Density and Reproductive Success of California Towhees

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Abstract: *Models of habitat selection commonly asume that higher-quality source habitats will be occupied at higher densities than sink habitats. We examined an apparent sink habitat for California Towhees (*Pipilo crissalis*) in which densities are greater than in nearby source habitats. We estimated territory density using spot-mapping and monitored nests of towhees in grazed and ungrazed oak-pine woodland habitat. Breeding density of California Towhees was higher in ungrazed oak-pine woodlands than in grazed areas, yet birds in the ungrazed site experienced lower reproductive success. Predation during the nestling period was primarily responsible for the lower nest success. Clutch size and the number of young fledged were also lower in the ungrazed site. Towhees selected nest sites with high foliage density and cover of live oaks (*Quercus wislizenii*) in the understory. Grazed sites had greater cover of live oak than ungrazed sites, and successful nests were more often built in live oak than in other plant species. This pattern could not be explained by dominant birds settling in grazed sites and excluding subdominant individuals because a large proportion of adults continued to settle in the ungrazed area. Towhees may have perceived the dense foliage of the ungrazed area as suitable due to abundant nest sites, cover, and food, resulting in an "ecological trap." The resulting high density of birds there may have contributed to density-dependent predation. Alternatively, towhees are not ideally adapted to their habitats because of their sedentary habits and site tenacity that is not affected by persistent nest loss. We stress the need to examine the reproductive success and productivity of individual species within specific habitat types.*

Densidad y Exito Reproductivo del Rascador Californiano

Resumen: *Los modelos de selección de hábitat comunmente asumen que las fuentes de hábitat de alta calidad estarían ocupadas con densidades mas altas que en los hábitats pobres. Examinamos un hábitat aparentemente pobre para rascadores californianos (*Pipilo crissalis*) en el cual las densidades son mayores que en las fuentes de hábitat adyacentes. Estimamos las densidades territoriales utilizando mapeo de puntos y monitoreo de nidos en hábitats utilizados para pastoreo, así como en bosques de encino-pino no pastoreados. La densidad de crianza de los rascadores fue mas alta en los bosques de encino-pino libres de pastoreo que en las áreas utilizadas para pastoreo, sin embargo, las aves en el sitio sin pastoreo experimentaron un menor éxito reproductivo. La depredación durante el periodo de polluelos fue el motivo principal. El tamaño de puesta y el número de juveniles emplumando por nido fueron mas bajos en sitios libres de pastoreo. Los rascadores escogieron sitios de nidación con alta densidad de follaje y cobertura de encino siempreverde (*Quercus wislizenii*) en el sotobosque. Los sitios utilizados para pastoreo tuvieron mas encino siempreverde, en los cuales las aves construyeron mas nidos que en caulquier otra especie de planta. No se puede explicar este modelo en base al establecimiento de individuos dominantes en las áreas utilizadas para pastoreo y excluyendo a las aves menos dominantes, puesto que una proporción grande de adultos se estableció en sitios sin pastoreo. Es posible que los rascadores percibieron el follaje denso del sitio libre de pastoreo como apropiado, con abundantes sitios para nidación, cobertura y alimento, resultando en una "trampa ecológica." La densidad alta de aves en el sitio sin pastoreo posiblemente contribuyó a una depredación denso-dependiente. Alternativamente, los rascadores no estan idealmente adaptados a sus hábitats debido a sus hábitos sedentar-*

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ios y a su tenacidad por sitios, misma que no es afectada por una pérdida persistene de nidos. Enfatizámos la necesidad de analizar el éxito reproductivo y la productividad de especies a nivel individual dentro de tipos de hábitat específicos.

Introduction

Populations of plants and animals often occur across a range of habitat types, and their rates of survival and productivity may differ among habitats. In sink habitats reproductive output is inadequate to maintain local population levels, so populations are maintained only through immigration from other populations (Wiens & Rotenberry 1981; Pulliam 1988). This apparent maladaptation is maintained by asymmetric gene flow between sources and sinks, with surplus fledglings being produced in source habitats (Blondel et al. 1993; Dias 1996). Models of habitat selection commonly assume that higher-quality source habitats will be occupied at higher densities than sink habitats (Fretwell & Lucas 1970). Also—perhaps more important—management of many wildlife species has adopted this same assumption, despite warnings (Van Horne 1983).

We examined an apparent sink habitat for California Towhees (*Pipilo crissalis*) in which densities are greater than in nearby source habitats. We provide data on the abundance and reproductive success of California Towhees breeding in grazed and ungrazed habitats in the western foothills of the central Sierra Nevada. We compared habitat characteristics of successful and depredated nests, compared habitat characteristics of nest sites and available sites, and explored habitat differences between grazed and ungrazed habitats to investigate habitat selection. California Towhees are permanent residents in our study area, building open nests in shrubs or trees. They have recently expanded their range in response to increases in edge-type habitat due to grazing, logging, farming, and suburbanization (Ehrlich et al. 1988), and they may benefit from the effects of grazing and browsing by cattle (Bent 1968). California Towhees are commonly found in chaparral habitats, in low-elevation riparian deciduous habitat, and in the dry foothills of the western slope of the Sierra Nevada. The population we studied is near the upper elevational limit of its distribution, although California Towhees are common in these habitats, which include oak-pine woodlands and blue oak (*Quercus douglasii*) woodlands.

Study Area

The San Joaquin Experimental Range (hereafter SJER) is approximately 1875 ha of oak-pine woodlands, ranging in elevation from 215 to 520 m, in the western foothills of the Sierra Nevada, Madera County, California. The climate is characterized by cool, wet winters and hot, dry summers. Annual precipitation averages 48.6 cm, with most falling as rain between November and March. A sparse woodland overstory of foothill pine (*Pinus sabiniana*), blue oak, and interior live oak (*Q. wislizenii*) occurs over most of the SJER. Understory shrub species include wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*Ceanothus leucodermis*), Mariposa manzanita (*Arctostaphylos viscida mariposa*), redberry (*Rhamnus crocea*), and coffee berry (*Rhamnus californica*). SJER has been lightly to moderately grazed at least since 1900, as has the land surrounding it. A research natural area of approximately 29 ha has been ungrazed since 1934. This is the only extensive ungrazed habitat in this area.

Methods

In 1985–1993, numbers of all territorial bird species were estimated by the spot-mapping method (Anonymous 1970; Robbins 1970) on two 30-ha plots. One plot was in the ungrazed research natural area (2.9 ha were not within the natural area because of its irregular shape); the other was in grazed pastures similar to the ungrazed plot in terms of total canopy cover and general topography. The two plots were 1.33 km apart. To facilitate mapping, the plots were gridded at 30-m intervals and labeled with alphanumeric codes. One (in 1985 and 1986) to four (1988 through 1993) observers made 12 visits to each plot. All observers received training in both bird vocalizations and the spot-mapping method. Beginning within 15 minutes after sunrise, observers walked alternate lines, recording all birds seen or heard. Starting points and directions were chosen randomly in advance, as was the order of visits by observers. Species maps were analyzed each year by all observers jointly.

Seventy-six nests of California Towhees were located in 1988–1994 on the two plots and were checked every 4–7 days. Seven additional nests were monitored in other grazed areas of the SJER. High nests were checked with a mirror on a pole. Data for all variables except laying date were pooled across years after no significant year effects were found. Nests that fledged at least one young were considered successful. Predation was assumed when eggs or nestlings too young to have fledged disappeared. Nest success and daily mortality rates were calculated for grazed and ungrazed areas by the Mayfield

(1961, 1975) method, with variance calculated according to Hensler and Nichols (1981). Differences in nest success and nest predation rates between habitat types were tested using computer program Contrast (Hines & Sauer 1989), as described by Sauer and Williams (1989).

We calculated season-long estimates of fecundity for each habitat. We assumed (1) no age-related variation in fecundity, (2) no seasonal variation in nest success, (3) no seasonal variation in the number of young fledged per successful nest, and (4) a 50:50 sex ratio among fledglings. In addition, we assumed that all breeding-aged females attempted to nest. We have no evidence that towhees in this area attempt to renest following a successful first nest. We know, however, that towhees renested in some cases following a failed nest (a few individuals were individually color-marked or two nests were located within a single territory, with one nest initiated soon after the first one failed). Based on the range of first-egg dates, a third attempt is probably rare unless both earlier attempts fail early in the nesting period. Therefore, we assumed that no double brooding occurred and that all females would renest following only a first failed attempt. We used nest success rates and the mean number of female fledglings produced per successful attempt to calculate season-long fecundity (Donovan et al. 1995). For example, the observed nest success was 15% in ungrazed habitat, and an average of 1.1 female fledglings were produced per successful nest. Fifteen of 100 females (for ease of calculation) would produce 16.5 female fledglings, and the other 85 would produce none. All 85 females with a failed first attempt would renest; 15% of these would produce 14 fledglings and 85% of them would produce none. Thus, 30.5 female young would be produced per 100 adult females, or 0.305 female young per adult female per year. We assumed that juvenile survival was 0.50 of adult survival (Temple & Cary 1988; Thompson 1993), and we used two-stage population models to predict the minimum adult survival rates needed to achieve a lambda of 1, or a stable population, for each habitat.

Vegetative characteristics were measured in an 11.3-m-radius circular plot (0.04 ha) centered on each nest and on paired, randomly chosen trees or shrubs (paired random samples). Paired samples represented potential but unused nest sites within the same patch of habitat and potentially within the territory. These nonoverlapping sites were chosen by walking 30 m in a random direction from the nest, randomly choosing to go left or right, and locating the nearest appropriate substrate within a circular band 25–35 m from the nest. Nests in shrubs were paired with the nearest shrub, regardless of species; nests in trees were paired with the nearest tree, regardless of species.

We measured several vegetation variables around each active nest. We considered only three of these variables: foliage density of the focal tree or shrub, measured on a scale of 0–5, 5 being the most dense and 0 being a snag or dead shrub; percent cover of live oak shorter than 1.3 m high; and percent cover of wedgeleaf ceanothus shorter than 1.3 m high. The cover variables were based on 80 points 0.5 m apart on four perpendicular transects centered on the nest. We recorded "hits" on a vertical rod up to 1.36 m or the height of the understory canopy, whichever was higher.

In comparing grazed and ungrazed habitat characteristics, we used random plots measured during the same period for 17 other bird species, including both open- and cavity-nesting species. Although these samples were not systematically stratified over the plots, because of the diversity of species and the fact that most species were abundant and used most of the area of the plots, we believe they more than adequately represent the plots. Vegetation samples at nests of towhees were compared with their paired random plots (paired random samples) and with random samples for nests of other bird species (plot-level random samples). Some observations from the random sample data set were randomly deleted so that the proportions of samples centered on shrubs and trees and in grazed and ungrazed areas were equal to those centered on nests.

Variables were tested for normality and homogeneity of variance and transformed when appropriate. When transformation was unable to correct variance heterogeneity, unequal-variance t tests were used (SAS Institute 1988). We used Bonferroni error rates to control for experimentwise error. Differences between proportions were tested by means of a z test (Zar 1974:297). Power was tested for two-tailed tests and an alpha of 0.05 (Abramowitz & Stegun 1964).

Results

Density, Reproductive Success, and Source-Sink Models

The number of territories on the ungrazed plot was greater in all 9 years, and the mean density of California Towhees was significantly higher in the ungrazed area than in the grazed area (Table 1). Excluding 1985 through 1987, years when we collected no data on reproductive success, the difference was still significant ($t = 3.84, p = 0.012$).

California Towhees nesting in the ungrazed area had significantly lower nest success and higher predation rates than those nesting in grazed areas (Table 1). Nest success in the ungrazed area was only 14.7%. Of 31 nests followed to completion in the ungrazed plot, only 5 were successful. Daily mortality rates differed by nesting stage. More nests failed in the ungrazed area during the nestling period than during laying or incubation ($\chi^2 = 7.69$, df = 2, $p = 0.021$), but nest success did not differ between stages in grazed areas ($\chi^2 = 0.011$, df = 2, $p =$

Table 1. Abundance,[a] nest success, laying date, and productivity of California Towhees breeding at the San Joaquin Experimental Range in grazed[b] and ungrazed[c] areas.

	Grazed site	*Ungrazed site*		
	mean (SE)	*mean (SE)*	t *or* χ^2	p
Number of territories/30 ha/year	4.38 (0.58)	6.22 (0.66)	$t = 5.68$	0.0005
Daily mortality rate[d]	0.0288 (0.0069)	0.0739 (0.0139)	$\chi^2 = 8.45$	0.0037
Nest success (%)	48.2	14.7		
Daily predation rate[d]	0.0254 (0.0065)	0.0710 (0.0137)	$\chi^2 = 9.04$	0.0026
Predation rate (%)	47.4	84.1		
Laying date (Julian)	109.7 (2.2)	115.0 (2.2)	$t = 1.74$	0.0895
Clutch size	3.88 (0.08)	3.52 (0.12)	$t = 2.54$	0.0144
Number fledged/attempt	1.64 (0.30)	0.35 (0.16)	$t = 3.86$	0.0003
Number fledged/successful attempt	2.95 (0.27)	2.20 (0.37)	$t = 1.32$	0.1991

[a] *Data on abundance are from 9 years of territory mapping.*
[b] *n = 45 nests; 589.5 observation days.*
[c] *n = 30 nests; 353 observation days.*
[d] *Based on 589.5 and 352 observation days for grazed and ungrazed sites, respectively.*

0.995). Significantly more nests failed during the nestling period in the ungrazed area than in grazed areas ($\chi^2 = 7.04$, df = 1, $p = 0.008$). Nest predation followed the same pattern.

Nearly all failed nests were lost to predation. Western Scrub-jays (*Aphelocoma californica*) were the main predator of towhee nests in our study area (unpublished data). Jays were more abundant on the ungrazed plot in 7 of 9 years, although the mean number of territories did not differ significantly ($\bar{x} = 8.1$ versus 6.8 territories on ungrazed and grazed sites, $t = 1.61$, $p = 0.147$). Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) was directly responsible for the complete loss of only two nests: one nest on the grazed plot appeared to have been abandoned after a cowbird egg was laid, and a nest on the ungrazed plot fledged only two cowbird nestlings. Parasitism rates did not differ between all nesting attempts in grazed and ungrazed areas (31.8% versus 29.0% for grazed and ungrazed plots, respectively, $z = 0.300$, $p > 0.50$), but second nesting attempts were parasitized more frequently than first attempts (22.5% versus 81.8% for first and second attempts, respectively, $z = 4.385$, $p < 0.001$).

First nesting attempts occurred more than 5 days later in the ungrazed area, although the difference was not significant at the $\alpha = 0.05$ level (Table 1). Power to detect a difference of 4 days was only 0.24; power to detect a difference of 7 days was 0.60. When year effects were controlled, differences between plots became unimportant ($F = 1.17$, $p = 0.287$).

Clutch size was smaller in nests in the ungrazed area (Table 1). The number of young fledged per attempt was significantly lower in the ungrazed area (Table 1), reflecting the higher predation rates there. The number of young fledged per successful attempt did not differ between habitats (Table 1; $t = 1.32$, df = 22, $p = 0.1991$), but the sample size of successful nests on the grazed area was small ($n = 5$). Power to detect a difference of one nestling per successful attempt was 0.83; power to detect a difference of 0.5 nestling was 0.31.

The two-stage models predicted that adult survival rates of towhees would have to be greater than 0.86 to achieve a lambda of 1 in ungrazed habitat and greater than 0.65 in grazed habitat.

Habitat Characteristics

Combined over both habitats, towhees nested most often in live oaks and secondarily in wedgeleaf ceanothus. Nests in grazed areas were built more often in live oaks than in other shrub and tree species; nests in the un-

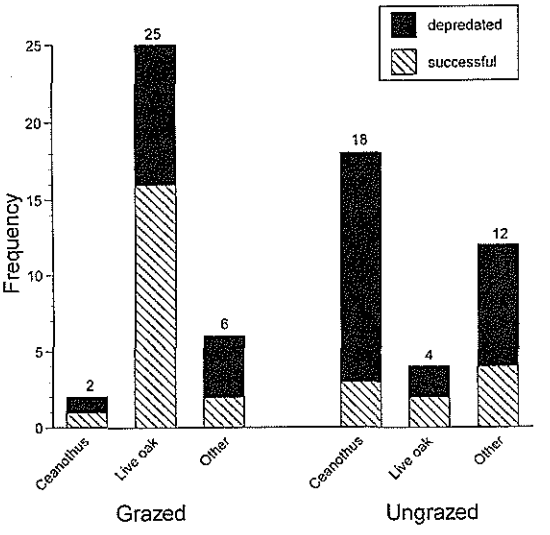

*Figure 1. Frequency of nests built in wedgeleaf ceanothus (*Ceanothus cuneatus*), live oak (*Quercus wislizenii*), and other species in grazed and ungrazed sites, and for successful and depredated nests. Total number of nests is shown above each bar.*

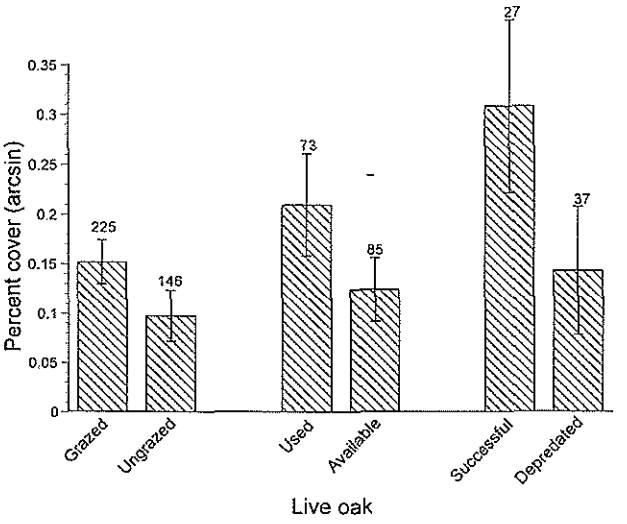

*Figure 2. Percent cover of live oak (*Quercus wislizenii*) (arcsin transformed; ±2 SE) in grazed and ungrazed sites, used and random (available) sites, and successful and depredated nests.*

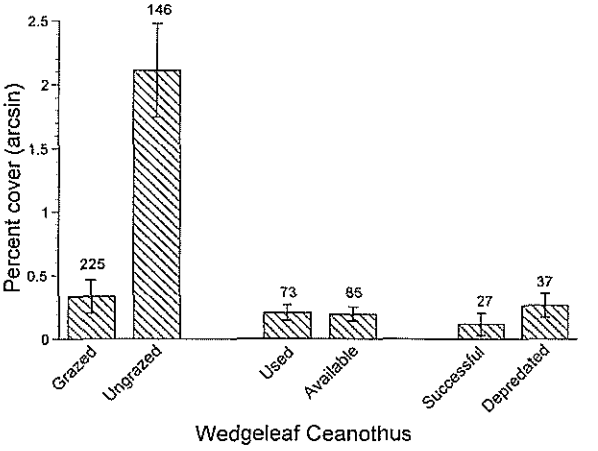

*Figure 3. Percent cover of wedgeleaf ceanothus (*Ceanothus cuneatus*) (arcsin transformed; ±2 SE) in grazed and ungrazed sites, used and random (available) sites, and successful and depredated nests.*

grazed area were more often in wedgeleaf ceanothus (Fig. 1; $\chi^2 = 39.004$, df = 2, $p < 0.0001$). Nests in grazed areas were higher than nests in the ungrazed area ($t = 3.18$, $p = 0.0021$), as expected from the higher proportion of nests in trees versus shrubs. Successful and unsuccessful nests were not evenly distributed across plant species (Fig. 1; $\chi^2 = 9.335$, df = 2, $p = 0.009$). Nests in live oaks were more often successful than nests built in other plant species; nests in wedgeleaf ceanothus suffered higher predation.

We compared differences in three habitat variables of (1) grazed and ungrazed sites, (2) nest sites and paired random and plot-level random samples, and (3) successful and depredated nests. Habitat characteristics of nest sites were more similar to the paired random samples than to the plot-level random samples. None of the comparisons between nest sites and paired random samples for the three variables considered here was significantly different after the Bonferroni adjustment, and few differences were found for other habitat variables. Results of the comparisons of nest sites to paired random samples are not included.

The grazed plot had a higher percent cover of live oak in the understory than did the ungrazed plot (Fig. 2; $t = 3.16$, df = 369, $p = 0.0017$). Combined over both habitats, towhees selected nest sites with more live oak in the understory than in random sites (Fig. 2; $t = 2.82$, df = 123, $p = 0.006$), although nest sites on the ungrazed plot did not have more live oak ($t = 1.10$, df = 72, $p = 0.277$). Successful towhee nests occupied sites with more live oak in the understory than occurred in sites of depredated nests (Fig. 2; $t = 3.13$, df = 62, $p = 0.003$).

The most obvious and probably most important difference between the grazed and ungrazed plots was the greater shrub cover of the ungrazed plot, especially of wedgeleaf ceanothus, with nearly nine times greater cover on the ungrazed plot (Fig. 3; $\bar{x} = 9.29$ and 1.06 for the ungrazed and grazed plots, $t = 9.18$, df = 182, $p = 0.0001$). Towhees, however, did not select nest sites with more ceanothus (Fig. 3; $t = 0.29$, df = 156, $p = 0.775$). Successful towhee nests tended to have less ceanothus around them, although this difference was not significant after the Bonferroni adjustment (Fig. 3; $t = 2.23$, df = 62, $p = 0.029$). Power to detect a 10% difference in cover of ceanothus was 0.99; power to detect a 5% difference was 0.85.

Foliage density of the focal tree or shrub did not differ between the grazed and ungrazed plots (Fig. 4; $t = 1.21$, df = 342, $p = 0.226$). Towhees selected nest trees or shrubs that had greater foliage density than random trees and shrubs (Fig. 4; $t = 3.06$, df = 154, $p = 0.003$). Successful towhee nests were built in trees or shrubs that had greater foliage density, although this difference was again not significant after a Bonferroni adjustment. Power to detect a difference of 1 was 0.878; power to detect a difference of 0.5 was 0.27.

Discussion

Because we did not have data on survival and because we found no data on survival rates of California Towhees in the literature, we looked at adult survival rates of closely related species reported in the literature. Survival rates of Rufous-sided Towhees (*Pipilo erythrophthalmus*) and Green-tailed Towhees (*Pipilo chlorurus*) were reported as approximately 0.56 (Savidge & Davis 1974; King &

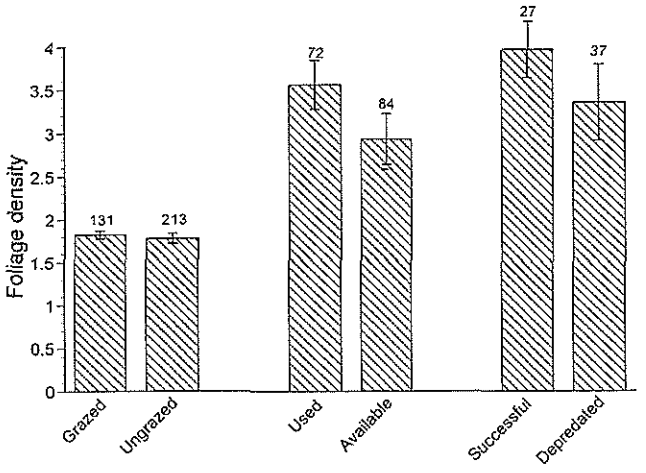

Figure 4. Foliage density (measured on a scale of 0–5, 5 being the most dense (±2 SE) in grazed and ungrazed sites, used and random (available) sites, and successful and depredated nests.

Mewaldt 1987; Martin 1995*a*). Survival values of 31 shrub- or low-foliage-nesting species averaged 0.53, and none was over 0.58 (Martin 1995*a*). Given our estimate of adult survival of 0.86 needed to maintain a stable population size for birds nesting in ungrazed habitat, we consider it unlikely that survival of California Towhees nesting on the ungrazed site was sufficient to compensate for their low reproductive success and likely that ungrazed habitat at the SJER represented a sink for California Towhees.

Compared to survival values in the literature, populations nesting in grazed habitat would also appear to be declining because our estimate of adult survival of 0.65 needed for a stable population there is higher than reported values. Survival estimates based on return rates such as those reported here generally are negatively biased (Martin 1995*b*) and, because most of this study took place during a drought period, clutch sizes might have been smaller than normal, leading to low estimates of fecundity. If model assumptions were violated or model parameters were biased, the discrepancy between the survival estimates needed for a stable population of towhees in grazed habitat and those reported in the literature is within reason, and grazed habitat is probably not a sink. We think it is unlikely, however, that these biases are large enough to account for the larger discrepancy between survival rates needed and those reported in the literature for a stable population size in ungrazed habitat.

Van Horne (1983) warned that density may not be a good indicator of habitat quality because confusion about habitat quality may arise when a negative correlation between abundance and reproductive success exists. Several authors have identified sink habitats for the species they studied (Thompson & Nolan 1973; Wray et al. 1982; Rodenhouse & Best 1983; King & Mewaldt 1987; Donovan et al. 1995), although few studies have found significantly higher densities of breeding birds in those sink habitats. Ribaut (1964) found that reproduction was disrupted by intense territorial activity in areas with high densities of blackbirds (*Turdus merula*). Fretwell (1969) found higher densities of Field Sparrows (*Spizella pusilla*) in a habitat with lower nest success than another habitat with lower densities, although data were from only one year. Studying three species of sparrows, Vickery et al. (1992) found that the highest reproductive success did not occur at the highest density for any of the species. Savannah Sparrows (*Passerculus sandwichensis*) were more successful at low density and least successful at high density.

What might account for these results? One hypothesis involves species with social hierarchies that defend nonoverlapping territories (Van Horne 1983). Dominant individuals maintain and defend more than their proportional share of area in the more productive habitat (Brown 1969). Subdominant juveniles, precluded from settling in good habitat, are forced to emigrate and settle in less suitable habitat (Krebs 1971; Vickery et al. 1992). These young birds may be the counterpart of nonbreeding "floaters" in other species, the difference being that they attempt to breed and sometimes succeed. In addition, they receive the benefits of holding territories, which can include increased winter survival, a food supply, nest sites, and a reduction of interspecific interference (Catchpole 1972). These subpopulations are important to healthy populations as replacement individuals. This type of sink habitat may be evolutionarily stable if gene flow from source populations prevents adaptive evolution in sinks (Pulliam 1988; Dias 1996).

For this hypothesis to hold, we would expect a predominance of young birds in the sink habitat. Banding data from the ungrazed plot from 1981–1986 and 1991–1993 yielded a mean recapture rate of 0.43, based on 100 birds banded (unpublished data). Assuming conservatively that all birds were first-year birds when first banded, 43% of the birds nesting on the ungrazed plot were second-year birds or older on average. That older birds remained in the ungrazed habitat is also confirmed by the recapture of three, two, and one birds 5, 6, and 7 years, respectively, after they were first banded. It is interesting that the mean recapture rate for birds banded on the grazed plot in 1991–1993 was also 0.43, although this was based on only seven banded birds.

An additional test of this hypothesis involves the nature of site fidelity. Unpaired male Ovenbirds tended to be more site-faithful than paired males that were unsuccessful (Porneluzi 1996). If there were more unpaired, site-faithful males in ungrazed habitat, perhaps pairing status could account for the larger number of older birds there. Territory spot-mapping data do not indicate any unpaired males on the ungrazed grid. All territories in-

cluded registrations of pairs and/or nests. On the grazed grid, however, most daily registrations in two territories each in 1991 and 1993 were of single, singing males, and no nests were found. An additional territory in 1988 could also have been that of an unpaired male.

Why, then, do older birds remain in unsuitable habitat? Most studies that show older birds remaining in unsuitable habitat have been done in altered or changing habitat, which suggests that the site tenacity of breeding birds is responsible. Morrison and Meslow (1984) found no difference in overall density and diversity of birds after herbicide application had removed understory foliage. Wiens and Rotenberry (1985) found no evidence of an immediate response by bird populations to sagebrush removal and planting of crested wheatgrass (*Agropyron cristatum*). They found that incorporating a 1-year time lag improved the fit of observed to predicted values in some cases but made no significant difference overall. Wiens et al. (1986) found that birds of the shrub-steppe did not respond to changes in habitat structure within territories as a result of mechanical sagebrush removal. In the stable, unaltered habitat in our study, however, a time lag cannot explain the higher density of towhees in the ungrazed site.

Nest sites of California Towhees were thick and brushy, with good cover, as indicated by their use of areas with more live oaks and the fact that they selected and were more successful nesting in trees and shrubs with dense foliage. If the dense foliage of the ungrazed area is a proximate environmental cue capable of eliciting the settling response, California Towhees would perceive the dense shrub layer of the ungrazed area as suitable habitat. Ungrazed habitat may have structural cues indicative of suitable nest sites, food availability, and cover, and they may function as an "ecological trap" (Gates & Gysel 1978). Nests may be easier for predators to find in the simpler structure of a ceanothus shrub than in a multiple-stemmed live oak. The high density of birds in the ungrazed area may lead to smaller clutch sizes (Kluijver 1951; Perrins 1965; van Balen 1973; Sasvári et al. 1987), density-dependent predation (Martin 1988*a*, 1988*b*), and lower reproductive success (Arcese & Smith 1988). Individuals in these sink habitats would represent all age classes, and these sink habitats would be detrimental, especially if they lure high-quality individuals away from more productive habitats (Howe & Davis 1991).

If the low productivity we observed in the ungrazed habitat is due to depressed fecundity or increased nest predation resulting from high densities, then ungrazed habitat could be a pseudo-sink (Watkinson & Sutherland 1995). In this case the intrinsic quality of ungrazed habitat could be equal to that of grazed habitat, but poorly adapted settling responses increase density beyond that which can be supported. Regardless of the mechanism, however, the result is still the same: reproduction within the habitat is insufficient to balance mortality, and the population is not viable.

Locations of our banding recaptures showed that California Towhees were very sedentary, remaining close to the area where they were first captured, with distances between recapture locations much less than the average territory diameter. This site tenacity, which does not seem to be affected by persistent nest loss, may be more influenced by previously established site attachments than by habitat affinity (Krebs 1971; Wiens & Rotenberry 1985). Fledglings may imprint on the habitat in which they were raised and may breed in similar habitat (Hildén 1965). In the tradeoff between survival and reproduction for towhees, survival may be more important. The benefits of territory ownership and the accompanying increase in survival may outweigh the potential advantages of moving to more productive habitat.

It is important to note that this study lacks true replication. Data on territory density are from only one ungrazed and one grazed plot. Although we included data from some nests in other grazed areas of the SJER, all of the ungrazed nests we monitored came from one plot because this is the only ungrazed habitat. The density of towhees on the grazed plot appears to be representative of towhee densities in grazed habitat in the surrounding area. The density and productivity of towhees in other ungrazed habitat is the biggest gap in our knowledge. Lack of replication may result in an underestimate of the true variability and may increase the Type I error rate. We believe, however, that the results presented here represent true differences for this species in this study area. Additional data on the abundance and reproductive success of California Towhees nesting in other ungrazed areas and in other habitats are needed.

The differences between analyses using paired random and plot-level random habitat samples warrant mention. Ultimately, the choice between comparing nest sites to paired or random samples depends on the question addressed. Comparisons of used sites and paired random sites reveal how other available, unused nest sites differ from the used nest site; analysis of plot-level random samples reveal habitat selection at the stand scale. The larger sample size of plot-level random samples than of paired random samples, and the resulting greater power, were responsible, in part, for the greater differences between used and plot-level random samples. Paired random samples tended to be closer to the nest, however—often within the same territory—so differences would be harder to detect. Similar results were obtained when several variables were examined simultaneously by discriminant analysis (Purcell 1995): nest sites were more similar to random paired samples than to plot-level random samples. The comparison of characteristics of nest sites and paired random sites had slightly lower sample classification rates and showed fewer significant differences (Purcell 1995).

Habitat similar to the ungrazed habitat at the SJER may once have been fairly rare and patchy in distribution. Fire was once an important component of the disturbance regime in oak woodlands of the Sierran foothills. Native Americans burned extensively for at least 3000 years (Lewis 1973) to modify plant and animal communities for their benefit (Kay 1995). Following Euro-American settlement in the mid-nineteenth century, ranchers burned to maintain forage production, with fire intervals of 8–15 years (Sampson 1944; McClaran & Bartolome 1989). Fire reduces brush cover and results in an open woodland of grasses, trees, and intermittent brush fields (Lewis 1973), creating the open woodland habitat with shrub-grassland edges that California Towhees require. Since the 1940s, fire suppression has dominated land-management practices. Livestock grazing, however, may mimic the once-frequent fires in some respects by reducing fuels and brush (Duncan & Clawson 1980) and may result in habitat similar to that existing before fire suppression.

Because a sink habitat for one species may be a source habitat for another, these results do not support a hypothesis that grazing benefits wildlife species in general. For example, ungrazed coastal scrub habitat was more productive than grazed habitat for White-crowned Sparrows (*Zonotrichia leucophrys*; G. Geupel, personal communication). Rather, we stress the need to examine the reproductive success and productivity of individual species within specific habitat types. Although data on survival, especially age-specific survival, are limited and needed, habitat-specific productivity may be more important (Pulliam 1988). We need to identify productive and nonproductive habitats and the processes underlying the differences in abundance.

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