence was 50% was 4 years for the Cactus Wren, 13 for the California Quail, 21 for the California Thrasher, 41 for the Spotted Towhee, and 48 for the Wrentit (calculated from Fig. 1b).

After we controlled for area and age effects, isolation was a significant predictor of the probability of occurrence only for Bewick's Wren, which was more likely to be found in less isolated fragments (Fig. 1c). The degree

of isolation at which probability of occurrence was 50% was 3.5 km (calculated from Fig. 1c).

Multiple logistic regression models of the combined effect of area and age generated "extinction surfaces," which consisted of plateaus of occupancy at larger and more recently isolated fragments that declined to basins of local extinctions at smaller and older fragments (Fig. 2). The effect of the interaction between age and area, and hence the contour of the extinction surfaces, varied among species. The estimated fragment size at which probability of occurrence was 95% after 100 years of isolation was 344 ha for Cactus Wrens, 173 for California Quail, 157 for Greater Roadrunners, 146 for Spotted Towhees, 118 for Gnatcatchers, 29 for Wrentits, 29 for California Thrashers, and 13 for Bewick's Wrens (calculated from Fig. 2).

LOCAL EXTINCTION AND COLONIZATION

Backward-elimination logistic regression indicated that models that accounted for fragment area significantly pre-

Table 3. Density indices, occupancy, body weight, proportion of extinctions, and proportion of recolonizations for scrub-specialist bird species in southern California.

Species	Average density index ^a					No. of fragments ^d	No. of fragments ^e	Body weight (g)	Proportion of extinctions ^f	Proportion of recolonizations ^g
	urban 250 m ^b	urban 500 m	urban 750 m	urban 1000 m	all urban ^c					
Wrentit	0.00	0.00	0.00	0.00	0.00	0.97	23	14	0.22	0.00
Spotted Towhee	0.03	0.00	0.03	0.00	0.02	0.80	21	37	0.00	0.13
Bewick's Wren	0.03	0.07	0.10	0.03	0.06	0.76	29	9	0.05	0.60
California Thrasher	0.00	0.00	0.00	0.00	0.00	0.54	12	94	0.33	0.56
California Quail	0.00	0.00	0.00	0.00	0.00	0.49	7	184	0.69	0.00
California Gnatcatcher	0.00	0.00	0.00	0.00	0.00	0.22	5	8	0.50	0.11
Cactus Wren	0.00	0.00	0.00	0.00	0.00	0.13	1	40	1.00	0.00
Greater Roadrunner	0.00	0.00	0.00	0.00	0.00	0.04	1	304	0.90	0.00

^aAverage number of detections per point-count survey within 100 m of point-count station.

^bDensity index per station along urban transect 250 m from the boundary of Mission Trails Regional Park.

^cDensity index per station among all urban stations.

^dDensity index per station per fragment detected.

^eNumber of fragments occupied by each species among the 34 fragments surveyed in 1997.

^fNumber of extinctions experienced by each species, accounting for number of fragments occupied in 1987.

^gNumber of colonizations experienced by each species, accounting for number of fragments not occupied in 1987.

dicted the probability of local extinction for the California Quail, Wrentit, and California Thrasher (Table 4). Local extinctions of these species were more likely in smaller fragments (Table 2). Fragment age predicted extinction probability for Wrentits; higher extinction probabilities were found in older fragments. Isolation did not significantly predict extinction probability for any species.

Backward-elimination logistic regression indicated that models that accounted for fragment area significantly predicted the probability of colonization for Bewick's Wrens, California Gnatcatchers, California Thrashers, and Spotted Towhees (Table 4). Colonization of Bewick's Wrens, California Gnatcatchers, and California Thrashers was more likely in larger fragments, whereas the two colonizations for Spotted Towhees occurred in smaller and younger fragments (Table 2). A model incorporating fragment isolation significantly predicted the probability of colonization for California Thrashers; paradoxically, the association was negative, with the one colonization for this species occurring in a highly isolated fragment.

Intrinsic Factors

Bewick's Wrens, Wrentits, and Spotted Towhees were frequently detected, California Quail and California Thrashers were less abundant, and Greater Roadrunners, Cactus Wrens, and California Gnatcatchers were detected only rarely (Table 3). The negative correlation between body size and average density index was not significant ($r = -0.521$, $p = 0.186$). After we accounted for differences in body size, multiple regressions revealed a significant effect of average density index on occupancy ($\beta = 8.70$, $p = 0.008$), proportion of local extinctions ($\beta = -0.791$, $p = 0.035$), relative-area requirements ($\beta = -0.844$, $p = 0.019$), and relative time to local extinction ($\beta = 0.901$, $p = 0.003$). Relative-area requirements and proportion of local extinctions were

inversely related to the average density index, whereas time to local extinction and occupancy increased with the average density index (Fig. 3).

In contrast, after we accounted for abundance effects, multiple regressions revealed that body size was not related to occupancy ($\beta = -0.095$, $p = 0.657$), proportion of local extinctions ($\beta = 0.255$, $p = 0.369$), or relative-area requirements ($\beta = 0.141$, $p = 0.556$). Body size, however, was negatively related to relative time to local extinction ($\beta = -0.231$, $p = 0.041$); larger animals disappeared from fragments more rapidly than smaller species after we accounted for differences in abundance. Neither average density index ($\beta = 0.236$, $p = 0.627$) nor body size ($\beta = -0.361$, $p = 0.467$) was related to proportion of colonizations.

Discussion

Local extinctions of one or more scrub bird species occurred in 16 out of 30 (53%) habitat fragments, and local extinctions were almost two times more frequent than colonizations. The Greater Roadrunner and California Gnatcatcher have already been extirpated from most urban fragments, today occurring in only the largest sites. The Cactus Wren disappeared from the one fragment in which it occurred in 1987 and was detected in only one additional site in the current surveys, a relatively large (44 ha) and young (8 years) fragment. The Cactus Wren, however, specializes on patchily distributed maritime succulent scrub habitat (Unitt 1984) and may not have been present in many of these sites at the time of isolation from urban development. The California Quail, Wrentit, and California Thrasher exhibited 18 local extinctions since 1987 and only one colonization; local extinctions were more common in fragments that were small (<10 ha) and,

Table 4. Results of backward-elimination logistic regression models of the effect of fragment size, age, and isolation on the probability of occurrence, probability of extinction, and probability of recolonization of scrub-breeding birds in San Diego habitat fragments.

	<i>Whole-model log-likelihood χ^2</i>	<i>p^a</i>	<i>Parameter estimate</i>	<i>χ^2 to remove^b</i>	<i>p</i>
Occurrence					
Bewick's Wren	13.29	0.001			
intercept			5.70		
area			6.46	10.56	0.001
isolation			-3.23	3.55	0.060
Cactus Wren ^c	6.25	0.012			
intercept					
age					
California Gnatcatcher	19.13	<0.001			
intercept			-12.09		
area			7.60		
California Quail	16.71	<0.001			
intercept			2.07		
area			4.42	11.97	<0.001
age			-6.03	5.41	0.020
California Thrasher	34.89	<0.001			
intercept			-7.25		
area			22.97	30.70	<0.001
age			-10.64	5.59	0.018
Greater Roadrunner	3.98	0.046			
intercept			-13.95		
area			6.78		
Spotted Towhee	29.37	<0.001			
intercept			18.73		
area			3.53	6.70	0.010
age			-13.73	22.07	<0.001
Wrentit	28.48	<0.001			
intercept			14.04		
area			6.15	9.26	0.002
age			-11.67	18.05	<0.001
Extinction					
Bewick's Wren ^d	n.s. ^e				
California Quail	3.10	0.078			
intercept			4.22		
area			-2.49		
California Thrasher	10.70	0.001			
intercept			12.00		
area			-13.26		
Wrentit	11.84	0.003			
intercept			10.63		
area			-5.97	5.27	0.022
age			9.27	8.31	0.004
Recolonization					
Bewick's Wren	4.21	0.040			
intercept			-3.24		
area			5.11		
California Gnatcatcher	11.56	<0.001			
intercept			-10.74		
area			6.54		
California Thrasher ^c	7.72	0.021			
intercept					
area					
isolation					
Spotted Towhee ^c	9.03	0.011			
intercept					
area					
age					

^aSignificance of final model was tested by comparing the whole-model log-likelihood χ^2 statistic against the log-likelihood statistic of an intercept-only model. For final models with only one independent variable, this test therefore also evaluated the significance of the removal of that variable from the model.

^bDifference in whole-model χ^2 with and without independent variable in model. Calculated only for models with two or more independent variables.

^cParameters and their significance could not be calculated reliably due to ill-conditioning of correlation matrix and resulting instability of estimates.

^dNo independent variables were retained in the model.

^eNot significant.

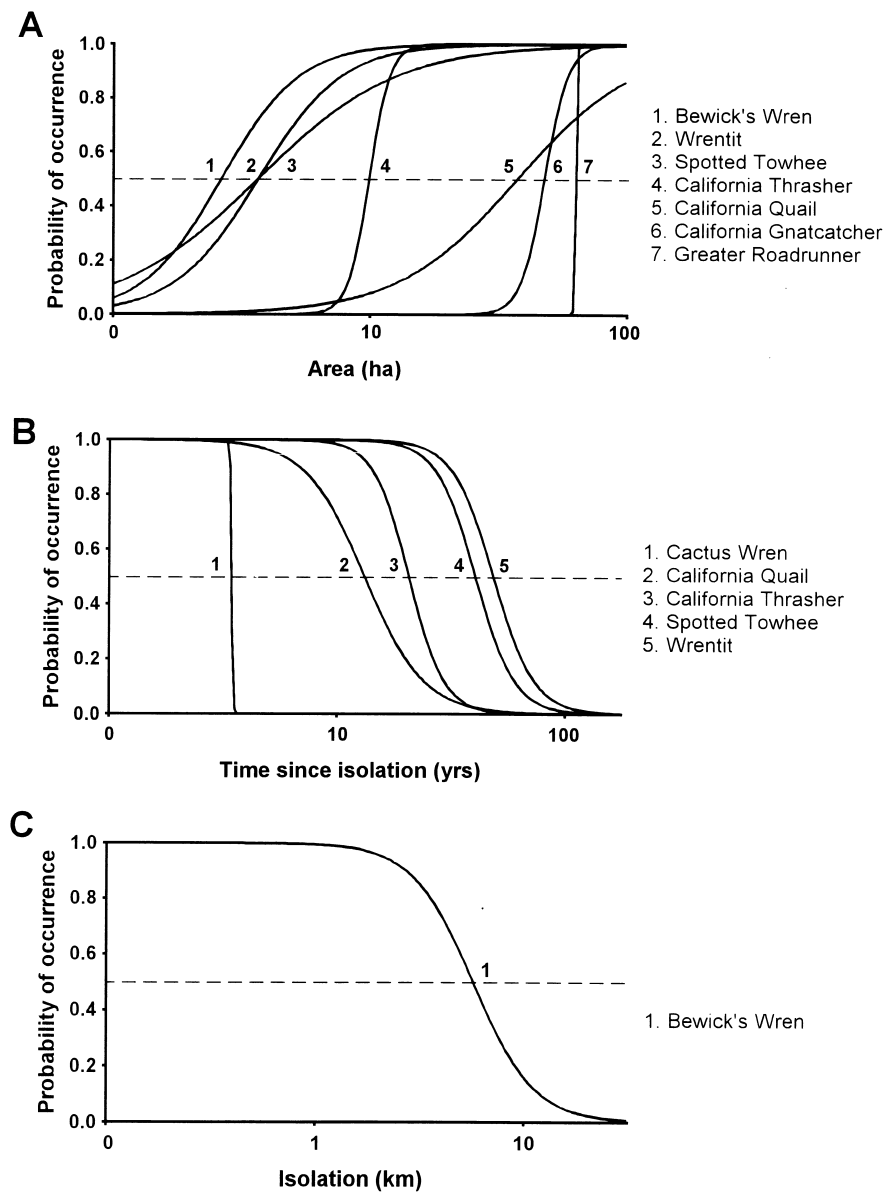


Figure 1. Logistic regression models of the probability of occurrence of eight scrub-breeding bird species as a function of fragment (a) area, (b) age, and (c) isolation. Area, age, and isolation curves were constructed after the other two independent variables were held constant by substituting their median values into a three-way logistic regression model. Only species with significant area, age, or isolation effects in the multiple logistic regression models are presented. Dashed line represents 50% probability of occurrence.

for the Wrentit, fragments that were relatively old (32–86 years). Colonizations, although relatively infrequent, occurred more often than local extinctions for Bewick's Wren, California Gnatcatcher, and Spotted Towhee. Thus, species-occurrence patterns in habitat remnants appear to result from extinction and colonization dynamics, modified by a combination of extrinsic and intrinsic factors.

Extrinsic Factors

The size of the fragment was the most important extrinsic factor determining occupancy patterns, local extinc-

tions, and colonizations of scrub species, confirming the prediction of Soulé et al. (1988). Most scrub species were more likely to go extinct and less likely to colonize small fragments over the last decade and were more likely to occur in larger fragments during this study. Likewise, smaller fragments experienced higher local extinction rates and lower colonization rates over the last decade. Higher relative extinction rates in small fragments are likely explained in part by the fact that these fragments supported fewer scrub species in 1987. Thus, any extinctions would result in higher proportional extinction rates. Nevertheless, the high rate of local extinc-

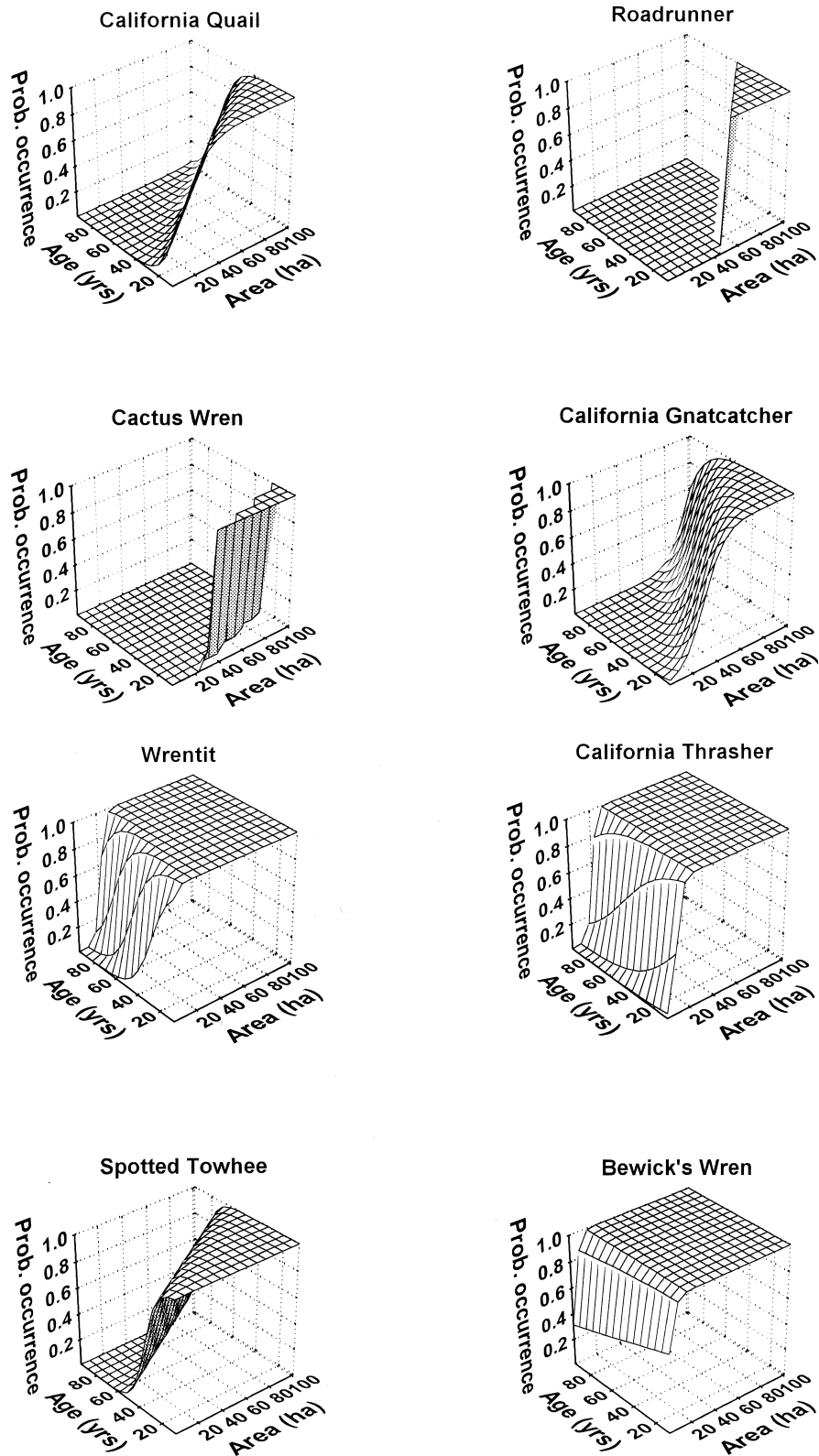


Figure 2. Multiple logistic regression models of the probability of occurrence of eight scrub-breeding bird species as a function of fragment area and age. Local extinction surfaces are parameterized with occupancy data from the 1997 surveys.

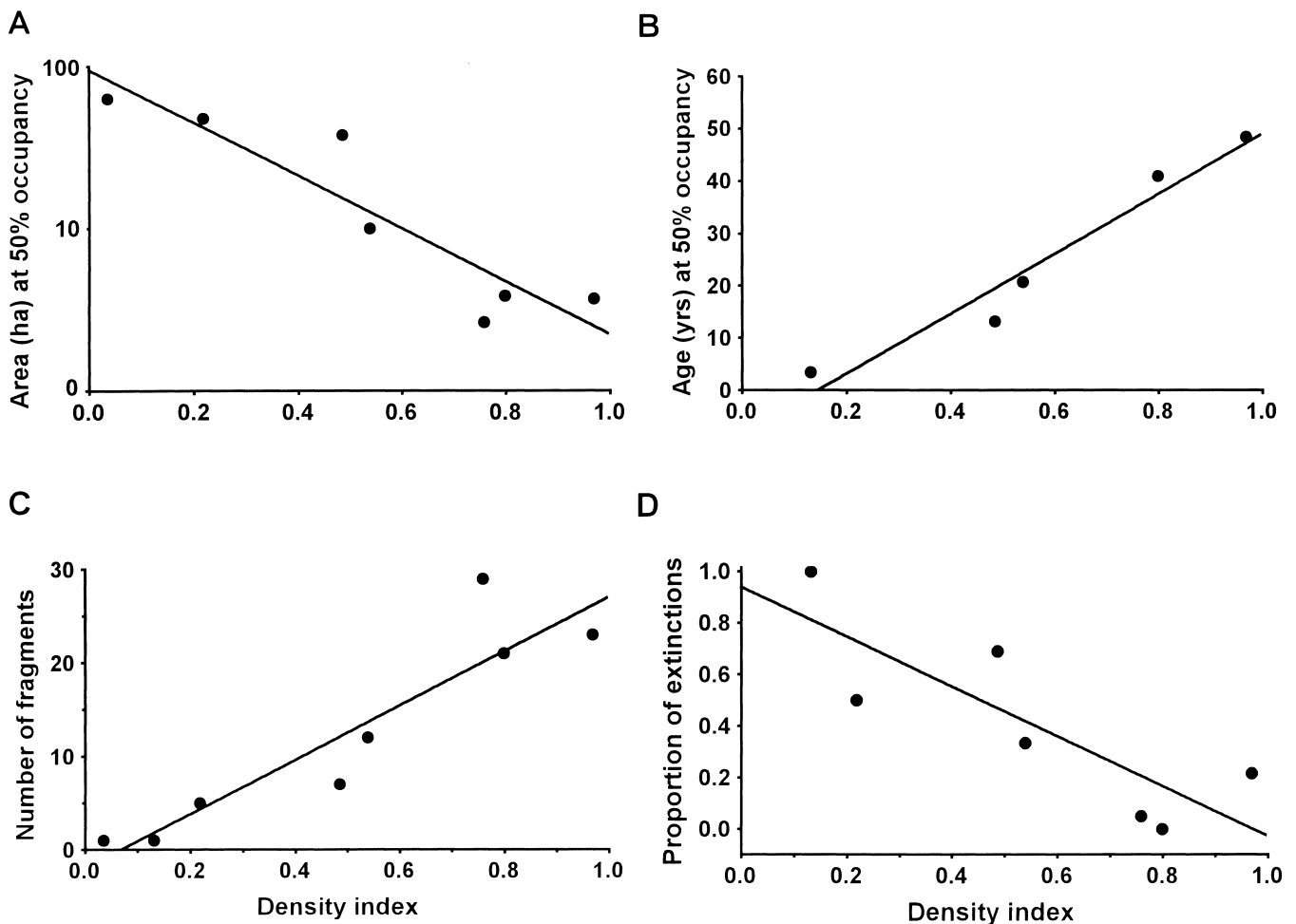


Figure 3. Relationship between density indices of each scrub bird species and (a) relative-area requirements, or the fragment area at which the logistic model predicted a 50% probability of occupancy for the seven species with significant area logistic regressions; (b) relative time to local extinction, or the fragment age at which the logistic model predicted a 50% probability of occupancy for the five species with significant age logistic regressions; (c) number of fragments occupied; and (d) proportion of local extinctions (accounting for the number of fragments occupied in 1987).

tions emphasizes the instability of bird populations in small, isolated, and old fragments (Hinsley et al. 1995).

As predicted by Soulé et al. (1988), fragment age was also an important extrinsic factor determining occupancy and extinction probabilities. The effect of age, however, appeared to be less than that of area: the proportion of local extinctions in each fragment varied with fragment area but not with age. Fragment age, however, was an important determinant of probability of occurrence for some scrub species: most scrub species were more likely to occur in recently isolated fragments. In the earlier surveys, older fragments had already lost many scrub birds, whereas the youngest habitat fragments, even the smallest ones, still contained most scrub species. This study revealed extinctions in these younger fragments since 1987. For example, four of the youngest fragments (Mil Cumbres, Montanosa, Oak Crest, and Solana) each supported most scrub species in 1987, and these young

fragments accounted for 11 of the 30 (37%) recorded local extinctions over the previous 10 years.

Unlike area and age, isolation of a fragment did not significantly predict probability of occurrence or number of local extinctions for most scrub bird species. A weak effect of fragment isolation may be caused in part by the low vagility of scrub-breeding birds. Dispersal has not been studied explicitly in these birds, but they are generally considered to be restricted to coastal sage scrub and chaparral habitat, usually feeding on the ground or within shrub cover, flying low through the scrub canopy, and rarely flying far (Unitt 1984; Soulé et al. 1988). Indeed, the California Quail, Greater Roadrunner, Cactus Wren, Wrentit, and California Thrasher were not detected in urban counts, and all of these species except the California Thrasher (which colonized only one fragment) were not detected in fragments in which they were previously absent. These results are therefore con-

sistent with restricted dispersal for some scrub bird species. If developed areas do not represent suitable habitat, the habitat fragments may emulate true islands for these species. In other insular systems, it has been suggested that the documented disappearance of birds might not represent actual "extinctions" of isolated populations on islands, but rather movement of individuals among islands within large regional populations (Haila & Hanski 1993; Simberloff 1994). In this system, however, movement between fragments appears to have been limited, so in most cases the disappearances we recorded are likely actual population extinctions. Local extinctions in excess of colonizations suggest that these particular species are still disappearing.

Although it appears that dispersal is limited and extinctions ongoing for most scrub bird species, we did record 12 colonizations. Three species—Bewick's Wren, California Gnatcatcher, and Spotted Towhee—had experienced more colonizations than local extinctions since 1987 (although they were still absent from a number of fragments that seemed capable of supporting them). Bewick's Wrens and Spotted Towhees were also detected within the urban matrix. In particular Bewick's Wren appears to be the scrub species most capable of dispersal and colonization across the urban matrix. We recorded six apparent colonizations of Bewick's Wren, and it was the most frequent scrub bird in the urban counts. Furthermore, Bewick's Wren, the only scrub species to show a significant relationship with fragment isolation, was more likely to occur in less isolated fragments, consistent with an ability to occasionally recolonize nearby fragments across the urban matrix. Our estimates of the permeability of the urban matrix also may be underestimates; our urban counts were conducted during the spring and thus reflect use of the urban matrix as breeding habitat, but dispersal might occur in late summer and fall when young are leaving natal areas (Thaxton & Hingtgen 1996).

Thus, Bewick's Wrens, and perhaps the California Gnatcatchers and Spotted Towhees, appear to exist in discrete subpopulations connected by occasional colonization. For these species, a metapopulation perspective (Levins 1969), in which the overall persistence of a species across the landscape is a function of recolonizations of populations from nearby patches, may be an appropriate model (Akçakaya & Atwood 1997). A metapopulation approach predicts that the entire network of habitat fragments, including fragments currently unoccupied, may be critical to the long-term persistence of these species (Hanski 1998).

Intrinsic Factors

In accordance with Soulé et al.'s (1988) prediction, we found that for scrub species the average density index was significantly related to the number of sites occupied, to relative-area requirements, to relative time to local ex-

tingtion, and to local extinction rates. Extinction on islands is thought to result frequently from the effects of environmental, demographic, and genetic stochasticity in small, isolated populations (Gilpin & Soulé 1986). Because both population density and fragment area were highly significant and independent predictors of local extinction rates for scrub species, population size appears to be a factor driving extinction rates for scrub species.

Body mass incorporates physiological, life-history, and ecological characteristics of species (Peters 1983). The relationship between body size and extinction risk in birds, however, has been the subject of considerable debate, and evidence of a generalized pattern remains equivocal (Terborgh 1974; Pimm et al. 1988; Tracy & George 1992; Gaston & Blackburn 1995; Johst & Brandl 1997). In our study, body size did not significantly predict occupancy and number of local extinctions in scrub species. Body size, however, was correlated with time to local extinction: extinction was more rapid for larger species, even after we accounted for abundance differences in birds of different sizes. Indeed, all but one of the extirpations in the four youngest canyons were of California Quail, Greater Roadrunners, and California Thrashers, the three largest birds; over all the fragments, we recorded 23 local extinctions but only one colonization of these three species. Thus, although large-bodied animals may live longer, have lower population variation, and be better buffered against short-term environmental stress (Pimm et al. 1988; Tracy & George 1992), larger species in this system also may be less vagile and may have higher resource requirements, thereby limiting colonization and increasing extinction probabilities (Terborgh 1974).

The probability of extinction for any species depends on complex interactions of species characteristics and environmental variables that affect both individuals and populations (Tracy & George 1992). Although density appears to be a good predictor of extinction vulnerability of scrub birds, other ecological differences will clearly affect their persistence. All species in this study breed in scrub habitats in this region, but they vary greatly in ecological traits such as trophic level, fecundity, longevity, territory size, and food and nesting requirements. For example, Roadrunners, a top predator on vertebrates, occupy relatively large territories (approximately 40–50 ha per breeding pair; Hughes 1996) and therefore would be able to persist in only the largest fragments. Given the ecological heterogeneity of these birds, idiosyncratic autecological features of individual species must be considered in the design of conservation measures for these species in fragmented landscapes.

Possible Mechanisms

The loss and degradation of habitat certainly contributes to extinctions within fragments. Native vegetative cover

declines closer to the urban edge (Suarez et al. 1998), fragments with proportionally more urban edge have an increased diversity of ruderal and ornamental plant species (Alberts et al. 1993), and the proportion of native shrub cover declines with fragment age (Soulé et al. 1988; Suarez et al. 1998). Changes in microhabitat availability within fragments may particularly affect species with strict habitat requirements, such as the Cactus Wren, which specializes on maritime succulent scrub (Unitt 1984), and the California Gnatcatcher, which requires coastal sage scrub (Akçakaya & Atwood 1997). Local extinctions can also occur before there is much loss of habitat, however. We recorded disappearances of scrub birds in young fragments that were isolated only recently, and we recorded nine local extinctions in fragments that still retained a high proportion (>75%) of native shrub cover.

In addition to overt habitat degradation or other physical changes in the fragments, other factors likely contribute to extirpations of scrub birds. For example, the matrix surrounding habitat islands may support competitors and predators whose interactions with species within islands may alter population persistence and community structure (Wilcove 1985; Andren & Angelstram 1988). Exotic carnivores (opossums, domestic cats) and native carnivores (gray foxes, striped skunks, and raccoons) occur within the developed matrix and are predators on birds and bird nests in this system (Soulé et al. 1988; Langen et al. 1991; Crooks & Soulé 1999) and elsewhere (Wilcove 1985; Churcher & Lawton 1987; Leimgruber et al. 1994). Numbers and activities of these opportunistic "mesopredators" increase with the disappearance of the dominant predator, the coyote, in the fragments, a process termed *mesopredator release* (Soulé et al. 1988; Crooks & Soulé 1999). In turn, the species richness of scrub-breeding birds was lower in fragments with more mesopredators and fewer coyotes, even after we accounted for the positive effect of fragment area and the negative effect of fragment age on scrub bird persistence (Crooks & Soulé 1999).

Conclusions

Urban habitat fragments in coastal southern California continue to show a net loss of scrub bird species. A few species, however, particularly Bewick's Wren, seem capable of recolonizing fragments across the urban matrix. Logistic regression models predict that most species have low probabilities of persisting in the smallest fragments over time. The logistic models for several species, such as Bewick's Wren, Wrentit, and California Thrasher, predict high probabilities of occurrence in old fragments, but only if they are large. Other species, such as the California Quail, Greater Roadrunner, Cactus Wren, and California Gnatcatcher, have little chance of long-

term persistence in even the largest of these fragments. No fragments were large enough to support the full complement of scrub-breeding bird species with 95% probability over the next 100 years.

Although these projections do not evoke optimism, native species can still persist within the fragments. Because of their habitat specializations and limited dispersal abilities, the scrub-breeding birds we surveyed are the most sensitive birds in this system to the loss and fragmentation of habitat. Despite this vulnerability, some of their populations have persisted for up to a century in a rapidly developing landscape and might continue to persist, particularly in the largest fragments. The urban habitat fragments also support many other native bird species, such as those that are less specialized and better dispersers than the scrub-breeding birds (Crooks et al., unpublished data), a wide range of native plants (Alberts et al. 1993), rodents (Bolger et al. 1997b), invertebrates (Suarez et al. 1998; Bolger et al. 2000), and mammalian carnivores (Crooks & Soulé 1999). The persistence of these native populations in the urbanizing landscape depends on the persistence of the fragments themselves.

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