

ANNUAL SURVIVORSHIP OF THE SEDENTARY RUFIOUS-CROWNED SPARROW (*AIMOPHILA RUFICEPS*): NO DETECTABLE EFFECTS OF EDGE OR RAINFALL IN SOUTHERN CALIFORNIA

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ABSTRACT.—The Rufous-crowned Sparrow (*Aimophila ruficeps*) is a nonmigratory passerine that displays an area-sensitive distribution pattern of abundance in fragmented coastal sage-scrub habitat of southern California. To determine if habitat fragmentation negatively affected adult survival, we used Cormack-Jolly-Seber models to compare annual survival probabilities of adult sparrows breeding in habitat adjacent to urban-developed edges to those of birds breeding in the interior of large habitat expanses in San Diego County, 1997–2000. During that period, an El Niño event brought heavy rainfall to the study area, and a La Niña event brought drought. Annual survival probabilities were relatively high for a small passerine (females: 0.69 ± 0.05 SE; males: 0.74 ± 0.04 SE) but, given our data, did not differ between habitat types or with rainfall. Annual resighting probabilities for the birds were strongly associated with variation in rainfall, being high in the wet year and low in the dry year. Mate- and site-fidelity were apparently high, and surveys during the nonbreeding season documented that the sparrows stayed paired and on territories year-round. We hypothesize that the high apparent survivorship of this species is related to its nonmigratory habit and its tendency to curtail reproductive effort during periods of food scarcity. Although our survivorship analysis suggests that the urban-wildland interface does not adversely affect survival of territorial Rufous-crowned Sparrows, our power to detect an effect of habitat edge on survival was low. Thus, we urge caution in concluding that edge effects do not have an ecologically important influence on survival rates in this species. Received 10 February 2003, accepted 28 March 2004.

RESUMEN.—*Aimophila ruficeps* es un ave paseriforme no migratoria que presenta un patrón de distribución de abundancia afectado por la fragmentación del matorral costero en el sur de California. Para determinar si la fragmentación de hábitat afecta la supervivencia de los adultos, utilizamos modelos de Cormack-Jolly-Seber para comparar la probabilidad de supervivencia anual de los adultos que nidifican en hábitats adyacentes a los bordes urbanos con adultos que nidifican en el interior de grandes extensiones de hábitat en el condado de San Diego, entre 1997 y 2000. Durante este período un evento El Niño produjo fuertes lluvias en el área de estudio y un evento La Niña produjo sequía. Las probabilidades de supervivencia anual fueron relativamente altas para este paserino de pequeño tamaño (hembras: 0.69 ± 0.05 EE; machos: 0.74 ± 0.04 EE) pero, de acuerdo a nuestros datos, no difirieron entre los tipos de hábitat o con las precipitaciones. Las probabilidades anuales de re-avistamiento de estas aves estuvieron fuertemente asociadas con las variaciones en las precipitaciones, siendo alta en el año húmedo y baja en el año seco. Las fidelidades de sitio y de pareja fueron aparentemente altas, y los censos realizados durante la época no reproductiva mostraron que estas aves permanecieron apareadas y en sus territorios durante todo el año. Proponemos la hipótesis de que la alta supervivencia aparente de esta especie se relaciona con su hábito no migratorio y con la tendencia a restringir su esfuerzo reproductivo durante los periodos de escasez de alimento. A pesar de que los análisis de supervivencia sugieren que la interfase de hábitat urbano-silvestre no afecta negativamente la supervivencia de *A. ruficeps*, el poder de nuestros análisis para detectar un efecto de borde de hábitat sobre la supervivencia fue bajo. Por esto, recomendamos suma precaución al concluir que los efectos de borde no tienen una influencia ecológica importante sobre las tasas de supervivencia en esta especie.

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IN MANY FRAGMENTED landscapes—including North American mid-Atlantic forests (Robbins et al. 1989), midwestern grasslands (Herkert 1994, Winter and Faaborg 1999), and southwestern scrubland (Bolger et al. 1997)—as the area of remaining habitat is reduced, some songbird species decline more sharply in abundance than others. When natural habitat is fragmented, it is concurrently reduced in area, dispersed in a matrix of human-modified habitat, and exposed to that matrix along its edges (Wilcox and Murphy 1985). Biotic and abiotic factors may “spill over” from the matrix and degrade the quality of the remaining habitat (Murcia 1995). Edge effects may generate area-sensitive distribution patterns in abundance, because smaller fragments have higher edge:area ratios. Most research on the mechanisms underlying avifaunal collapse following fragmentation have focused on relative nesting success in habitat isolates and along habitat edges. Numerous studies have documented edge-related declines in songbird nesting-habitat quality because of elevated brood-parasite and nest-predator abundance (Paton 1994, Morrison et al. 1999). Reduced nest-success may result from declines in food-resource availability coincident with fragmentation (Zanette et al. 2000). But edge effects may affect other demographic processes as well (e.g. pairing success of males; Gibbs and Faaborg 1990), and an understanding of such effects may be necessary to mitigate declines in native diversity following fragmentation. Changes in predator communities or food availability near habitat edges, for example, could directly or indirectly affect the mortality rates of birds. To our knowledge, however, no published studies have addressed edge effects on survivorship of adult songbirds.

A standard method for quantifying avian survival rates entails marking individuals with unique combinations of colored leg-bands, then surveying the study area in subsequent years to count those marked individuals that have “returned” (Lebreton and North 1993). However, simple return rates (i.e. proportion of marked individuals that are detected in the following year) provide biased survival-rate estimates, because it is unlikely that all birds not detected in subsequent years have actually died. Some birds may have temporarily emigrated off-plot, whereas others may have gone undetected during a survey period. Therefore, statistical

methods, such as Cormack-Jolly-Seber models (Pollock et al. 1990; Lebreton et al. 1992), must be used to correct the bias of missed detection on survival-rate estimates. Probability of permanent emigration from study areas, however, is much more difficult to quantify (Turchin 1998), and usually remains subsumed in the estimates of survival. Such estimates thus reflect apparent (rather than true) survival.

Consequently, comparative studies addressing effects of relative habitat quality on survivorship must be aware of behavioral factors that could obscure patterns in survival. For example, birds in territories abutting habitat edges may have relatively fewer conspecific neighbors—resulting, perhaps, in less territorial defense, less conspicuous activity, and therefore reduced detectability during resighting surveys. If nesting-habitat quality is lower in edges, and if birds respond to low nesting success by not returning to the same breeding territory in subsequent years (Haas 1998, Forero et al. 1999), then survival could appear lower in edges not because of higher mortality but because of lower fidelity to breeding sites. Edge-associated changes in vegetative composition (Gates and Gysel 1978) or arthropod prey biomass (Burke and Nol 1998) might also influence habitat selection by birds breeding in fragmented landscapes. Area-sensitive patterns in abundance could be generated by either higher mortality in or higher dispersal from edge habitat, and distinguishing between them has clear biological importance. Given that those two processes can confound one another, species that exhibit high territorial fidelity are best suited for assessment of edge effects on survival.

Coastal sage-scrub habitat in California has been a focus of ornithological research on effects of habitat fragmentation (reviewed in Bolger 2002). The habitat is characterized by a drought-deciduous plant community that once formed a contiguous mosaic with chaparral and grassland in the lowlands between Los Angeles, California, and northwestern Baja California, Mexico (Mooney 1977). Extensive fragmentation by urban development has resulted in loss of as much as 90% of coastal sage scrub's historic coverage (Westman 1981). The pattern of urban development in the region exposes a high proportion of the remaining habitat to developed edges (Soulé et al. 1988). Thus, an understanding of the suite of biotic and abiotic changes that

occur near edges will be important for conservation of native diversity in the region. Nearly 100 species that reside in coastal sage scrub have been listed as endangered, threatened, or of conservation concern (Atwood 1993).

The Southern California (or "Ashy") Rufous-crowned Sparrow (*Aimophila ruficeps canescens*) is a nonmigratory songbird resident in California coastal sage-scrub habitat (Grinnell and Miller 1944, Unitt 1984). In San Diego County, the Rufous-crowned Sparrow exhibits an area-sensitive distribution pattern: its abundance in small (1–100 ha) fragments is only 2% of its abundance in larger habitat expanses (>1,000 ha), where it tends to be common (Bolger et al. 1997; Crooks et al. 2001, 2004). The subspecies is listed as a California species of special concern (California Department of Fish and Game 1992). A three-year study of Rufous-crowned Sparrow reproductive biology in San Diego County found that the annual mean number of fledged offspring of birds nesting in habitat adjacent to urban edges did not differ from that of birds nesting in the interior of large habitat expanses (Morrison and Bolger 2002a). That lack of an urban edge effect on fecundity occurred despite a higher abundance in edge plots of some putative nest predators and a lower abundance of some arthropod taxa that are important prey for breeding Rufous-crowned Sparrows (Bolger 2002, Patten and Bolger 2003, D. T. Bolger unpubl. data). Lower food-availability could potentially affect adult survivorship (Boag and Grant 1981), as could elevated abundance of predators of adult songbirds (e.g. house cats [*Felis catus*]; Crooks and Soulé 1999) along edges. Predator scans conducted regularly over the course of the present study found that small raptors (e.g. Cooper's Hawks [*Accipiter cooperii*], Sharpshinned Hawks [*A. striatus*], American Kestrels [*Falco sparverius*], and White-tailed Kites [*Elanus leucurus*]) were significantly more abundant in edge plots (D. T. Bolger unpubl. data). Perhaps urban edges attract such predators by providing more nesting or perching sites (e.g. ornamental vegetation, utility poles) than low-stature scrub vegetation.

Here, we present the results of a four-year mark-resighting study, in which we compared annual survivorship and detection probabilities of Rufous-crowned Sparrows between edge and interior habitats. Given the area-sensitive distribution pattern of this species in San Diego County,

we hypothesized that annual survival rates of adults would be lower in edge habitats. We also examine within- and between-year patterns of mate- and site-fidelity in the species and characterize its tendency to disperse after breeding.

METHODS

To examine the effects of edges while controlling for fragmentation effects that result from area reduction (see Crooks and Soulé 1999) or isolation (see Crooks et al. 2001), we selected large habitat expanses. We established eight research plots in habitat interior areas (mean distance from residential development = 1.1 km, range 0.6–1.5 km), and seven edge plots (<250 m from linear edge with high-density residential development), distributed over three publicly owned habitat expanses in San Diego County, California (Fig. 1). Age of adjacent housing developments ranged from 11 to 27 years in 1997. Plots ranged in size from 5 to 10 ha; size varied because of constraints encountered in our efforts to encompass similar vegetative characteristics across all plots and juxtapose similar human land-use

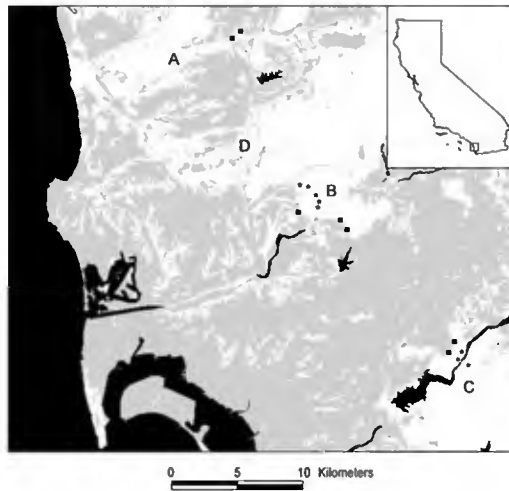


FIG. 1. Research sites in San Diego County, California. All are publicly owned nature reserves: (A) Los Peñasquitos Canyon Preserve (3,720 acres); (B) Mission Trails Regional Park (5,760 acres); and (C) San Diego National Wildlife Refuge, Sweetwater Unit (6,100 acres). Weather data were collected at the U.S. Marine Corps Air Station Miramar (D; approximately 32.9°N, 117.1°W). Gray areas represent urban or residential development; black areas represent water; white areas represent undeveloped natural habitat. Stars indicate location of research plots in interior habitat; squares indicate edge plots. Location of study area in California is indicated on inset map.

characteristics across all edge plots. Vegetative cover and structure were similar between edge and interior plots (see Morrison and Bolger 2002a) although, in the interior of one site (Peñasquitos Canyon), coastal sage-scrub habitat was interdigitated with chaparral and grassland, such that no appropriate interior plots could be located there. A 50-m² grid system was staked into each plot.

The mediterranean climate of coastal San Diego County is characterized by winter rainfall and summer drought. Rufous-crowned Sparrows are seasonal breeders that typically begin breeding in February–March, as the winter rainy season wanes (Wolf 1977). Reproductive effort and success appear to be highly dependent on rainfall (Morrison and Bolger 2002b). In dry years, birds may not attempt to breed. In more favorable breeding conditions, sparrows may be multibrooded, with renesting tapering off at onset of summer drought in June–July.

We studied Rufous-crowned Sparrows from 1997 through 2000. Birds were captured with mist nets and marked during the 1997–1999 breeding seasons. Each individual was marked with a unique combination of colored leg-bands. Tarsus and wing-chord lengths and body mass were measured prior to release. Mean (± 1 SE) mass of Rufous-crowned Sparrows in the study was 17.3 \pm 1.0 g for males ($n = 157$) and 17.0 \pm 1.2 g for females ($n = 106$). The species is sexually monochromatic, but sex of breeding individuals can be determined at capture by presence of breeding characters—cloacal protuberance in males, brood patch in females. Age of birds cannot be determined reliably beyond the hatch year (Pyle 1997). Although males aggressively defend breeding territories (~1 ha in area) from conspecifics, behaviors of both sexes are generally inconspicuous. During the 1998–2000 breeding seasons, we used binoculars to resight banded birds on the research plots. In each year, we recorded locations of all Rufous-crowned Sparrow sightings within the grid system on our plots, noting in particular the area defended by males and used by breeding pairs. From those data, we established territory boundaries for all birds residing on the plots. Throughout the 1997–1999 breeding seasons, we also surveyed those plots extensively for reproductive and other data (Morrison and Bolger 2002a, b). We did not collect reproductive data during the 2000 breeding season, but instead worked exclusively on resighting birds during March and April. Each plot was surveyed until we had mapped all territory boundaries and determined whether all individuals detected were marked. Playbacks of recorded Rufous-crowned Sparrow vocalizations were used occasionally in 2000 to facilitate detection of birds.

Climatic conditions.—Annual rainfall was highly variable over the course of the study. In the San Diego region, variation in rainfall is coupled with the El Niño Southern Oscillation (ENSO; Pavia and Badan 1998).

The study spanned both El Niño and La Niña phases of the ENSO cycle. During the winter of 1997 and spring of 1998, a powerful El Niño event brought heavy rains. In 1999, and continuing through 2000, a La Niña event brought prolonged drought conditions.

To examine the effect of rainfall on annual survivorship, we calculated total precipitation over the year-long census interval, which we defined as April through March of the subsequent year. Rainfall data were provided by the Weather Service Branch of the U.S. Marine Corps Air Station, Miramar, located near the center of our study area (Fig. 1). Total rainfall between April and the following March was 518 mm in 1997–1998, 235 mm in 1998–1999, and 173 mm in 1999–2000. Mean annual rainfall over the period 1950–1999 was 279 mm.

Survival analysis.—Cormack-Jolly-Seber (CJS) models (Pollock et al. 1990, Lebreton et al. 1992) and the program MARK (White and Burnham 1999) were used to estimate annual survival (ϕ) and resighting (p) probabilities from capture histories of 46 females and 61 males in edge plots, and 60 females and 96 males in interior plots. To exclude potential transients (i.e. nonterritorial birds) from data analysis, we did not include individuals that were banded and never detected post-release in the same season (two females and no males from edge plots, four females and five males from interior plots). Models were constructed using a logit link function and design matrices. Fit of the global model was verified with the program RELEASE goodness-of-fit procedure (tests 2 and 3; Burnham et al. 1987) implemented in MARK.

Based on our knowledge of Rufous-crowned Sparrow biology and on the limitations inherent in our data set, we considered 21 candidate CJS models. We hypothesized that the following factors influenced survival and resighting rates: habitat type (“hab”; i.e. edge and interior), sex, and annual rainfall (“rain”). Rainfall was included in models as a covariate. We did not consider age-specific parameterizations of ϕ because of our inability to accurately age adult sparrows and the lack of transient individuals in the modeled population (see above). Because survival in small passerines often differs between females and males (Breitwisch 1989, Payevsky et al. 1997), ϕ was always modeled as a function of sex. Given that constraint, we included all one- and two-factor parameterizations of ϕ , and constant as well as all one- and two-factor parameterizations of p , in the candidate set of CJS models. We also modeled three-way interactions among sex, habitat, and rain for both ϕ and p (i.e. [$\phi_{\text{sex-hab-rain}}, p_{\text{sex-hab-rain}}$]; see Table 1). In the global model, ϕ and p were functions of sex, habitat, and year: [$\phi_{\text{sex-hab-year}}, p_{\text{sex-hab-year}}$].

Model-selection methods using second-order Akaike’s Information Criterion values, or AIC_c (Lebreton et al. 1992, Burnham and Anderson 1998) were used to (1) provide the best estimates of annual

TABLE 1. Models of annual survival (ϕ) and recapture (p) probabilities for adult Rufous-crowned Sparrows in San Diego County, California, 1997–2000. Columns give model notation, number of estimable parameters (K), second-order Akaike’s Information Criterion values (AIC_c), AIC_c differences (Δ_i), and AIC_c Weights (w_i). Statistics for the best-fit model are in bold. Subscripts define parameterizations of ϕ and p : “sex” = sex-specific; “rain” = linear function of annual rainfall (see text); “hab” = different between edge and interior habitats; no subscript = constant; subscripts joined by a multiplication sign indicate a factorial model. Based on the program RELEASE (Burnham et al. 1987), the global model ($\phi_{\text{sex}\cdot\text{hab}\cdot\text{year}} p_{\text{sex}\cdot\text{hab}\cdot\text{year}}$) provided a good fit to the data ($\chi^2 = 11.04$, $df = 12$, $P = 0.53$). Models with low statistical support ($w_i \leq 0.01$) are not presented, with the exception of model [$\phi_{\text{sex}\cdot\text{hab}\cdot\text{rain}} p_{\text{sex}\cdot\text{hab}\cdot\text{rain}}$] and the global model (10).

Model	K	AIC_c	Δ_i	w_i
(1) $\phi_{\text{sex}} p_{\text{rain}}$	4	649.06	0	0.45
(2) $\phi_{\text{sex}} p_{\text{sex}\cdot\text{rain}}$	6	650.94	1.89	0.18
(3) $\phi_{\text{sex}} p_{\text{hab}\cdot\text{rain}}$	6	652.23	3.18	0.09
(4) $\phi_{\text{sex}\cdot\text{hab}} p_{\text{rain}}$	6	652.78	3.73	0.07
(5) $\phi_{\text{sex}\cdot\text{rain}} p_{\text{rain}}$	6	653.11	4.06	0.06
(6) $\phi_{\text{sex}\cdot\text{rain}} p_{\text{sex}\cdot\text{rain}}$	8	654.63	5.57	0.03
(7) $\phi_{\text{sex}\cdot\text{hab}} p_{\text{sex}\cdot\text{rain}}$	8	654.71	5.66	0.03
(8) $\phi_{\text{sex}\cdot\text{hab}} p_{\text{hab}\cdot\text{rain}}$	8	655.29	6.23	0.02
(9) $\phi_{\text{sex}\cdot\text{hab}\cdot\text{rain}} p_{\text{sex}\cdot\text{hab}\cdot\text{rain}}$	12	658.91	9.86	0.00
(10) $\phi_{\text{sex}\cdot\text{hab}\cdot\text{year}} p_{\text{sex}\cdot\text{hab}\cdot\text{year}}$	16	661.24	12.18	0.00

ϕ and p for the Rufous-crowned Sparrow and (2) assess statistical support for habitat-, sex-, and rainfall-related differences in those parameters. Relative likelihood of each model in the candidate set was estimated with AIC_c weights (w_i ; Burnham and Anderson 1998). We used MARK’s model-averaging procedure to compute average annual estimates of ϕ and p from all models in the candidate set. Statistical support for sex-, habitat-, and rainfall-related differences in ϕ and p was assessed by summing the w_i for all models in which a parameter of interest occurred.

After running the initial set of 21 candidate models, we considered a larger model set containing all additive models that complemented the factorial models described above (e.g. [$\phi_{\text{sex}\cdot\text{hab}\cdot\text{rain}} p_{\text{sex}\cdot\text{hab}\cdot\text{rain}}$]). Model-averaged estimates from that expanded model set (containing all additive and factorial models) did not substantially differ from those in Table 2. Thus, for clarity, we have not presented those results.

Retrospective analysis of edge effects on sparrow survival.—We conducted a retrospective analysis, following Steidl et al. (1997), to determine if our data enabled detection of ecologically relevant differences in ϕ between edge and interior habitats, given possible variation in ϕ with rainfall and sex. For that analysis, we considered a proportional difference in ϕ , or effect size, of ≥ 0.2 to be ecologically important. A 20% reduction in annual survival probability (see below) would reduce by ~50% the estimated number of both females and males that would survive for four years, the average interval between ENSO events (Trenberth 1991, Enfield and Mestas-Nuñez 1999). Reproductive

success of Rufous-crowned Sparrows in San Diego County covaries with the ENSO cycle: reproductive output is high during wet El Niño years and low during dry La Niña years (Morrison and Bolger 2002b). Surviving for four breeding seasons would, on average, increase the likelihood of experiencing favorable breeding conditions. Therefore, a 50% decline in number of sparrows surviving for four years could have a strong effect on population dynamics.

Annual, sex-specific, and habitat-specific estimates of ϕ from model [$\phi_{\text{sex}\cdot\text{hab}\cdot\text{rain}} p_{\text{sex}\cdot\text{hab}\cdot\text{rain}}$], and their associated variances and covariances, were used in retrospective analysis of edge effects. That model was chosen because it allows ϕ and p to vary with sex, habitat, rainfall, and all possible interactions among those three factors. For both females and males in each year, we calculated the proportional difference in survival probability between edge and interior habitats (i.e. $\hat{\phi}_{\text{edge}}/\hat{\phi}_{\text{interior}}$), hereafter $\Delta\hat{\phi}$. Associated variance in $\Delta\hat{\phi}$ for each sex \times year group (e.g. 1998 females) was next estimated with the delta method (Williams et al. 2002) as

$$\text{var} \Delta\hat{\phi} = \Delta\hat{\phi}^2 \left[\frac{\text{var}(\hat{\phi}_{\text{edge}})}{\hat{\phi}_{\text{edge}}^2} + \frac{\text{var}(\hat{\phi}_{\text{interior}})}{\hat{\phi}_{\text{interior}}^2} - \frac{2 \text{cov}(\hat{\phi}_{\text{edge}}, \hat{\phi}_{\text{interior}})}{\hat{\phi}_{\text{edge}} \times \hat{\phi}_{\text{interior}}} \right]$$

TABLE 2. Model-averaged estimates of annual survival (ϕ) and recapture (p) probabilities, unconditional standard errors, and profile-likelihood 95% confidence intervals for adult Rufous-crowned Sparrows in edge and interior coastal sage-scrub habitats in San Diego County, California, 1997–2000.

Year	$\phi \pm 1 \text{ SE}$ (95% CI)		$p \pm 1 \text{ SE}$ (95% CI)	
	Edge	Interior	Edge	Interior
Female				
1997–1998	0.685 \pm 0.050 (0.579–0.775)	0.691 \pm 0.050 (0.587–0.779)	0.974 \pm 0.029 (0.792–0.997)	0.968 \pm 0.034 (0.776–0.996)
1998–1999	0.682 \pm 0.048 (0.582–0.768)	0.689 \pm 0.045 (0.590–0.773)	0.863 \pm 0.050 (0.734–0.935)	0.851 \pm 0.046 (0.737–0.921)
1999–2000	0.681 \pm 0.050 (0.577–0.770)	0.688 \pm 0.049 (0.586–0.775)	0.799 \pm 0.082 (0.592–0.916)	0.789 \pm 0.078 (0.600–0.904)
Male				
1997–1998	0.742 \pm 0.045 (0.644–0.820)	0.743 \pm 0.045 (0.647–0.821)	0.983 \pm 0.021 (0.835–0.998)	0.978 \pm 0.023 (0.810–0.998)
1998–1999	0.740 \pm 0.043 (0.647–0.815)	0.742 \pm 0.043 (0.649–0.817)	0.854 \pm 0.045 (0.743–0.922)	0.844 \pm 0.041 (0.744–0.909)
1999–2000	0.739 \pm 0.045 (0.642–0.817)	0.741 \pm 0.045 (0.644–0.819)	0.764 \pm 0.078 (0.580–0.884)	0.755 \pm 0.073 (0.587–0.870)

We approximated a 95% confidence interval (CI) around each $\hat{\text{var}} \Delta\hat{\phi}$ as

$$\Delta\hat{\phi} \pm 1.96\sqrt{\hat{\text{var}}\Delta\hat{\phi}}$$

and an 80% CI as

$$\Delta\hat{\phi} \pm 1.28\sqrt{\hat{\text{var}}\Delta\hat{\phi}}$$

Before graphing and interpreting the estimates described above, we subtracted 1 from all values of $\Delta\hat{\phi}$ and their associated upper and lower confidence intervals; those numbers can be used as follows. If AIC model selection supports the hypothesis of reduced survival rates in edge habitats, the retrospective analysis would indicate whether a difference in survival was (1) ecologically relevant (e.g. CI includes only values $\phi \leq -0.2$) or (2) merely statistically significant (i.e. CI includes only negative numbers). If AIC model selection fails to reject the null hypothesis of no difference among habitats, retrospective analysis would provide insight about the power of our CJS models to detect an edge effect on survival. Statistical power would be acceptable for a given group, meaning that we would be confident that survival was habitat-independent, if the CI does not include values less than or equal to -0.2 or ≥ 0.2 . A CI that includes 0 as well as values less than or equal to -0.2 would indicate that our power to detect a negative edge-effect on sparrow survival is low.

Nonbreeding-season habitat use.—To characterize the tendency of Rufous-crowned Sparrows to disperse after breeding, we described the species' habitat use

during the nonbreeding season. Between 14 and 21 December 1999, we attempted to resight all banded birds on nine of our plots (four edge, five interior) that had the highest numbers of banded individuals during the previous breeding season. When overwintering, Rufous-crowned Sparrows tend to be even more cryptic than when breeding. Occasionally, playbacks of a recorded song or contact call (Collins 1999) instigated a response and thus facilitated detection. Contact calls between birds were not frequent, but they were heard consistently during the surveys. We considered birds to be paired if we observed them foraging and moving together and exchanging contact calls. In general, we surveyed for birds by walking transects through plots; we often deviated from the transect, however, because infrequency of detections rendered systematic surveys inefficient, compared with investigating any bird sighting or vocalization. We recorded locations of resighted birds and their paired status within the grid system of the plots and then compared locations of birds during the nonbreeding season with their previous breeding territories. Resighting data from winter surveys were not included in survivorship analysis.

RESULTS

Survivorship.—Annual apparent-survival probabilities of adult Rufous-crowned Sparrows in our study area did not clearly differ between edge and interior habitats, and did not vary with interannual variation in rainfall (Tables 1 and 2). In the best-fit model, [$\phi_{\text{sex}} p_{\text{rain}}$; Table 1], females

(0.69 ± 0.05 SE) had lower estimated survival than males (0.74 ± 0.04 SE). Based on the sum of AIC_c weights (ϕw_i), simple sex-specific survival (e.g. models 1–3; Table 1) was 5.8× more likely than habitat-specific survival (e.g. models 4, 7, 8), and 5.9× more likely than survival varying by rainfall (e.g. models 5, 6).

Resighting probability.—Resighting probability varied positively with annual rainfall (Table 1). Detection probability was ~0.97 in 1998, following the wet El Niño of 1997–1998, versus 0.77 in 2000, following the dry La Niña of 1999–2000 (Table 2). Our data indicate that resighting probability varying with rainfall was 52.6× more likely than constant p , and 41.4× more likely than p being solely a function of habitat. Resighting probability did not differ strongly by sex (Table 2).

Retrospective analysis of edge effects on annual survival.—The CJS analysis failed to reject the null hypothesis of habitat-independent survival of Rufous-crowned Sparrows in San Diego County. Given our data, power to detect an edge effect was apparently low for females and males in all three years, based on 95% confidence intervals (CIs) around estimates of ϕ (Fig. 2). With the exception of females in 1999, retrospective analysis indicated that proportional difference in survival rates of edge birds was not >0.4 (Fig. 2).

Site and mate fidelity.—Adult Rufous-crowned Sparrows appeared to have strong site-fidelity to breeding territories. In only 2 instances out of 293 total breeding-season returns did we resight a banded bird outside of the neighborhood (~100 m radius) where it was initially captured as an adult. In one case, an edge male abandoned a female and established a breeding territory ~300 m distant; in the second case, an interior female dispersed and formed a pair ~250 m distant. We stress, however, that our mark-recapture analyses could not distinguish between individuals that died and those that permanently emigrated from the study area.

The majority of banded Rufous-crowned Sparrows stayed paired between years (Table 3) and remained paired on their territories year-round. In most cases, if a bird paired with a different mate in a subsequent breeding season, the mate from the previous season was not seen again and was presumed dead. During the nonbreeding-season survey in December 1999, all 40 of the marked birds we detected were

found in the location of their 1999 breeding territory and of their subsequent 2000 breeding territory, if they were seen again. Five banded pairs were located within their previous breeding territories, where they were again resighted during the subsequent breeding season. We located two additional banded pairs during December within their previous season’s territories, but only one individual from each pair was breeding in those locations in 2000 (we assume that the second individual did not survive the winter). Two birds that were not paired during the 1999 breeding season were observed paired in December of that year, where they were also resighted in the 2000 breeding season. We resighted five banded birds mated with unbanded birds during the 2000 season in the same places they were located in December, when they were also observed in association with an unbanded bird (i.e. perhaps the same bird). In four of those cases, the banded bird

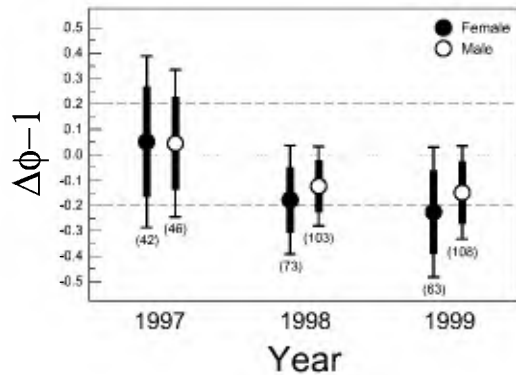


FIG. 2. Retrospective analysis indicated low statistical power to detect an ecologically relevant edge-effect on apparent annual survival of adult Rufous-crowned Sparrows in San Diego County, California. The y-axis gives estimated proportional difference in annual survival between females and males in edge and interior habitats ($\Delta\phi - 1$); x-axis gives capture year. Positive values of $\Delta\phi - 1$ indicate that $\hat{\phi}$ was greater in edge habitat, whereas negative values indicate that $\hat{\phi}$ was greater in interior habitat. Estimates of ϕ were taken from model $[\phi_{\text{sex} \times \text{hab} \times \text{rain}} / p_{\text{sex} \times \text{hab} \times \text{rain}}]$ (Table 1). Circles indicate $\Delta\hat{\phi} - 1$; thick vertical bars give 80% confidence intervals; thin vertical bars with caps give 95% confidence intervals. Numbers in parentheses give sample sizes for each sex × year class. Dotted horizontal line denotes that $\Delta\phi - 1 = 0$; dashed horizontal line denotes our estimate of an ecologically relevant differences in ϕ between edge and interior habitat. See text for further detail.

TABLE 3. Between-year mate fidelity of Rufous-crowned Sparrows in San Diego County, California. "Banded pairs" represents numbers of pairs of banded birds breeding at the beginning of the indicated interval. Row 1 tallies the number of those pairs that were mated together in the following breeding season; row 3 shows the number of pairs that did not remain together. Of the latter, row 4 counts the instances in which one of those banded birds either died or emigrated (i.e. inferred because the remaining bird was observed with a different mate), and row 5 counts the occasions of confirmed dissolution of a pair.

Row		1997–1998	1998–1999	1999–2000
Banded pairs		33	64	51
	Paired the following season?			
1	Yes	17	24	18
2	Uncertain ^a	5	18	9
3	No	11	22	24
	If no, were both individuals resighted?			
4	No	8	15	20
5	Yes	3	7	4
Dissolution rate ^b		0.11	0.15	0.10

^a Neither individual located with confirmed mate in subsequent year.

^b Dissolution rate = (row 5)/(row 1 + row 3).

resighted in 2000 had been mated with a banded bird during the previous breeding season, but that bird had since disappeared. Throughout the nonbreeding-season resighting period, we observed no groups of more than two Rufous-crowned Sparrows.

DISCUSSION

The present study is the first to investigate the effect of proximity to edge on survival of adult songbirds. To our knowledge, only two other published papers (Porneluzi and Faaborg 1999, Zanette 2000) have quantified the influence of habitat fragmentation on songbird survival. Like the present study, neither found statistical support for a fragmentation effect. However, Porneluzi and Faaborg (1999) and Zanette (2000) did not examine statistical power and had smaller sample sizes of marked birds than those analyzed here. Thus, we urge caution in concluding that habitat fragmentation does not have an ecologically important influence on survival rates of adult passerines.

Our failure to reject the null hypothesis of habitat-independent survival could be attributable to (1) insufficient data to detect the edge effect or (2) lack of an edge effect. Our

retrospective analysis, in contrast to AIC model selection and the model-averaged parameter estimates, suggested that survivorship was lower in edge areas in two of the three years of the study (see 80% CIs in Fig. 2). That trend seems consistent with the observation that some putative predators of songbirds are more abundant, and food less abundant, in edge as compared with interior plots (D. T. Bolger unpubl. data). On the other hand, an apparent paradox in the Rufous-crowned Sparrow reproductive study underscores the plausibility of habitat-independent survival probabilities: although abundance of some putative nest-predator taxa increased in edge habitat, there was no significant difference in nest predation rates between edge and interior plots (Morrison and Bolger 2002a). Statistically differentiating between the two alternative hypotheses described above would require a considerably larger number of marked individuals, years, or both, and replication of climatic conditions. Given the study region's highly variable climate, a full understanding of the ecological consequences of habitat fragmentation on this species will require longer-term studies.

Rufous-crowned Sparrows resident in southern California appear to have higher annual adult survivorship (females: 69 ± 0.05 SE; males: 0.74 ± 0.04 SE) than most sparrow species, including other ground-nesting species (Martin 1995, DeSante et al. 1998, Sandercock and Jaramillo 2002). However, Rufous-crowned Sparrows are nonmigratory, which likely contributes, in part, to their relatively high annual survival rates (Dobson 1990; but see Sandercock and Jaramillo 2002). Greater mortality risk appears to be associated with dispersal (Daniels and Walters 2000) or migration (Sillett and Holmes 2002), as compared with stationary life stages. It is important to emphasize that the survival estimates presented here are based on observations of territorial adults. The importance of nonterritorial birds, or floaters (Smith 1978, Arcese et al. 1992), to Rufous-crowned Sparrow demography is unknown. It is also not clear whether the difference in ϕ between males and females represents differences in mortality or site fidelity.

Our data indicated that apparent survival of Rufous-crowned Sparrows did not differ strongly among years, at least in interior habitats, despite considerable variation in climatic conditions during the study. An El Niño

event increased cumulative rainfall during the 1997–1998 survey interval to 1.9× the long-term mean, and a La Niña in 1999 and 2000 brought severe drought conditions to the semiarid study region. Those contrasting precipitation regimes apparently caused high interannual variation in food-resource availability for the granivorous and insectivorous Rufous-crowned Sparrow (Morrison and Bolger 2002b). Observed variation in reproductive output provided indirect evidence that food supplies were coupled to rainfall: in the wettest year, many of the birds were multiple-brooded and fecundity was high; in the subsequent dry year, few nests were attempted and fecundity was low (Morrison and Bolger 2002b). Investment in reproduction can reduce adult survivorship (Lack 1968; reviewed in Martin 1987). Yet, adult Rufous-crowned Sparrows seemingly maintained stable survivorship between 1997 and 2000, despite considerable variation in climatic conditions, reproductive effort, and food supply. Perhaps, by scaling reproductive effort to food availability (Morrison and Bolger 2002b), Rufous-crowned Sparrows avoid exceeding a threshold of energy expenditure that might compromise future survival (Martin 1987).

Birds of arid regions often have adaptations that enable them to tolerate extreme environmental conditions and exploit resources that become available episodically (Wiens 1991). The Rufous-crowned Sparrow's apparently high survivorship may be an adaptation to long periods of unsuitable breeding conditions. During two consecutive years of our four-year study, for example, Rufous-crowned Sparrow reproduction was substantially limited by dry La Niña conditions (Morrison and Bolger 2002b; S. A. Morrison and D. T. Bolger unpubl. data). Yet, although the bird's fecundity varied strongly between years, its apparent survivorship did not. That combination of life-history traits—high survivorship plus high fecundity during occasional good years—might be categorized as a “bet-hedging” strategy (Sæther et al. 1996). In such species, population growth rates tend to be most sensitive to variation in adult survival rates (Sæther and Bakke 2000). If the population growth rate of Rufous-crowned Sparrows is indeed highly sensitive to adult survival, then knowledge of survivorship may be particularly important for conservation and management of the species.

Site- and mate-fidelity.—Our data indicate that adult Rufous-crowned Sparrows are highly sedentary and have strong fidelity to territory sites within and between seasons. Pair bonds were also maintained year-round, and dissolution of pairs between years was only infrequently observed (Table 3). Dissolution rates may be underestimates (Sandercock et al. 2000), however, because only confirmed divorces were included in our calculations. We documented two short-distance (~300 m) breeding-dispersal events. It is difficult to draw conclusions about breeding-dispersal rate or distance on the basis of those two observations, because the probability of detecting a dispersed individual is inversely related to its distance from the study plot (Barrowclough 1978, Koenig et al. 1996). We did, however, observe natal dispersal over greater distances within our research sites (S. A. Morrison and D. T. Bolger unpubl. data). We banded 473 nestling or recently fledged Rufous-crowned Sparrows. We do not know how many of those birds survived to independence, but 11 hatch-year birds banded on their natal territory were subsequently resighted on breeding territories; one settled ~1.5 km from his natal plot. The observed high mate- and territory-fidelity within and among breeding seasons suggest that breeding dispersal is rare in the study population.

Biases in estimation.—Detectability of Rufous-crowned Sparrows varied strongly with climatic conditions (Table 2). In general, birds were most detectable when they were engaged in breeding activities (e.g. territory defense, mate guarding, nest building, nest provisioning). Consequently, in the driest years of the study, when breeding activity was reduced (Morrison and Bolger 2002b; S. A. Morrison and D. T. Bolger unpubl. data), our resighting success declined (Table 2). The El Niño and La Niña climatic events were not replicated during the course of the study, however, so the steady decline in detectability could also be attributable to factors unrelated to rainfall.

If unaccounted for, a sampling bias resulting from variable detectability could have led us to very different conclusions. Based on *ad hoc* return rates alone (i.e. simple proportion of birds marked in one year that return the following year), Rufous-crowned Sparrow survival appeared to decline with dry, La Niña conditions. The mean (± 1 SE) of the proportion of marked individuals resighted per plot was

0.74 ± 0.06 for the 1997–1998 interval, 0.63 ± 0.04 for 1998–1999, and 0.55 ± 0.04 for 1999–2000. Other field methods that rely on a consistent probability of detection across surveys (e.g. point counts) seem prone to similar confounding. Our findings underscore the importance of using field methods that can allow for an explicit accounting of detectability (e.g. double-observer sampling; Nichols et al. 2000), especially when studying species of conservation concern, or secretive species like the Rufous-crowned Sparrow. Estimates of population viability, for example, could be overly pessimistic if based on uncorrected parameter estimates from drier years.

Area sensitivity.—Understanding the mechanisms underlying area-sensitive distribution patterns is difficult, because habitat fragmentation triggers a multitude of confounding effects. Although our data do not clearly indicate an edge effect on survival of Rufous-crowned Sparrows, it is nonetheless intriguing that the trend toward lower apparent survival in edge habitat was observed during the two driest years of the study. It may be that fragmentation effects in the semiarid study region, where primary and secondary productivity is highly sensitive to within- and between-year patterns in rainfall (Noy-Meir 1973, Polis et al. 1997), are themselves dependent on climatic conditions. Rufous-crowned Sparrow offspring production, for example, is similar in edge and interior habitat in wet years (when it is uniformly high) and in dry years (when it is uniformly low). However, in “average” rainfall years, number of nestlings per fledged nest appears to be relatively lower in edge habitat, and that may be attributable to lower food-availability in edges (Morrison and Bolger 2002a). If edge effects are manifest only during years of particular rainfall regimes, population consequences of those effects will depend on patterns of climatic variability.

The apparent area-sensitivity of Rufous-crowned Sparrows in southern California may be attributable in part to their high sedentaryness. Highly sedentary species could be limited in their ability to locate high-quality habitat (Pulliam and Danielson 1991) and to disperse through human-modified landscapes (Wiens 1995, Reed 1999, Thomas 2000). Dispersal limitation can preclude colonization of fragments or rescue of insular populations undergoing stochastic decline (e.g. Bellamy et al. 1998,

Robinson 1999). Mounting evidence suggests that an isolation effect contributes to the area-sensitive distribution patterns displayed by many of the mostly nonmigratory coastal sage-scrub songbirds (see Soulé et al. 1988, Bolger et al. 1997, Crooks et al. 2001, Bolger 2002). Colonization, however, probably depends more on natal dispersal than breeding dispersal, which we examined here. A better understanding of area sensitivity in this species will likely require data on natal dispersal and juvenile survival in fragmented landscapes.

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