ABUNDANCE AND SITE FIDELITY OF MIGRATORY BIRDS WINTERING IN RIPARIAN HABITAT OF BAJA CALIFORNIA

STEVEN C. LATTA, PRBO Conservation Science, 3820 Cypress Drive, Suite 11, Petaluma, California 94954 (current address: National Aviary, Allegheny Commons West, Pittsburgh, Pennsylvania 15212); steven.latta@aviary.org

HORACIO DE LA CUEVA, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Departamento de Biología de la Conservación, Ensenada, Baja California, Mexico

ALAN B. HARPER, Terra Peninsular, A.C., PMB 189003, Suite 88, Coronado, California 92178

ABSTRACT: The ecology of migratory landbirds in Baja California has been little studied, yet the nonbreeding season is of critical importance in the life cycle of any bird. We used mist netting to quantify the relative abundance and demographic indices of six species of landbirds wintering in riparian habitat at two sites in Baja California. In addition, we assessed their persistence at the sites through area searches for and recapture of individuals marked with a unique combination of color bands. From the winter of 2004–05 through the winter of 2006–07 we captured 561 individuals of the six species along the Río Santo Tomás and Río San Vicente. The most abundant species, the Hermit Thrush (*Catharus guttatus*), Yellow-rumped Warbler (*Setophaga coronata*), and Ruby-crowned Kinglet (*Regulus calendula*), together accounted for 83.1% of all net captures of target species. The sex ratios of the six target species were not significantly different from 1:1 except for the Yellow-rumped Warbler, of which we found significantly more males than females. Persistence beyond one day and annual rates of return of the color-banded target species were generally low and did not differ by sex.

The Baja California peninsula is considered an important area for avian conservation (Rodríguez-Estrella 2005), a critical region for wintering shorebirds, waders, and aquatic migrants (Massey and Palacios 1994, Mellink 2005), and large portions are included in two Endemic Bird Areas (Stattersfield et al. 1998). However, knowledge of the avifauna of Baja California is mostly limited to studies of the occurrence and distribution of breeding species and migrants (Erickson and Howell 2001, Rodríguez-Estrella 2005) and of the biology of waterbirds; few studies of the ecology of the region's migratory landbirds have been published (Rodríguez-Estrella 2005).

Riparian ecosystems represent one of the most important habitats for landbirds, especially in arid regions of western North America. Riparian habitat is more diverse and more productive than surrounding uplands despite covering a small percentage of the landscape (Knopf et al. 1988, Skagen et al. 2005). The riparian areas of northwest Baja California are structurally similar to those of coastal southwestern California and share similar animal and plant communities (Mellink 2002, Roberts 2004, González-Abraham et al. 2010), despite the lower diversity of riparian plants in Baja California (Minnich and Franco-Vizcaíno 1997). While many of the upland ecosystems of Baja California are in a very good state of conservation in comparison to those of similar areas in southern California (Minnich and Franco-Vizcaíno 1998), this is not true for the riparian habitats, many of which have been

heavily affected by development, agriculture, and water extraction (Minnich and Franco-Vizcaíno 1997).

This habitat is used not only by riparian-obligate songbirds but also often supports higher densities of non-obligate birds than do adjoining habitats during the breeding season and migration (Knopf et al. 1988, Finch and Yong 2000, Kelly and Hutto 2005, Skagen et al. 2005). In California, riparian areas have been identified as the single most critical habitat for the protection and conservation of songbirds (Miller 1951, RHJV 2004), with many terrestrial and aquatic species dependent on riparian systems during the breeding season (Knopf et al. 1988, Jensen et al. 1993). Among the many studies addressing birds' use of California's riparian habitats, Gardali et al. (2006) recorded breeding bird abundance with point counts in riparian remnant forests along the Sacramento River, while Nur et al. (2008) investigated relationships between abundance of breeding birds and characteristics of riparian vegetation. Songbirds' use of riparian habitat has also been studied during fall migration; Humple and Geupel (2002) used mist netting and area censuses of landbirds to show that numerous migrants use remnant riparian sites.

For the nonbreeding season, similar data for riparian areas in western North America are few. The nonbreeding season is of critical importance in the ecology and life cycle of migratory species (Faaborg et al. 2010). Conditions in the nonbreeding season may affect a bird's body condition or timing of migration and so its reproductive fitness in the following breeding season (Marra et al. 1998, Webster and Marra 2005). Abundance data for the nonbreeding season alone, however, can be a misleading indicator of population size and habitat preference because the latitudes and habitats used by many winter visitors vary with sex and age class (Ketterson and Nolan 1976, Morton 1984, Holmes et al. 1989, Latta and Faaborg 2001, 2002). Moreover, abundance cannot be equated with survival, so data on site fidelity, persistence at a site through the winter, and annual return rates are needed for habitat quality to be assessed. Thus, to investigate migrants' winter ecology, recent studies have focused on their demography and site fidelity by habitat (Ketterson and Nolan 1982, Holmes et al. 1989; Latta and Faaborg 2001, 2002).

In this study we used mist netting to quantify the relative abundance and demographic indices of six species of landbirds wintering in riparian habitat at two sites in Baja California. In addition, we banded birds with unique combinations of colors and used area searches to assess their persistence at the sites. We use these data to discuss suitability of riparian sites for visiting migratory birds under the assumption that a greater proportion of males, and longer persistence at the site, indicate higher quality for a species.

METHODS

Study Sites

In October 2004 we established study plots at two sites of conserved riparian habitat with well-developed vegetative cover, of extremely high conservation importance in Baja California (Figure 1). The sites were typical of riparian habitats in northwestern Baja California, which are found in small

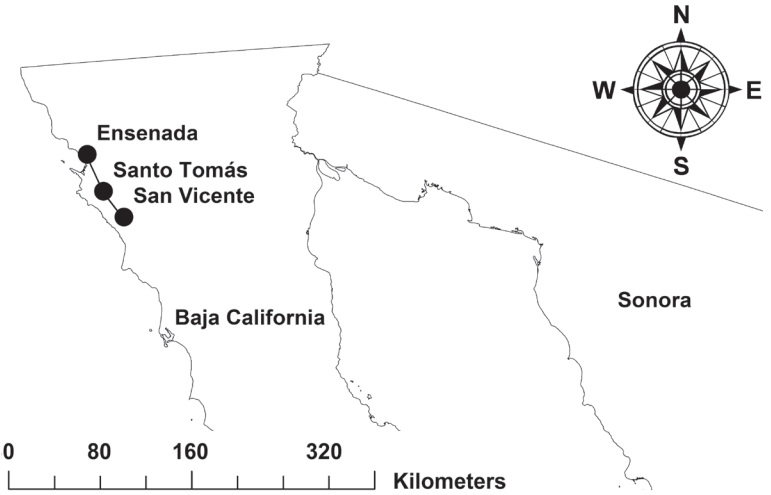

Figure 1. The location of San Vicente and Santo Tomás near the Pacific coast of Baja California.

canyons and along streams that run through coastal scrub and chaparral. One 12-ha site (Santo Tomás) was located at 31° 34′ 14″ N, 116° 28′ 42″ W, ~34 km south of Ensenada. The upper reaches of the Río Santo Tomás are nearly intact and roadless, but the lower reaches are affected by water extraction for agriculture. Although water flow is ephemeral, the streambed is not heavily modified by gravel extraction or other disturbances. The second 20-ha site (San Vicente) was a well-conserved riparian area along a seasonal stream ~60 km south of Ensenada and south of La Bocana de Santo Tomás (31° 22′ 13′ N, 116° 19′ 12′ W). The stream flows through some of the best-preserved coastal sage scrub in Baja California (Terra Peninsular unpubl. data). At both sites the surrounding uplands are vegetated with coastal scrub and chaparral. Both sites are located in the Northwestern Coastal Slope biogeographic region (Howell 2001).

Avian Sampling

At each site we sampled birds with 10 mist nets (12 m, 32-mm mesh). Nets were placed in fixed locations scattered to best sample each site's habitat. At each site, we netted for 2 or 3 days 3 or 4 times each year from November to March, 2004–2007 (Table 1). A final round of mist netting in January 2008 provided data on annual return rates. When we netted for 2 days, we opened the nets at 07:30 (~15 min after sunrise) and closed them at 16:00. When we netted for 3 days, we opened mist nets for 3 hr the first afternoon, from 07:30 to 16:00 the next day, and 3 hr the last morning. The length of mist netting was always consistent at the two sites, so if nets were opened for 2 days at Santo Tomás then they were also opened for 2 days at San Vicente. Thus effort at both sites was equivalent.

Table 1 Schedule of Mist Netting and Searching for Color-Banded Birds at Riparian Sites near Santo Tomás and San Vicente, Baja California, 2004–2008

	San Vicente	Santo Tomás
2004–05		
Nov	12–14 Nov	9–11 Nov
Jan	27–28 Jan	22–23 Jan
Feb	17–18 Feb	19–20 Feb
Mar	5–6 Mar	3–4 Mar
2005–06		
Nov	20–21 Nov	18–19 Nov
Dec	18–19 Dec	16–17 Dec
Jan	11–12 Jan	13–14 Jan
2006–07		
Nov	4–6 Nov	25–27 Nov
Dec	11–13 Dec	8–10 Dec
Jan	25–26 Jan	27–28 Jan
Feb	10–11 Feb	12–13 Feb
2008		
Jan	25–26 Jan	27–28 Jan

Whenever possible we identified all mist-netted birds to species and sex by plumage and other criteria (Pyle 1997). We banded six target species, selected because the probability of their capture was high, with a numbered metal band and a unique combination of three color bands: the Ruby-crowned Kinglet (*Regulus calendula*), Hermit Thrush (*Catharus guttatus*), Orange-crowned Warbler (*Oreothlypis celata*), Yellow-rumped Warbler (*Setophaga coronata*), Lincoln's Sparrow (*Melospiza lincolnii*), and White-crowned Sparrow (*Zonotrichia leucophrys*). Color banding enabled us to identify individuals in the field and so to evaluate site fidelity. Such banding during the winter can provide information on birds' survival and persistence at a site over the winter and can be helpful in determining individuals' home ranges and habitat use (Latta et al. 2005).

Sampling by mist net is subject to several biases (Ralph and Scott 1981, Remsen and Good 1996). For example, in some habitats nets do not sample all strata of the vegetation, very small or very large birds may be ineffectively sampled, and nets may overestimate the abundance of species that travel widely in search of food in comparison to those that forage in a more limited area. While recognizing these biases, in this study we minimized most of them because the vegetation structure at the two sites was similar, the nets' mesh size is effective in capturing the target species, the species differ relatively little in size, we limited analyses of net captures to comparisons within a species, and we assumed that the probabilities of capturing a species at the two sites were equal.

Resightings

To estimate winter site fidelity, we designed surveys for the color-banded birds to supplement recapture data from mist netting. After banding, two or

three observers searched each plot for color-banded birds for 3 or 4 days, with effort at the two sites consistent. Search areas extended approximately 100 m beyond the net lines or plot boundaries. Although very few color-banded birds in each plot may have remained unidentified, the number of newly resighted birds declined rapidly with effort such that we rarely encountered a newly identified bird in the last 12 person-hours of searching. We defined persistence as the proportion of birds detected (either resighted or by recapture in a mist net) at any time >24 hr after banding (Holmes et al. 1989, Latta and Faaborg 2001, 2002). We defined the annual return rate as the proportion of birds that persisted at the site at least 24 hr in the previous winter and returned to the same site the following winter.

Habitat Structure

In the winter of 2004–05, we used a method adapted from James and Shugart (1970) to characterize the species composition and vegetative structure of plants within an 11.3-m radius of 30 randomly selected points at each banding station, depending on site size. To create a foliage-height profile, we recorded the presence or absence (contacts with a pole) of broadleaf trees, shrubs, and ground cover at height intervals of 0–0.5 m, 0.5–1 m, 1–1.5 m, 1.5–2 m, 2–2.5 m, 2.5–3 m, 3–4 m, 4–6 m, 6–8 m, 8–10 m, 10–12 m, and 12–15 m.

Statistical Analyses

For statistical tests we used Excel and on-line worksheets provided by McDonald (2009). We accepted a probability of Type I error of 0.05 or less as significant unless otherwise noted. We did not analyze variation by year but pooled data for all years to increase sample sizes. Similarly, for the same reason, we did not analyze variation between the two sites but pooled their data. We used a two-tailed exact binomial test to test for significant differences in each species' sex ratio, with the expectation that the sex ratio was 1:1. We used the same test to test for a significant difference in sex ratios of birds persisting at the sites. In these tests the expected sex ratio was based on the ratio observed in mist-netted birds.

RESULTS

Habitat Structure

The vegetation at the two sites was similar, with a well-developed understory, mid-story, and canopy at both (Figure 2). Mean canopy cover at Santo Tomás was 57.2% (standard error [SE] 6.1), at San Vicente, 44.5% (SE 5.8). The most abundant trees at the Santo Tomás site were the coast live oak (*Quercus agrifolia*), western sycamore (*Platanus racemosa*), and willow (*Salix* sp.); at San Vicente they were sycamore and willow.

Wintering Birds

Over the first three winters of our study we captured 561 individuals of the six target species (Table 2). The winter residents more frequently captured were the Hermit Thrush, Yellow-rumped Warbler, and Ruby-crowned

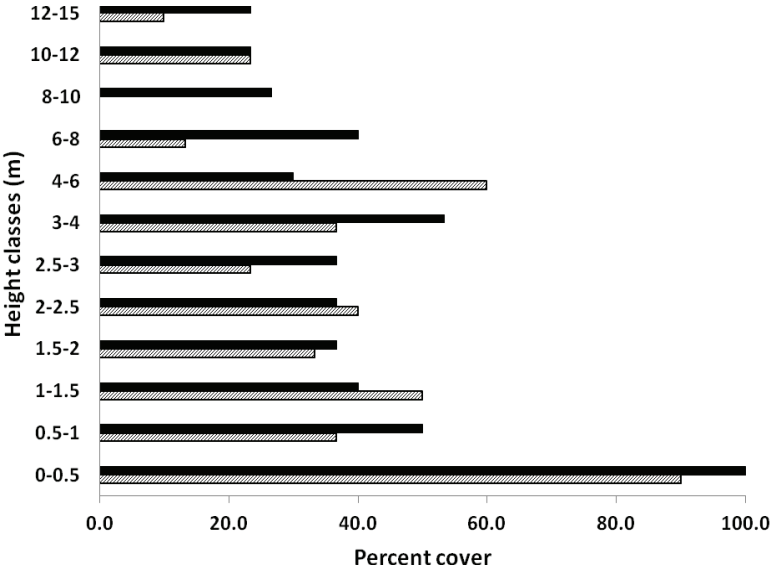

Figure 2. The percent cover of vegetation in each of 12 height classes in riparian vegetation at our study sites at San Vicente (light bars) and Santo Tomás (black bars), Baja California.

Kinglet, which together accounted for 83.1% of all net captures of our target species.

Our samples of three sexually dimorphic species were large enough for analysis. We found no significant difference in the sex ratio of the Ruby-crowned Kinglet (64% male, $P = 0.108$) or Orange-crowned Warbler (56% male, $P = 0.271$), but there were significantly more male than female Yellow-rumped Warblers at our sites (67% male, $P < 0.001$).

With both sexes combined, persistence at the site for ≥24 hr varied from zero for the White-crowned Sparrow to 13.7% for the Yellow-rumped Warbler (Table 3). In the latter species persistence of males and females did not differ significantly ($P = 0.334$). Because calculation of annual return rate is based on site-persistent individuals only, and because site persistence was universally low, small sample sizes allowed us to calculate annual return rates for only two species. This rate was low for the Hermit Thrush (19.0%) and only slightly higher for the Yellow-rumped Warbler (26.1%; Table 3).

DISCUSSION

The riparian habitats we studied supported substantial numbers of wintering migratory birds, especially the Hermit Thrush, Ruby-crowned Kinglet, and Yellow-rumped Warbler. The stratification, high foliage volume, and complex foliage-height profile of riparian woodland promotes bird diversity in similar habitat in California (Gaines 1977).

Table 2 Numbers of Six Species of Winter Residents Captured at Two Riparian Sites over Three Winters at Santo Tomás and San Vicente, Baja California

Species	San Vicente			Santo Tomás			Total
	2004–05	2005–06	2006–07	2004–05	2005–06	2006–07	
Ruby-crowned Kinglet	15	15	11	9	61	5	116
Hermit Thrush	31	72	6	22	39	12	182
Orange-crowned Warbler	6	1	0	8	13	1	29
Yellow-rumped Warbler	58	24	15	40	19	12	168
Lincoln's Sparrow	4	11	6	6	4	3	34
White-crowned Sparrow	4	0	0	0	0	28	32

However, site-fidelity data suggest that a relatively small proportion of these birds remained within the sites through the winter. No more than 14% of individuals of any of the six target species persisted within our sites for >24 hr. These results contrast with data from a companion study in remnants and restored patches of riparian woodland in the Central Valley of California (Latta et al. 2012). In these, we found higher rates of persistence in four species, the Hermit Thrush (56.3%), Fox Sparrow (*Passerella iliaca*; birds older than 1 year only; 57.1%), Lincoln's Sparrow (59.7%), and White-crowned Sparrow (67.8%). Our data from Baja California are more similar to those of Sandercock and Jaramillo (2002), who estimated site persistence on the basis of mark–recapture models for some of the same species we report on here. Their estimates of site persistence of first-winter emberizids ranged from 6% for Lincoln's Sparrow to 18% for the Golden-crowned Sparrow (*Zonotrichia atricapilla*), while those for older birds ranged from 8% for Lincoln's Sparrow to 28% for the Golden-crowned Sparrow. Similar data from other sites across the range of species studied here are lacking, as few studies have attempted to measure site fidelity of winter residents. Other winter studies also based on resighting of color-banded birds (e.g., Latta and Faaborg 2001, 2002), focused on parulid warblers wintering in native forests and shade-coffee plantations in the Caribbean and Mexico, found site persistence ranging from 42 to 80% (Holmes et al. 1989, Wunderle and Latta 2000).

The annual rates of return of the two species of which we had adequate samples were also low. Rates of return of the Hermit Thrush and Yellow-rumped Warbler have not been quantified previously (Hunt and Flaspohler 1998, Jones and Donovan 1996), but a rate of 50% may not be unusual for warblers (Wunderle and Latta 2000). Although annual return rate has been used as a measure of habitat quality (Faaborg et al. 2010), it also reflects winter survival, breeding-season survival, two migrations, site fidelity, prob-

Table 3 Site Persistence and Annual Return Rate[a] of Six Species of Winter Residents in Riparian Woodland at San Vicente and Santo Tomás, Baja California

	Ruby-crowned Kinglet	Hermit Thrush	Orange-crowned Warbler	Yellow-rumped Warbler	Lincoln's Sparrow	White-crowned Sparrow
San Vicente						
Sample size						
2004–05	15	31	6	58	4	4
2005–06	15	72	1	24	11	0
2006–07	11	6	0	15	6	0
Site persistence						
2004–05	40.0	25.8	16.7	15.5	25.0	—
2005–06	—	4.2	—	4.2	9.1	—
2006–07	—	16.7	—	6.7	—	—
Annual return rate						
2004–05	—	37.5	—	11.1	100.0	—
2005–06	—	—	—	—	100.0	—
2006–07	—	—	—	100.0	—	—
Santo Tomás						
Sample size						
2004–05	9	22	8	40	6	0
2005–06	61	39	13	19	4	0
2006–07	5	12	1	12	3	28
Site persistence						
2004–05	22.2	31.8	—	20.0	16.7	—
2005–06	1.6	2.6	—	5.3	—	—
2006–07	—	8.3	100.0	25.0	—	—
Annual return rate						
2004–05	50.0	14.3	—	12.5	0.0	—
2005–06	—	—	—	—	—	—
2006–07	—	—	100.0	100.0	—	—
Sites combined						
Sample size	116	182	29	168	34	32
Site persistence	7.8	11.5	6.9	13.7	8.8	0.0
Annual return rate	—	19.0	—	26.1	—	—

[a]Because annual return rates are calculated on the basis of site-persistent birds only, annual return rates could not be determined when low site persistence reduced sample sizes.

ability of detection, and the birds' vagility in response to changes in weather and their food supply. Faaborg et al. (2010) concluded that persistence at a site through a single winter may be a better measure of habitat quality.

It is generally thought that sites occupied longest can be considered higher in quality than those abandoned sooner (Holmes et al. 1989, Faaborg et al. 2010). A bird that remains at a site throughout the winter may be more familiar with food and other critical resources, better able to cope with resource fluctuations, and better able to avoid predators (Shields 1984, Dobson and Jones 1986). Whether the low rates of site persistence we observed suggest poor habitat quality or something else is unknown. Persistence would have been low if color-banded birds had simply moved into adjoining sage scrub and chaparral, but we think this is an unlikely explanation as we regularly searched

for color-banded birds up to 100 m outside of plot boundaries. Although these birds may have also avoided detection if they occupied unusually large home ranges, the size of territories or home ranges of these species has not been quantified other than by Ralph and Mewaldt (1975), who reported a home range of subspecies *gambelii* of the White-crowned Sparrow of about 20 ha, on a scale similar to that of our study sites. Alternatively, some individuals' strategy may have been to wander through the winter (Lefebvre et al. 1994). In some species different individuals pursue different strategies, some remaining faithful to a site, others wandering, taking advantage of dispersed food sources (Brown and Sherry 2008, Faaborg et al. 2010).

We think it is more likely, however, that low site persistence results from species-specific differences in habitat preference that may vary by demographic group and geography. For example, Sandercock and Jaramillo (2002) showed that for some emberizids, rates of site persistence (or local survival) of first-year birds are lower than those of older birds. Because in this study we did not determine the age of our birds, we do not know whether first-year birds were represented disproportionately at our study sites, thus depressing mean rates of site persistence. Alternatively, or in addition, a species may segregate geographically, one age class or one sex wintering disproportionately at a different latitude than another (Komar et al. 2005, Faaborg et al. 2010). Using museum collections, Komar et al. (2005) found evidence of latitudinal sexual segregation in 9 of 45 migratory species wintering in Mexico. These included the Orange-crowned and Yellow-rumped warblers, in both of which males predominate in the northern part of the species' winter range. Given that geographic variation in no species' winter strategy is well understood (Faaborg et al. 2010), further studies of site persistence across the winter ranges of these migratory species are justified.

The use of riparian habitats at our study sites by numerous overwintering migratory species and individuals underscores the importance of this vegetation type for conservation. Riparian zones have been widely recognized as a priority for management because of their high conservation value (Rich et al. 2004, RHJV 2004) and the high levels of threats they face, as the recipient of uses and abuses upstream (Dudgeon et al. 2006). Further studies of the use of riparian zones by winter visitors, as well as by permanent residents and summer residents, are merited especially when the critically important demographic measures of survival and reproductive success are included.

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