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TERRITORIALITY, SITE FIDELITY, AND SURVIVORSHIP OF WILLOW FLYCATCHERS WINTERING IN COSTA RICA

THOMAS J. KORONKIEWICZ[1], MARK K. SOGGE, CHARLES VAN RIPER III, AND EBEN H. PAXTON

U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, AZ 86001

Abstract. We studied wintering Willow Flycatchers (*Empidonax traillii*) in two seasonal freshwater wetland habitats in northwestern Costa Rica during five boreal winters, to determine habitat occupancy, overwinter and between-year site and territory fidelity, and the degree to which the sexes maintain and defend winter territories. Both males and females used agonistic displays, song, and other vocalizations to maintain and defend mutually exclusive winter territories. Males were generally more abundant than females, but this varied by site and year. There was no significant difference in male and female territory size, nor any indication of sexual habitat segregation. Similarity in morphology and aggressiveness between the sexes may account for the lack of habitat segregation and the ability of females to maintain territories at wintering sites. Each year, 80%–92% of banded flycatchers that were present in midwinter remained at the site until late winter; of these, 86%–100% of individuals maintained the same territories throughout the entire period. We also observed nonterritorial floaters that subsequently established and held winter territories. Between-year site fidelity averaged 68%, and almost all returning birds established territories with boundaries similar to the previous year. Between-year apparent survivorship estimates ranged annually from 54%–72%, with no difference between sites but weak support for higher survivorship of males compared to females. Values for winter site and territory fidelity were generally higher than those reported for other species and for Willow Flycatchers on the breeding grounds; between-year survivorship estimates were similar to those reported for breeding flycatchers.

Key words: Empidonax traillii*, floaters, nonbreeding, site fidelity, survivorship, territoriality, Willow Flycatcher.*

Territorialidad, Fidelidad de Sitio y Supervivencia de *Empidonax traillii* en Costa Rica

Resumen. Estudiamos individuos de *Empidonax traillii* que se encontraban invernando en dos hábitats de humedales estacionales de agua dulce en el noroeste de Costa Rica durante cinco inviernos boreales. Determinamos la ocupación de hábitat, la fidelidad de sitio y de territorio durante el invierno y entre años, y el esfuerzo de los sexos para mantener y defender sus territorios de invierno. Tanto las hembras como los machos utilizaron despliegues agonísticos, cantos y otras vocalizaciones para mantener y defender sus territorios de invierno, que son mutuamente exclusivos. Los machos fueron en general más abundantes que las hembras, pero esta diferencia varió entre sitios y años. No hubo diferencia significativa entre el tamaño de los territorios de las hembras y de los machos, y no se observó nada que indicara segregación de hábitat entre sexos. La similitud en la morfología y la agresividad entre sexos puede estar dando cuenta de la falta de segregación de hábitat y de la capacidad de las hembras de mantener territorios en los sitios de invernada. Cada año, el 80% al 92% de las aves anilladas que se encontraban presentes a mediados del invierno permanecieron en el sitio hasta fines del invierno, y de estos, el 86% al 100% de los individuos mantuvieron el mismo territorio durante todo el periodo. También observamos individuos flotantes sin territorio que establecieron y mantuvieron territorios más tarde. La fidelidad de sitio entre años fue del 68% en promedio, y casi todas las aves que retornaron establecieron territorios con bordes similares a los del año anterior. La supervivencia aparente estimada entre años varió anualmente entre 54% y 72% sin que existan diferencias entre sitios, pero con una diferencia, apoyada débilmente, de mayor supervivencia para los machos que las hembras. Los valores de fidelidad de sitio y de territorio fueron más altos que los reportados para otras especies y para esta misma especie en los sitios de cría. Las estimaciones de supervivencia entre años fueron similares a aquellas reportadas para *E. traillii* en los sitios de cría.

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[1] Present address: SWCA, Inc., 114 North San Francisco St., Flagstaff, AZ 86001. E-mail: tkoronkiewicz@swca.com

INTRODUCTION

A great deal of new ecological information has been obtained about migratory passerines in tropical regions since the pioneering work of Rappole and Warner (1980), yet the details of behavioral ecology and habitat use of many Neotropical migratory species in winter remains poorly understood (Marra 2000, Stutchbury et al. 2005). Some early research suggested that migrants are highly mobile generalists on the winter grounds, exploiting only superabundant resources and unable to compete with resident tropical species for food and space (Leck 1972, MacArthur 1972, Karr 1976). Over the last decade, food resource and habitat partitioning have been more widely accepted as an explanation for the integration of migratory and resident species in the Neotropics (Greenberg 1995, Johnson et al. 2005). Increasingly, evidence from studies of marked individuals has demonstrated that many species of migratory passerines occupy specific niches in tropical habitats, form stable components of winter tropical avian communities, and exhibit behaviors suggestive of highly developed territorial social systems (Holmes and Sherry 1992, Rappole et al. 1992, Greenberg and Salewski 2005, Stutchbury et al. 2005).

Studies have documented individuals of over 60 species of Neotropical migrant passerines within eight families returning to tropical sites in successive years or exhibiting intraspecific territoriality on the winter grounds (Rappole et al. 1983, Rappole 1995, Koronkiewicz 2002, Greenberg and Salewski 2005). Although such statistics might imply that winter territoriality and site fidelity are widespread among most Neotropical migrant passerines, information actually exists for only a small subset of species. The vast majority of studies on the wintering grounds have focused on sexually dichromatic species or on the wood-warblers (Parulidae). Although tyrant flycatchers (Tyrannidae) comprise the largest family of Neotropical passerines, including approximately 25 boreal migrant species (DeGraff and Rappole 1995), detailed information on wintering ecology exists only for the Yellow-bellied Flycatcher (*Empidonax flaviventris*) and Least Flycatcher (*E. minimus*, Rappole and Warner 1980, Rappole et al. 1992).

Here, we report a study of Willow Flycatchers (*Empidonax traillii*) wintering in northwestern Costa Rica. Strongly territorial on the breeding grounds (Sedgwick 2000, Sogge 2000), this sexually monomorphic tyrant flycatcher is also suspected to exhibit winter territoriality (Gorski 1969), but this and other aspects of its winter behavioral ecology are largely unknown. Furthermore, the southwestern subspecies (*E. t. extimus*) was listed as an endangered species in 1995, and the U.S. Fish and Wildlife Service identified the need for additional knowledge about its winter ecology. Using color-banded individuals monitored over five consecutive boreal winters, we addressed the following questions: (1) how are populations structured at wintering sites? (2) to what degree are seasonal and between-year site fidelity exhibited? and (3) are winter territories defended against conspecifics?

METHODS

We conducted this study from 1998 to 2003 at two sites in northwestern Costa Rica where Willow Flycatchers are resident throughout the boreal winter, Chomes (Puntarenas Province; 10°05′N, 85°05′W) and Bolson (Guanacaste Province; 10°20′N, 85°25′W). This region experiences pronounced annual rainy and dry seasons, with wintering Willow Flycatchers arriving just prior to the height of the rainy season (September–October), and departing at the end of the dry season (April–May). Study sites were visited all five years, with multiple field visits each year distributed variably from September through May. Throughout this manuscript, our designation for specific boreal winters (i.e., nonbreeding seasons) includes the year in which the nonbreeding season started and in which it ended; e.g., winter 1999–2000 designates the nonbreeding season that started in September 1999 and continued through April 2000.

The Chomes study site was located on a large, privately owned ranch approximately 25 km northwest of the city of Puntarenas. The study area consisted of a large seasonal freshwater wetland, or laguna, bordered entirely by patches and narrow strips of tropical evergreen and deciduous forest, woody shrubs, and man-made savanna pastures. Willow Flycatchers were distributed along the periphery (approximately 2700 m in length) of the wetland edge.

Predominant wetland vegetation included dense woody shrubs (*Mimosa pigra*) and swamp herbs (primarily *Thalia* spp.). Dominant trees bordering the wetland were *Guazuma ulmifolia*, *Pithecellobium dulce*, *P. saman*, *Enterolobium cyclocarpum*, and *Cocoloba* spp. Although large areas of the wetland completely dried up as the dry season advanced, some standing water and saturated soils were present year-round.

The Bolson study site, approximately 25 km northeast of the city of Santa Cruz, was also located on a large, seasonal freshwater wetland, and had a vegetation structure and species composition similar to Chomes. As with the Chomes site, Willow Flycatchers were distributed along the periphery (approximately 4000 m in length) of the wetland edge. Standing water and saturated soils were present year-round. Slow-moving waterways and muddy seeps bordered the wetland to the north and south. Seasonal inundation here was much more pronounced than at Chomes, due to the annual flooding (October and November) of the Tempisque River, approximately 1 km to the west.

We captured and color-banded as many Willow Flycatchers as possible at each site, primarily during December and January of each year. We located flycatchers by traversing the study areas and broadcasting conspecific vocalizations, listening for responding individuals (similar to the breeding survey protocol of Sogge et al. 1997). Once detected, we captured flycatchers using a targeted mist-net technique (Sogge et al. 2001); an *Empidonax* decoy was occasionally used. We captured some flycatchers by "passive netting," whereby mist nets were erected and periodically checked. Each captured flycatcher was given a unique combination of colored leg bands (including a color-anodized, numbered federal aluminum band; Koronkiewicz et al. 2005) and its capture location was marked on a high-resolution aerial photograph. We also collected a drop of blood by clipping a toenail (Busch et al. 2000) for later sex determination in the laboratory (Fridolfsson and Ellegren 1999).

We conducted spot-mapping by repeatedly and systematically visiting the study sites and visually searching for color-banded individuals. Resightings of individual flycatchers occurred in a variety of ways, ranging from a single detection per day to focal-individual observations that recorded successive movements of a flycatcher over the course of 30 min or more. During the second year of the study, we also erected three 3.5 m tall portable observation platforms at the Chomes site to allow viewing of a large area of the wetland interior. Most surveying and resightings were conducted from 06:00–11:00 and 15:00–17:30 CST, when Willow Flycatcher activity was greatest. To maximize the number of detections, we used a combination of conspecific playback surveys and passive surveys. We also recorded the locations, movements, and details of conspecific interactions between individuals, following the terminology of Stein (1963) and Sedgwick (2000).

All flycatcher detections were mapped on high-resolution aerial photographs taken in November 1997 (Ministero del Ambiente y Energia, San Jose, Costa Rica). We determined the borders of each flycatcher territory by forming a minimum convex polygon that connected the outermost points of each individual's detections (Odum and Kuenzler 1955, Holmes et al. 1989, Staicer 1992). Nonoverlapping or minimally overlapping use areas, in combination with multiple observations of conspecific, territorial interactions (especially along territory borders), were considered evidence of territoriality. We digitally rectified the aerial photographs using ArcView GIS© (ESRI, Redlands, CA) with the Image Warp extension, calculating territory size and distance of any flycatcher movements using the X Tools extension. To differentiate among territory holders and possible nonterritorial "floaters," we used the definitions of Rappole and Warner (1980) and Rappole (1995). A flycatcher was considered a floater if: (a) it was seen only once, or very irregularly; (b) it was typically observed in quiet, "skulking" behavior; and (c) it did not display territorial behaviors toward conspecifics, but did so once it became a territory-holding individual.

We calculated seasonal site fidelity by determining (through resightings) which of the color-banded flycatchers present during early and mid winter were still present during late winter. If an individual's territory shifted <100 m over a winter period, it was considered to have held the same territory over that season. To calculate between-year return, we revisited study sites over five consecutive years and

TABLE 1. Willow Flycatcher abundance and within-season site and territory fidelity at two study areas in Costa Rica. Site fidelity is defined as the percentage of banded flycatchers that was known to remain at the same wintering site throughout the boreal winter season. Territory fidelity is the percentage of site-faithful banded birds that held the same territory throughout the winter season; thus, territory fidelity is a subset of site fidelity. Due to differences in field effort, territory and site fidelity could be calculated only for the 1999–2000 through 2001–2002 seasons; nc = not calculated.

Site	Winter season	Total flycatchers detected	Total flycatchers banded (females, males)	Within-season site fidelity (%)	Within-season territory fidelity (%)
Chomes	1998–1999	24	13 (6, 7)	nc	nc
	1999–2000	29	24 (15, 9)	92	100
	2000–2001	29	26 (11, 15)	85	86
	2001–2002	17	15 (8, 7)	80	100
	2002–2003	17	12 (4, 8)	nc	nc
Bolson	1998–1999	15	7 (3, 4)	nc	nc
	1999–2000	19	15 (7, 8)	87	92
	2000–2001	18	15 (6, 9)	80	100
	2001–2002	18	18 (7, 9) (plus 2 undetermined)	89	94
	2002–2003	15	11 (3, 7) (plus 1 undetermined)	nc	nc

divided the number of flycatchers that returned each year by the number present during the previous winter period. Individuals were considered to have returned to the same territory in a subsequent winter period if: (a) >50% of an individual's locations and movements (spot observations) in a winter period were located within an area determined to be its territory the previous year, or (b) an individual's capture location from a previous winter was located within the area determined to be its territory the following winter.

STATISTICAL ANALYSES

We used program MARK (White and Burnham 1999) to derive the maximum-likelihood estimate of between-year apparent survival of birds wintering at our sites. We predicted that site, sex, or yearly variation could influence survivorship, and used Akaike's information criterion (AIC; Burnham and Anderson 2002) to select the best models. We used SPSS version 10.1 (SPSS 2000) for all other statistical analyses. Data were tested for a normal distribution using Shapiro-Wilk *W*-tests. Because male-female territory size data did not conform to a normal distribution, we used a two-tailed Mann-Whitney *U*-test to compare the means; a statistical significance level of $P \leq 0.05$ was chosen to reject the null hypothesis. Data presented are means ± SE unless otherwise stated.

RESULTS

CAPTURE EFFORT

During five consecutive boreal winters, we spent 198 days color-banding, resighting, and spot-mapping Willow Flycatchers at Chomes and Bolson; greatest field effort occurred in 1999–2000 (n = 104 days) and 2000–2001 (n = 51 days). Over all years, flycatcher annual abundance was more constant at Bolson than at Chomes, with an average of 17 and 23 individuals per year, respectively (Table 1). Based on data from our longest field season (2001), Willow Flycatchers were observed for a maximum of just over eight months at our winter sites. Each year, 47%–100% of the flycatchers that we detected were color-banded. Overall, males were more abundant than females, though this varied by year and site (Table 1).

TERRITORIALITY

Based on minimum convex polygons generated by spot-mapping in 1999–2000, both female and male Willow Flycatchers maintained mutually exclusive, well-defined territories that had little or no overlap with territories of adjacent conspecifics. Females and males did not form consort pairs and territories of both sexes were interspersed throughout study areas (Fig. 1, 2). We observed no significant difference in territory size between the sexes at Chomes (males = 0.48 ± 0.04 ha; females = 0.46 ± 0.05 ha) or

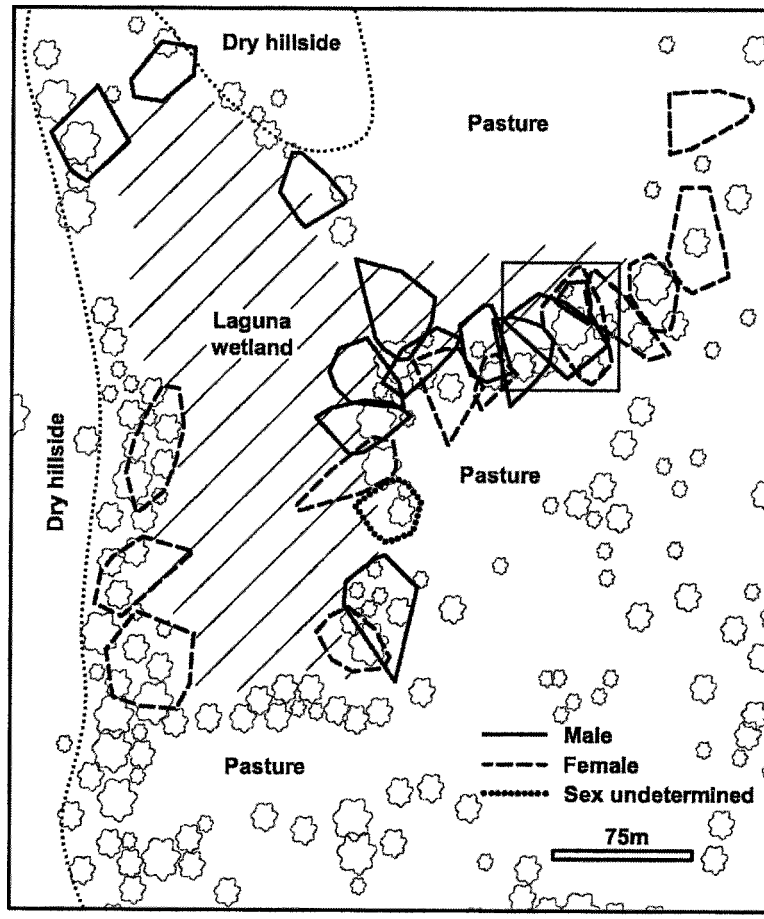

FIGURE 1. Willow Flycatcher territories at the Chomes, Costa Rica study site. Polygons depict territories based on spot-mapping of all movements of 25 individuals (including one unbanded individual) monitored from 17 December 1999 to 10 May 2000. Polygons within boxed area are territories that shifted as territory ownership changed over winter. Lobed circles represent trees. Flycatchers defended stable, exclusive territories that generally were nonoverlapping; most were located along the treeline–laguna interface.

Bolson (males = 0.82 ± 0.08 ha; females = 0.77 ± 0.18 ha); however, the mean territory size of 15 flycatchers at Bolson was significantly greater than that of 24 flycatchers at Chomes (Mann-Whitney *U*-test: $U = 52$, $P < 0.001$; Fig. 3).

By utilizing raised platforms, we were able to map flycatcher movements in the center of the wetland at Chomes that was unobservable on foot, adding greatly to the number of resightings of color-banded individuals. In addition, we found two individuals, one of each sex, that maintained and defended two noncontiguous territories separated by an area of cattle-trampled wetland vegetation and short-grass pasture. During early mornings, and from late afternoon until dark, both individuals were consistently detected defending wetland areas that were separate from territories used in the middle of the day.

TERRITORIAL BEHAVIORS AND DISPLAYS

From arrival in September until spring departure in April and May, male and female wintering flycatchers responded aggressively toward other individuals and to playbacks. At both study sites, we repeatedly observed stereotyped agonistic interactions between individuals of both sexes, similar to those used in defense of breeding territories (Sedgwick 2000,

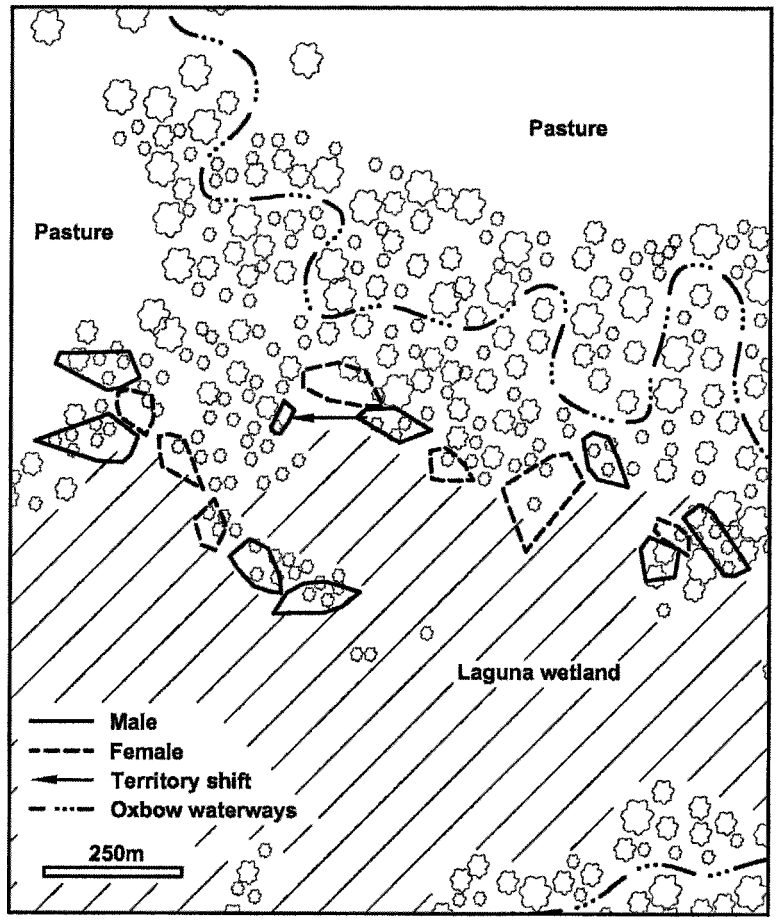

FIGURE 2. Willow Flycatcher territories at the Bolson, Costa Rica study site. Polygons depict territories based on spot-mapping of all movements of 15 individuals monitored from 23 December 1999 to 28 April 2000. Lobed circles represent trees. Flycatchers defended stable, exclusive territories that generally were nonoverlapping; most were located along the treeline–laguna interface.

Sogge 2000). We heard five vocalizations given in the context of territory defense: the *fitz-bew* and *creet* advertising songs, and *whit*, *wheet*, and *trill* calls (Stein 1963, Sedgwick 2000). Both males and females used all of these vocalizations. We heard *wee-oo* calls (common on the breeding grounds) only three times; once by each of three flycatchers immediately after they were released from capture. We also observed seven displays given by the sexes during aggressive intraspecific encounters, including rapid *tail-flicking/pumping*, *crest-raising*, *wing-flicking*, *wing-fluttering*, *supplants* (replacement of another flycatcher in position), *chases*, and rapid *bill-snapping* (Sedgwick 2000). Flycatchers used several aggressive visual displays in combination with advertising songs or calls. During the most intense confrontations, such as physical tussling, flycatchers gave a series of high-pitched, squeaky vocalizations, as have been described on the breeding grounds (Sogge et al. 2001). *Flight-songs*, in which a series of rapid *fitz-bews* or *wheets* are given during chases or direct flights at other individuals, were often accompanied by rapid bill-snapping. Most agonistic displays and vocalizations were given from an exposed perch, in close proximity to where intrusions by conspecific flycatchers occurred.

The degree to which both sexes aggressively respond to conspecific territory intrusion is illustrated by the efficacy of the target capture

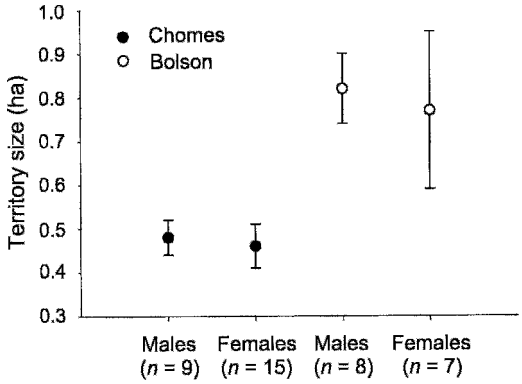

FIGURE 3. Mean territory size (ha) ± SE of wintering male and female Willow Flycatchers at the Chomes and Bolson, Costa Rica study sites, during the winter of 1999–2000. Statistics do not include noncontiguous territories. Territory size was not different between sexes, but did vary by site.

technique (Sogge et al. 2001), which simulates a conspecific intrusion. An average of 77% of the flycatchers detected at both sites were captured and color-banded, with the ratio of females to males approximately equal. In most cases, targeted individuals were captured within 5 min of the onset of call broadcast. Typical aggressive responses of individuals toward conspecific playbacks included almost immediate movements and flights toward the speaker locations, greatly increased singing and calling rates (up to 109 *fitz-bew* songs per 4 min), and direct flights at, or physical contact with, an *Empidonax* decoy. Furthermore, vocalizations from the first responding flycatcher typically initiated singing or calling from other, nearby Willow Flycatchers, and individuals could be heard responding up to 200 m away from the point of broadcast.

NONTERRITORIAL BIRDS

In addition to territorial individuals, we detected and color-banded two nonterritorial floaters (one male and one female) that each replaced a territory holder after the latter disappeared during the same winter season. Prior to territory acquisition, both floaters were quiet and submissive toward territorial individuals, and did not respond to conspecific playbacks; they were captured only by passive netting. After they acquired portions of the "empty" territory, both individuals became aggressive toward other flycatchers, vocalized regularly, responded strongly to conspecific playbacks, defended their territories until the end of winter, and returned as territory-holders in subsequent winters. We also observed one other nonterritorial floater in 1999–2000 that acquired a winter territory the following year; the previous territory-holding female was never detected again.

WITHIN-SEASON SITE AND TERRITORY FIDELITY

There was approximately half the number of Willow Flycatchers at sites in early winter compared to mid winter, as southbound individuals continued to arrive during this time. Thus, we defined within-season site fidelity as the percentage of flycatchers detected in mid-winter (December–January) that were still present in late winter (April–May). Each winter, site fidelity at Chomes and Bolson ranged from 80%–92% (Table 1). Within-season territory fidelity—the percentage of flycatchers known to be present throughout the winter that remained in the same territory—ranged from 86%–100% (Table 1). Flycatchers not present throughout the entire winter season were not included in the within-season territory fidelity calculations. It was uncommon for flycatchers to relocate their territories within a winter season. Only five individuals did so, and all of these moved to adjacent unoccupied areas, where they established and defended new territories until spring departure; the average distance moved was 264 ± 108 m (SD; range = 120–475 m).

BETWEEN-YEAR SITE AND TERRITORY FIDELITY AND SURVIVORSHIP

The percentage of individuals known to be present at a site during the later winter period and returning the following winter (between-year site fidelity) ranged from 43%–85% annually (Table 2). Overall, between-year site fidelity (sometimes used as a minimum estimate of survivorship) for four consecutive winter seasons combined was 68%, with approximately equal numbers of females and males not returning in subsequent years. Between-year territory fidelity for birds known to have survived from one year to the next ranged from 87%–100%, averaging 97% overall for four consecutive winter seasons. Only three Willow

TABLE 2. Willow Flycatchers exhibited very high between-year site and territory fidelity at two study areas in Costa Rica during four consecutive boreal winter seasons (numbers in parentheses represent numbers of returning flycatchers). Site fidelity was calculated by determining (through resightings) which of the color-banded flycatchers present during early and midwinter were still present during late winter. Territory fidelity is the percentage of flycatchers known to be present throughout the winter that remained in the same territory.

Site	Winter seasons	Site fidelity (%)	Territory fidelity (%)
Chomes	1998–1999 to 1999–2000	77	100 (10 of 10)
	1999–2000 to 2000–2001	68	87 (13 of 15)
	2000–2001 to 2001–2002	50	100 (11 of 11)
	2001–2002 to 2002–2003	79	100 (11 of 11)
Bolson	1998–1999 to 1999–2000	43	100 (3 of 3)
	1999–2000 to 2000–2001	85	91 (10 of 11)
	2000–2001 to 2001–2002	75	100 (9 of 9)
	2001–2002 to 2002–2003	69	100 (11 of 11)

Flycatchers were known to have returned and established different territories; two switched territories at Chomes, and one established a territory 130 m west of its previous year's location at Bolson.

Between-year apparent survivorship averaged 65%, ranging from 54%–72% over the years (Table 3), with an average detection probability of 95%. The best model selected using AIC was that of constant survivorship and detection probability (Table 4), indicating stability in the survivorship and detection of flycatchers across the groups we evaluated. However, yearly variation in survivorship was closely competitive with the top model, suggesting yearly variation in survivorship is important to consider. Finally, there was weak support for an effect of sex, with males predicted to have higher survivorship (69%) than females (62%), and a 13% higher detection probability. Although models with site effects had some weight, the survivorship estimates produced were almost identical to one another.

DISCUSSION

Based on our observations of flycatcher habitat occupancy, intraspecific agonistic behavior, and site fidelity, it is evident that Willow Flycatchers at our sites exhibited obligate territoriality during the nonbreeding period. Because of the overall paucity of detailed information on winter ecology of long-distance migrant tyrannids in tropical regions, many of the comparisons that follow will be to eastern U.S. wood-warblers, which have been the subjects of most long-term studies of marked individuals (Holmes et al. 1989, Holmes and Sherry 1992, Rappole et al. 1992, Staicer 1992, Latta and Faaborg 2001).

We observed no sexual habitat segregation in Willow Flycatchers wintering at our Costa Rica study sites, unlike what has been reported for many species of sexually dichromatic warblers (Lynch et al. 1985, Morton et al. 1987, Lopez Ornat and Greenberg 1990, Wunderle 1992, 1995, Parrish and Sherry 1994, Marra 2000, Latta and Faaborg 2001). At Bolson and

TABLE 3. Between-year apparent survivorship (%) was high for Willow Flycatchers wintering in Costa Rica, based on maximum-likelihood estimates from program MARK. AIC_c model selection results suggested constant survivorship as the best model, but also showed strong support for yearly variation in estimates. Detection probability of Willow Flycatchers for both annual and average apparent survivorship estimates was 95%.

Winter seasons	Survivorship (mean ± SE)	95% confidence interval
1998–1999 to 1999–2000	66 ± 11	49–79
1999–2000 to 2000–2001	72 ± 5	60–81
2000–2001 to 2001–2002	54 ± 6	43–65
2001–2002 to 2002–2003	69 ± 6	56–80
Mean	65 ± 3	59–70

TABLE 4. Models evaluating the effects of year, sex, and site on between-year apparent survival (Φ) and detection probabilities (p) of Willow Flycatchers wintering in Costa Rica, 1999–2003. Only the top seven models, representing 95% of the weight, are shown, ranked by Akaike's information criterion adjusted for small sample sizes (AIC_c). Model indicates which parameters were considered ("." denotes averaging across factors), Deviance is the amount of unexplained variance, K is the number of parameters, ΔAIC_c is the difference in the AIC_c value from the best model, and w_i indicates the model's weight in comparison to all other models. The best model was of constant survivorship and detection probability, indicating stability in the survivorship and detection of flycatchers across the groups we evaluated. However, yearly variation in survivorship (but not detection probability) was closely competitive with the top model, suggesting yearly variation in survivorship is important to consider.

Model	Deviance	K	ΔAIC_c[a]	w_i
Φ(.) p(.)	56.25	2	0.00	0.35
Φ(year) p(.)	50.78	5	0.72	0.25
Φ(sex) p(sex)	50.61	6	2.65	0.09
Φ(sex) p(.)	54.85	4	2.70	0.09
Φ(year) p(year)	48.57	7	2.71	0.09
Φ(site) p(.)	56.22	4	4.08	0.05
Φ(site, sex) p(.)	54.83	5	4.76	0.03

[a] The AIC_c value of the top-ranked model was 383.16, and of the lowest-ranked model (not shown) was 416.80.

Chomes, female and male Willow Flycatchers were interspersed throughout the study areas during each winter season and both sexes occurred in the same habitat type, with territories distributed along the homogenous peripheries of the wetlands. In addition, at neither of the sites were there differences in territory size between the sexes, with females and males defending mutually exclusive territories using the same stereotyped displays and vocalizations, which included primary song. Rappole and Warner (1980) found both sexes of Yellow-bellied and Least Flycatchers in the same habitat types in Veracruz, Mexico, and in both species the sexes defended separate territories using the same types of agonistic behaviors. Thus, defense of mutually exclusive winter territories by both sexes and a lack of sexual habitat segregation may be common life-history traits in *Empidonax*, and possibly other monochromatic migrants. However, because few studies have investigated the behavioral ecology of monochromatic species during the nonbreeding season, further research is needed to determine if such a pattern exists.

Winter territory defense included the use of song by both sexes of Willow Flycatchers, consistent with the finding of Rappole and Warner (1980) that advertising song acted as a mechanism in winter territory defense in Yellow-bellied and Least Flycatchers. Advertising song is innate in the Willow Flycatcher (Kroodsma 1984), and develops early, which could enable juveniles to acquire and defend resources during their first winter (Sogge 1997). Although it is impossible to age most wintering Willow Flycatchers, and therefore to know at what age they begin establishing winter territories, at least one territorial female at Bolson was a known first-year individual (originally banded five months prior as a nestling in Arizona; Koronkiewicz and Sogge 2001). This juvenile responded strongly with advertising song and visual displays during target capture, and defended a territory for her entire first winter. Thus, Willow Flycatchers of any age can potentially obtain and defend winter territories; this capability may be due to similarities in plumage and size among age classes as well as between sexes (Sedgwick 2000). This hypothesis is consistent with Stutchbury et al. (2005), who found that Neotropical migrant species that are territorial in the nonbreeding season are less dimorphic in size (based on wing length) than species that are nonterritorial.

Territorial defense during the nonbreeding season requires energy expenditure and the potential risk of injury, and so should convey fitness benefits compared to nonterritorial behavior. Brown (1964) and Kaufmann (1983) suggested that aggressive territorial defense may indicate that the defended resources are critical for survival. Therefore, one would expect that territorial Willow Flycatchers are

defending one or more important resources. Social behavior during the nonbreeding season appears to be at least partly a function of the kinds of food that a bird consumes (Rappole 1995), and we believe that the Willow Flycatcher's diet, predominantly insects during winter (Wetmore 1972), holds the key to understanding the high degree of winter territoriality that we observed. The Chomes and Bolson sites are wetland habitats that are greatly affected by seasonal inundation. When flycatchers arrive each fall, surface water inundates or is present throughout the sites. Although surface water dries up as the dry season advances, lagunas retain water and saturated soils year-round such that vegetation structure changes very little in flycatcher habitat compared to the surrounding habitats. Janzen (1980) found that as the dry season intensified in northwestern Costa Rica, large numbers of insects moved from dry hillsides to nearby wetland riparian vegetation, and remained in these "riparian refugia" over the dry season. Declines in insects as the dry season advances have been quantified at migrant passerine wintering sites in the West Indies (Strong and Sherry 2000, Latta and Faaborg 2002), and Morton (1980) reported that territorial insectivorous migrants in Panama were restricted to habitats that showed the least seasonal change in wetness. Thus, Willow Flycatchers are likely selecting habitats and strongly defending territories in areas that provide for persistent wet conditions, relatively little vegetation change, and large concentrations of insects over the entire winter period.

The value of obtaining and defending stable resources may be reflected in the high degree of within-season and between-year site and territory fidelity at our nonbreeding sites. The high winter site fidelity recorded here for the Willow Flycatcher is generally greater than that reported for most other long-distance Neotropical migrant passerines, although Northern Waterthrushes (*Seiurus noveboracensis*) in Venezuela remained at a wintering site for an average of slightly over six months (Schwartz 1964), and Holmes et al. (1989) documented winter residency of five to six months and overwinter fidelity of 80% for American Redstarts (*Setophaga ruticilla*) and 66% for Black-throated Blue Warblers in Jamaica. Also in Jamaica, 51% of American Redstarts and 46% of Black-throated Blue Warblers (*Dendroica caerulescens*) returned to the same sites the next year (Holmes and Sherry 1992). In Puerto Rico, 48%–54% of wintering warblers returned the year after banding (Staicer 1992), as did 49% of Yellow-bellied Flycatchers in Mexico (Rappole and Warner 1980).

However, reported fidelity rates of Neotropical migrant passerines are not always so high, and vary considerably among species and studies. Values as low as 0% and 15% have been reported for Common Yellowthroat (*Geothlypis trichas*, Kricher and Davis 1986), and American Redstart (Faaborg and Arendt 1984), respectively. Although some variation in these parameters is expected among species, years, and study sites, we concur with Holmes and Sherry (1992) and Staicer (1992) that studies based on general mist-netting activities and that report very low return rates undoubtedly underestimate site fidelity. Studies based on color-banded birds and intensive resighting show higher values of return and fidelity and most likely produce more realistic estimates of true site fidelity. Our 95% annual detection probability highlights the strength of our survey and resighting efforts. However, even though our results were consistent among years and at both study sites, we do not know if these results can be generalized across the flycatcher's wintering range. For example, Staicer (1992) showed flexibility in the winter social system of the Northern Parula (*Parula Americana*) in Puerto Rico, with some individuals defending territories and others not. Territory-holding Northern Parulas also had a higher probability of returning to the same sites in subsequent years. Willow Flycatcher winter ecology at sites that differ in important ways (such as habitat patch size or vegetation type) may be different than that reported here.

Given that Willow Flycatcher site fidelity is very high and overwinter movements occur relatively infrequently, site fidelity can be used as a minimum estimate of survival (Diamond and Smith 1973, Holmes et al. 1989, Mabey and Morton 1992, Staicer 1992), which allows comparisons with other studies that did not calculate apparent survivorship estimates. The overall fidelity values reported here for Willow Flycatchers are the highest yet published for a wintering Neotropical migrant passerine and suggest that for both sexes, overwinter mortality is relatively low and annual survival

relatively high. Furthermore, the between-year site fidelity estimates from our wintering sites are generally higher than those reported on the breeding grounds. In southern Oregon, 48% of adult males (152 of 314) and 50% of adult females (203 of 403) returned to the same breeding site in subsequent years (Sedgwick 2004). During a 10-year breeding demography study at Roosevelt Lake, Arizona (Newell et al. 2005), average return rates ranged from 53% to 69%. Our between-winter apparent survivorship estimates (54%–72%) are similar to between-year values for breeding Willow Flycatchers at Roosevelt Lake, which ranged from 58% to 73% (Newell et al. 2005).

As is true on the breeding grounds, nonterritorial floaters are difficult to detect and probably underreported in most winter ecology studies. We detected a small number of floater Willow Flycatchers, which replaced territorial individuals that disappeared during and between winters. Holmes et al. (1989) also reported floater American Redstarts and Black-throated Blue Warblers that replaced territorial individuals that disappeared, and Rappole and Warner (1980) documented floaters in banded populations of six species of migrants in Mexico. Winker et al. (1990) documented ''wanderers'' in wintering Wood Thrush (*Hylocichla mustelina*) in Mexico, and found higher mortality for wanderers than for territory holders. The presence of nonterritorial floaters at flycatcher wintering sites suggests that high-quality habitat (i.e., habitat worth defending) may be limited.

The possibility of winter habitat limitation was raised by Lynn et al. (2003), who found that suitable or high-quality Willow Flycatcher habitat is relatively rare on a landscape scale in the Pacific lowlands of Costa Rica. This, in combination with the very strong winter site fidelity exhibited by Willow Flycatchers, implies that the persistence and quality of a particular wintering site has important consequences for the flycatchers that return to overwinter each year. It may be difficult for flycatchers to find alternative sites because suitable wintering sites are relatively uncommon and, if territory-holding Willow Flycatchers already occupy those sites, it may prevent displaced birds from resettling. Flycatchers that are displaced from sites affected by human activities, or are attempting to find better quality sites, could be forced into the role of floaters, with unknown consequences to winter survivorship or subsequent reproductive success on the breeding grounds. High-quality wintering habitat may result in increased reproductive success (Winker et al. 1995), and high-quality wintering sites may be able to better support larger, more stable local populations. This is a critical consideration, since it is not presently known whether small-area sites provide the same overwinter survival value as larger-area sites. Further studies are needed, incorporating multiple sites of varying size and habitat components, to determine if there is a correlation between habitat characteristics and flycatcher winter survivorship, site fidelity, and territory fidelity.

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