INTRASPECIFIC TERRITORIALITY AND SITE FIDELITY OF WINTERING WILLOW FLYCATCHERS (*Empidonax traillii*) IN COSTA RICA

By

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ABSTRACT

Intraspecific Territoriality and Site Fidelity of Wintering Willow Flycatchers (*Empidonax traillii*) in Costa Rica

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I studied wintering Willow Flycatchers (*Empidonax traillii*) in two seasonal freshwater wetland habitats in northwest Costa Rica during the boreal winters of 1998/99, 1999/2000, and 2000/01. I target captured, color-banded, re-sighted, and spot mapped Willow Flycatchers to quantify over-winter and between-year site and territory fidelity, and the degree to which the sexes maintain and defend winter territories. The sexes occurred in approximately equal numbers at sites, and there was no indication of sexual habitat segregation as has been recorded for wintering sexually dimorphic passerines. Males and females maintained and defended well defined, mutually exclusive winter territories, using stereotyped agonistic displays and vocalizations. Females were able to maintain and defend long-term winter territories in the presence of male territory holders and floaters. Winter site fidelity results are the highest yet recorded for a Neotropical migrant passerine. I also exposed Willow Flycatchers to simulated conspecific territory intrusions consisting of randomized sound playbacks; female and male agonistic response was not significantly different toward conspecific intrusion. Similarity in aggressiveness among the sexes in this monomorphic species may account for the observed pattern of winter population structure and lack of sexual habitat segregation at Costa Rica sites.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter I: Background

Van Tyne (1931) was the first to report a Neotropical migrant passerine (Indigo Bunting, *Passerina cyanea*), returning to a specific wintering site in successive years. For the next forty years, mist-netting studies demonstrated that individuals of many Neotropical migrant passerine species, including New World flycatchers, swallows, thrushes, vireos, wood warblers, grosbeaks and buntings, orioles, and tanagers, exhibited a relatively high degree of philopatry to specific wintering sites (see Appendix 1 for summary). However, the behavioral ecology of migrant passerines in tropical regions remains poorly understood. Some research (e.g. MacArthur 1972, Leck 1972, Karr 1976) suggested that migrant passerines were primarily generalists while in tropical regions, in competition with tropical residents for resources. Since 1980, studies incorporating intensive observation of color-banded birds have shown clearly that many species of Neotropical migrants exhibit a highly developed territorial social system during the non-breeding period and are integral members of tropical avian communities (Schwartz 1980, Rappole and Warner 1980, Keast 1980, Holmes and Sherry 1992, Rappole et al. 1992). Intraspecific non-breeding territoriality is now considered widespread in Neotropical migrant passerines (Greenberg 1985).

The Willow Flycatcher (*Empidonax traillii*), a Neotropical migrant passerine, breeds across most of the conterminous United States and parts of extreme southern Canada. As a Neotropical migrant, these birds spend over two thirds of their annual cycle in the subtropical and tropical regions of southern Mexico, Central America and northern South America, south to eastern Ecuador and east to northwestern Venezuela (Stiles and Skutch 1989, Howell and Webb 1995, Ridgely and Gwynne 1989, Ridgely and Tudor 1994, Unitt 1997, Meyer de Schauensee 1978, Sedgewick 2000) (Figure 1.1). Willow Flycatcher breeding habitat is largely confined to dense shrub and riparian habitats typically associated with slow moving or stagnant water (Sedgewick 2000, Paxton 2000). In tropical regions, flycatcher wintering habitat is similar to breeding areas and they favor areas near fresh water; winter habitat consists of humid to semi-arid, partially open areas such as woodland borders, brushy savanna edge, second growth, and scrubby fields (Stiles and Skutch 1989, Howell and Webb 1995, Ridgely and Gwynne 1989, Ridgely and Tudor 1994, Meyer de Schauensee 1978). One of the last spring migrants to arrive in North America, Willow Flycatchers have a short, approximately 100 day breeding season, with individuals typically arriving in May or June, and departing in fall in late August (Sedgewick 2000). From central Mexico to Costa Rica, southbound Willow Flycatchers have been recorded as early as mid-August, and northbound individuals have been recorded as late as May (Stiles and Skutch 1989, Howell and Webb 1995).

Figure 1.1. Breeding and wintering range of the Willow Flycatcher (after Sedgewick 2000).

During the breeding season, Willow Flycatchers are strongly territorial (Sogge 2000), with both sexes defending specific areas against intrusions from conspecifics (other than their mates) (Sogge et al. *in press*). Based on Willow Flycatcher response to conspecific playbacks in Panamá and Costa Rica, Gorski (1969), Koronkiewicz et al. (1998) and Koronkiewicz and Whitfield (1999) suggested that flycatchers are also territorial during the non-breeding season. However, winter territoriality in the Willow Flycatcher had not been proven, and overall, very little was known of its winter ecology. Determining the nature and degree of winter habitat use is important, because winter territorial behavior implies defense of a limited winter resource that may be critical for an individual's survival (Brown 1964, Kaufmann 1983). Furthermore, winter site fidelity could mean that Willow Flycatchers would be negatively affected by the loss of particular wintering sites (Holmes et al. 1989, Rappole et al. 1992, Staicer 1992). The southwestern subspecies (*E. t. extimus*) is federally-listed as endangered (USFWS 1995), and in California *E.t. brewsteri* and *E. t. adastus* are state-listed endangered species (Schlorff 1990). Clearly, knowledge of the behavioral ecology of wintering Willow Flycatchers is important to help guide management and conservation strategies for this and possibly other migrant bird species.

From late September through May in 1998/99, 1999/2000, and 2000/01, I conducted a demography and behavioral ecology study of wintering Willow Flycatchers at two sites in northwest Costa Rica. Utilizing target capture, color banding, extensive resighting, spot mapping color-banded birds, and a conspecific playback experiment, I attempted to determine how Willow Flycatcher winter populations are structured, the degree of over-winter and between-year site fidelity, and whether both sexes maintain and defend mutually exclusive winter territories. The following two chapters are a synthesis of this work. Chapter two addresses how Willow Flycatcher winter populations are structured, the intraspecific territorial behaviors exhibited by wintering flycatchers, and the degree of winter site fidelity. Chapter three details a conspecific playback experiment designed specifically to further describe and quantify agonistic behaviors used by Willow Flycatchers in intraspecific winter territory defense, and to test whether there are behavioral differences among the sexes.

Chapter II: Intraspecific Territoriality and Site Fidelity of Wintering Willow Flycatchers (*Empidonax traillii*) in Costa Rica

INTRODUCTION

Many Neotropical migrant passerines spend a large portion of each year in subtropical and tropical regions (Keast 1980, Rappole 1995). Mist-netting studies in the tropics have demonstrated that many species exhibit strong site fidelity to particular wintering sites (Van Tyne 1931, Schwartz 1964, Loftin 1977, Nickell 1968, Diamond and Smith 1973, Thurber and Villeda 1976). Some research suggests that migrants are highly mobile generalists on the winter grounds, exploiting only superabundant resources and unable to compete with tropical resident species for food and space (MacArthur 1972, Leck 1972, Karr 1976, Hutto 1980). However, behavioral ecology studies incorporating observations of marked individuals have challenged these theories, demonstrating that many species of migratory passerines occupy specific niches in tropical habitats, form stable parts of winter tropical avian communities, and exhibit behaviors suggestive of highly developed territorial social systems (Schwartz 1980, Rappole and Warner 1980, Keast 1980, Holmes and Sherry 1992, Rappole et al. 1992). Although much ecological information about migratory passerines in tropical regions has been obtained since the pioneering work of Rappole and Warner (1980), the vast majority of migrant passerine ecology studies on the wintering grounds have focused on the wood warblers (Family Parulidae).

Over 60 species of Neotropical migrant passerines within eight families have been recorded returning to tropical sites in successive years and/or have been documented as exhibiting intraspecific territoriality on the winter grounds (see Rappole et al. 1983, Rappole 1995, and Appendix 1 for summaries). However, although Tyrant Flycatchers (Family Tyrannidae), comprise the largest family of Neotropical passerines, including approximately 25 boreal migrant species (DeGraff and Rappole 1995), detailed winter ecology information exists for only Yellow-bellied Flycatcher (*Empidonax flaviventris*) and Least Flycatcher (*E. minimus*) (in Rappole and Warner 1980 and Rappole et al. 1992).

In this paper I report on the population structure and the territorial social system of Willow Flycatchers (*Empidonax traillii*) wintering in northwestern Costa Rica. Using color-banded individuals, monitored over three consecutive boreal winters, I addressed the following questions: (1) how are populations structured at wintering sites? (2) to what degree is seasonal and between-year site fidelity exhibited? and, (3) are winter territories defended against conspecifics?

METHODS

Study areas - I conducted this study at two sites in northwest Costa Rica where relatively large numbers of Willow Flycatchers are resident throughout the boreal winter (Figure 2.1). Sites are located in lowland areas (just above sea level) along the Pacific coast, between approximately 10^{o} and 10^{o} 30’ N latitude and from 85^{o} to 85^{o} 30’ W longitude. This region, intensively used for agriculture and human development, experiences two very pronounced seasons over the annual cycle. Wintering Willow Flycatchers arrive in this region late rainy season (September/October), and depart near the end of the dry season (April/May).

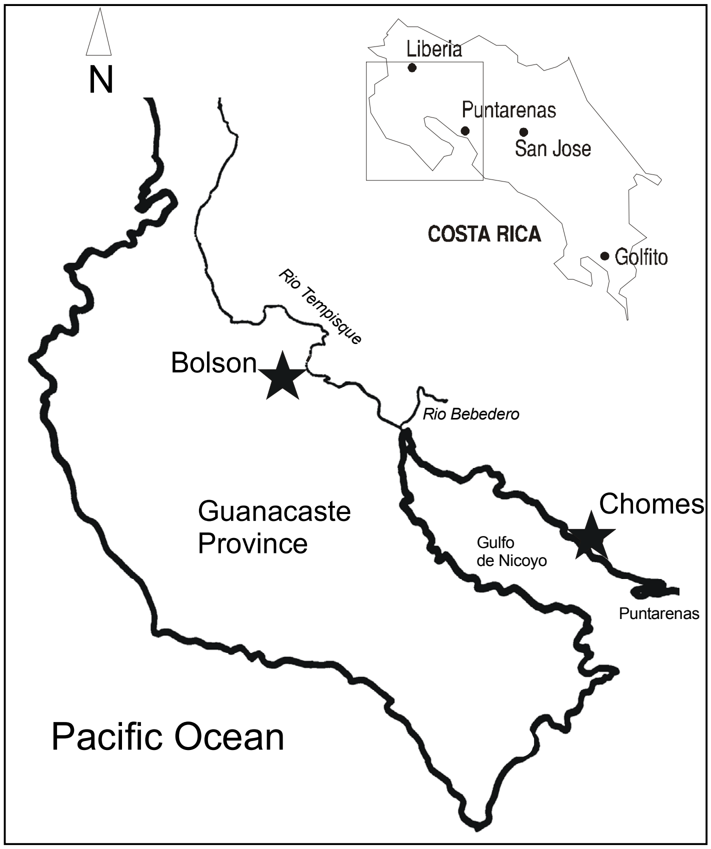

Figure 2.1. Location of Chomes and Bolsón study sites in northwestern Costa Rica.

The Chomes study site, Puntarenas Province, is located approximately 25 km northwest of the city of Puntarenas, and lies along the Pacific coast of northwest Costa Rica (Figure 2.1). The study area consists of a large seasonal freshwater wetland (hereafter refered to by its Spanish name *laguna*) bordered by patches and stringers of trees, woody shrubs and man-made savanna pastures. The periphery of the *laguna* study area is approximately 2700 m in length. Dominant plants include dense woody shrubs (*Mimosa pigra*) and swamp herbs (primarily *Thalia* sp.). Dominant trees bordering the *laguna* include *Guazuma ulmifolia*, *Pithecellobium dulce*, *P. saman*, *Enterolobium* *cyclocarpum*, and *Cocoloba sp*. Although large areas of the *laguna*-wetland dry up as dry season advances, standing water and saturated soils are present year round with the highest water levels occurring during the height of rainy season (October/November) when much of the area becomes inundated.

The Bolsón study site, Guanacaste Province, is located approximately 25 km northeast of the city of Santa Cruz, and lies within the Tempisque drainage of northwest Costa Rica (Figure 2.1). Structurally similar to Chomes but larger in size, the study area consists of a vast *laguna*-wetland and adjacent seasonally inundated man-made savanna pastures bordered by patches and stringers of forest and woody shrubs. The periphery of the *laguna* study area is approximately 4000 m in length. Vegetation height, structure and composition within and bordering the *laguna* are similar to the Chomes site, with standing water and saturated soils present year-round. Slow moving waterways and muddy seeps (*esteros*) meander through the forest and border the *laguna* to the north and south. The Tempisque River lies less than 1 km to the west. Seasonal inundation is much more pronounced than the Chomes site, due to the proximity of the Tempisque River which usually overflows its banks in October and November.

Field schedule – I conducted this study over three consecutive boreal winters: 1998/99, 1999/2000 and 2000/01. Study sites were visited all three seasons, with field visits distributed over the entire winter period: early winter (September/October), mid-winter (December/January), and late winter (April/May).

Capture and Color Banding - I captured and banded Willow Flycatchers, primarily focusing on December and January of each year. To locate wintering flycatchers I systematically traversed the study areas broadcasting Willow Flycatcher vocalizations from hand-held tape players, listening for responding flycatchers. After an individual Willow Flycatcher was detected, I broadcast a variety of conspecific vocalizations to lure flycatchers into a mist net (per Sogge et al. 2001); an *Empidonax* taxidermy mount ("decoy") was sometimes used to complement the broadcast. On several occasions I captured flycatchers via "passive netting", whereby mist nets were erected and periodically checked, with no broadcast of conspecific vocalizations. Each captured flycatcher was given a unique combination of colored leg bands (including a color-anodized and numbered federal aluminum band) and its capture location marked onto a high-resolution aerial photograph. During handling of birds for color banding, I collected a drop of blood (by clipping a toenail per Busch et al. 2000) for later gender determination (Fridolfsson and Ellegren 1999).

Winter Territoriality – To determine whether Willow Flycatchers maintain winter territories, locations, movements, and aggressive interactions (following the terminology of Stein 1963 and Sedgwick 2000) of color-banded flycatchers at both study sites, were mapped onto high resolution aerial photographs. Aerial photographs were taken in November 1997 (Ministero del Ambiente y Energia, San Jose, Costa Rica) and were of a resolution that facilitated pinpointing particular trees, shrubs and other landmarks, and ultimately flycatcher locations. The territory of each flycatcher was mapped by forming a minimum convex polygon that connected the outermost points of each individual's detections (per Odum and Kuenzler 1955, IBCC 1970, Holmes et al. 1989, Staicer 1992). I rectified the aerial photographs using ArcView GIS © software with the Image Warp extension, calculating territory size and distance of any flycatcher movements using X Tools extension; territory size was compared between the sexes. I considered nonoverlapping or minimally-overlapping use areas, in combination with observations of aggressive interactions (especially along border areas), as evidence of territoriality. In order to obtain the maximum number of flycatcher spot observations, I used a combination of playback surveys, which consisted of broadcasting conspecific vocalizations at a volume closely resembling that of a naturally singing bird, and "passive" surveys whereby no playbacks were used. I periodically and systematically traversed the study areas, covering all thoroughly and evenly. In 1999/2000, I erected three portable observation platforms at the Chomes site, each 3.5 m high, to map flycatcher movements within a selected portion of the *laguna*-wetland. Most resighting was conducted from 0600 - 1100 hrs and 1500 - 1730 hrs, when Willow Flycatcher activity is greatest.

Using the definitions of Rappole and Warner (1980) and Rappole (1995), I considered a Willow Flycatcher to be a floater if: (a) it was seen only once, or very irregularly, throughout a winter season excluding migration periods; (b) it was typically observed in quiet, "skulking" behavior; and/or (c) it did not display territorial behavior against other flycatchers or respond aggressively to conspecific playback, but did so once it became a territory holding individual.

Site Fidelity and Winter Survivorship – I calculated seasonal site fidelity by determining (through resights) which of the color-banded flycatchers present during the early (September/October) and middle (December/January) periods of winter were still at the sites at the end of winter (April/May). Individuals whose territory area did not shift >100 m were considered to have held the same territory over that winter period. To determine between-year site fidelity, I revisited study sites in subsequent winters and divided the number that returned to the site by the number of territory holding flycatchers present during April/May of the previous winter. In calculating between-year territory fidelity, individuals were considered to return to same territory in a subsequent winter if: (a) an individual's capture location from a previous winter was located within the area determined to be its territory the following winter; and/or (b) > 50% of an individual's locations and movements (spot observations) within a winter period were located within an area determined to be its territory the previous year.

It is impossible to know whether banded birds that disappear from a site during the winter have died, as opposed to moved, unless they are detected again at a different place or time. Therefore, my calculated survivorship rates, based on over-winter and annual site fidelity (per Holmes et al. 1989 and Holmes and Sherry 1992), must be considered *minimal* survival estimates.

I used the statistical package SPSS Version 10.1 for statistical analysis. Data were tested for normality using normal probability plots. Because data did not conform to normal distribution, I used a two-tailed Mann-Whitney *U*-test to compare the means of male-female territory size. A statistical significance level of $P \leq 0.05$ was chosen to reject the null hypothesis if male and female territory size differed significantly. Data presented are means ± SE unless otherwise stated.

RESULTS

During the 1998/99, 1999/2000 and 2000/01 winter field seasons I spent a total of 20, 104 and 51 days, respectively, color-banding and spot mapping Willow Flycatchers at the Chomes and Bolsón study areas (see Appendix 2 for dates). In 1998/99 I color-banded approximately half of the flycatchers detected within both study areas; 13 at Chomes and 7 at Bolsón (Table 2.1). In 1999/2000 and 2000/01 92% (44 of 48) and 89% (42 of 47), respectively, of the flycatchers detected in both study areas were color-banded (Table 2.1).

Table 2.1. Numbers of Willow Flycatchers detected and color-banded at the Chomes and Bolsón study areas in Costa Rica over four winter seasons.

Site	Winter Season	Total # of Willow Flycatchers detected	Total # of Willow Flycatchers color-banded
Chomes	1998/99	24	13
	1999/2000	29	27
	2000/01	29	27
Bolsón	1998/99	15	7
	1999/2000	19	17
	2000/01	18	16

Spot Mapping – During 1998/99, 14 Willow Flycatchers (10 at Chomes and 4 at Bolsón) were color-banded by mid-January; each site was revisited in mid-March and locations of color-banded individuals recorded. From 17 December to 10 May in 1999/2000, I conducted intensive spot mapping for 25 flycatchers at Chomes and 15 at Bolsón. Although flycatcher locations and movements were recorded at both study areas in 2000/01, overall field effort was reduced and intensive spot mapping conducted only within a pre-designated area at Chomes (in order to compare a sub-sample of flycatcher territories with those of previous winter seasons).

Willow flycatcher abundance remained relatively constant over this three year study, with an average of 27 and 17 Willow Flycatchers wintering at Chomes and Bolsón, respectively (Table 2.1). In 1999/2000, 15 of 25 spot-mapped flycatchers were females, 9 males, and 1 was undetermined; at Bolsón, there were 7 females and 8 males. In 2000/01, there were 24 wintering flycatchers at Chomes (11 females, 12 males and 1 undetermined); at Bolsón, 6 females and 8 males. Based on minimum convex polygons generated by spot mapping in 1999/2000 and 2000/01, both female and male Willow Flycatchers maintained mutually exclusive, well-defined territories that had little or no overlap with conspecific territories of adjacent individuals. Females and males did not form consort pairs and there was no noticeable skew in sex ratios at either site, with both sexes interspersed throughout study areas (Figures 2.2 and 2.3). I observed no significant difference in territory size between the sexes at Chomes or Bolsón. However, the mean territory size of 15 flycatchers at Bolsón was significantly greater than that of 25 territories at Chomes (Mann-Whitney *U*-test, $U = 52$, $P < 0.001$) (Figure 2.4).

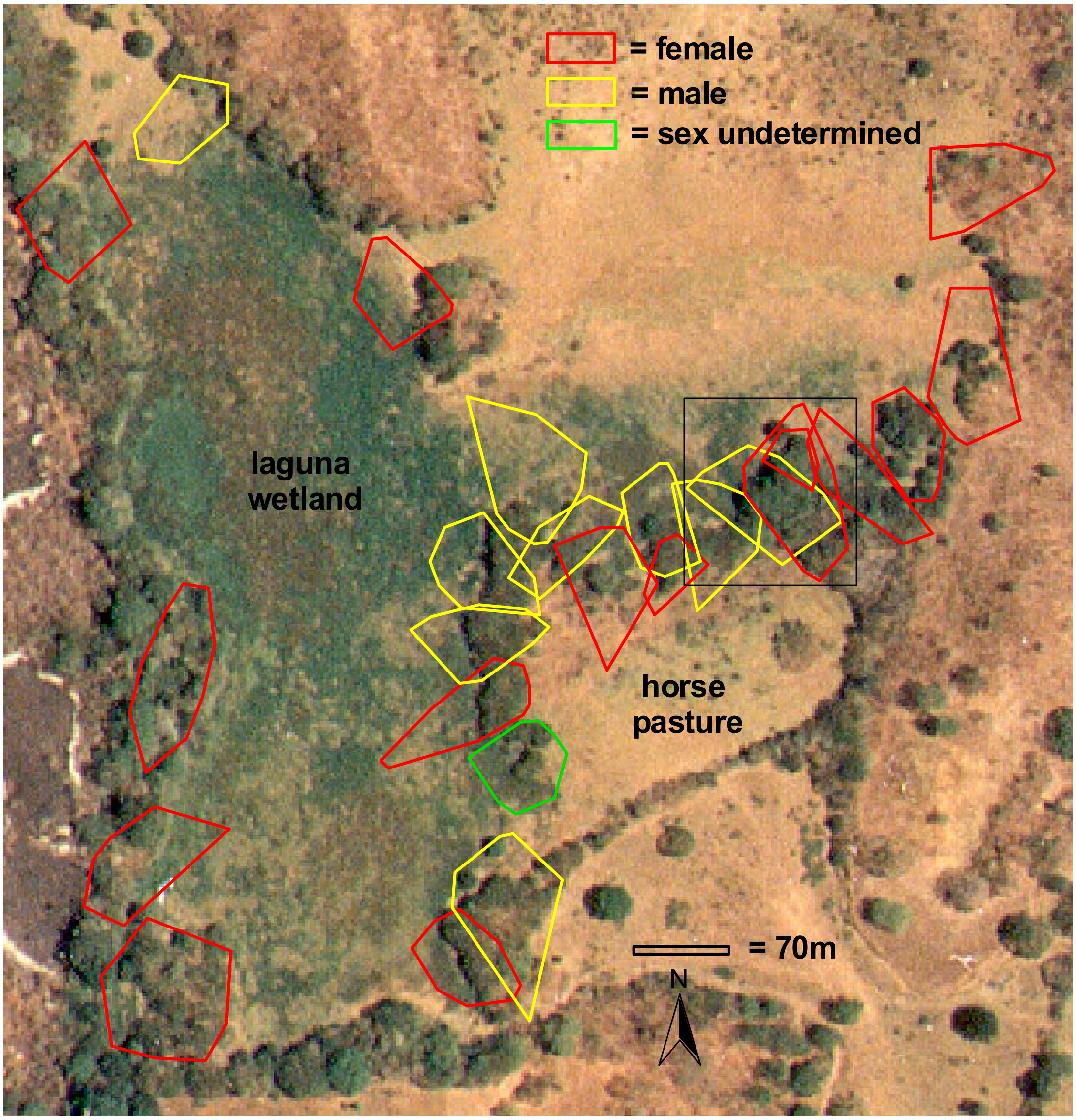

Figure 2.2. Willow flycatcher territories at the Chomes, Costa Rica study site. Polygons depict territories based on spot-mapping of *all* movements of 25 individuals that were monitored from 17 Dec 1999 to 10 May 2000. Red, yellow and green polygons are territories with boundaries that remained relatively constant during winter. Polygons within boxed area are territories that shifted as territory ownership changed (see Figure 2.5 for summary).

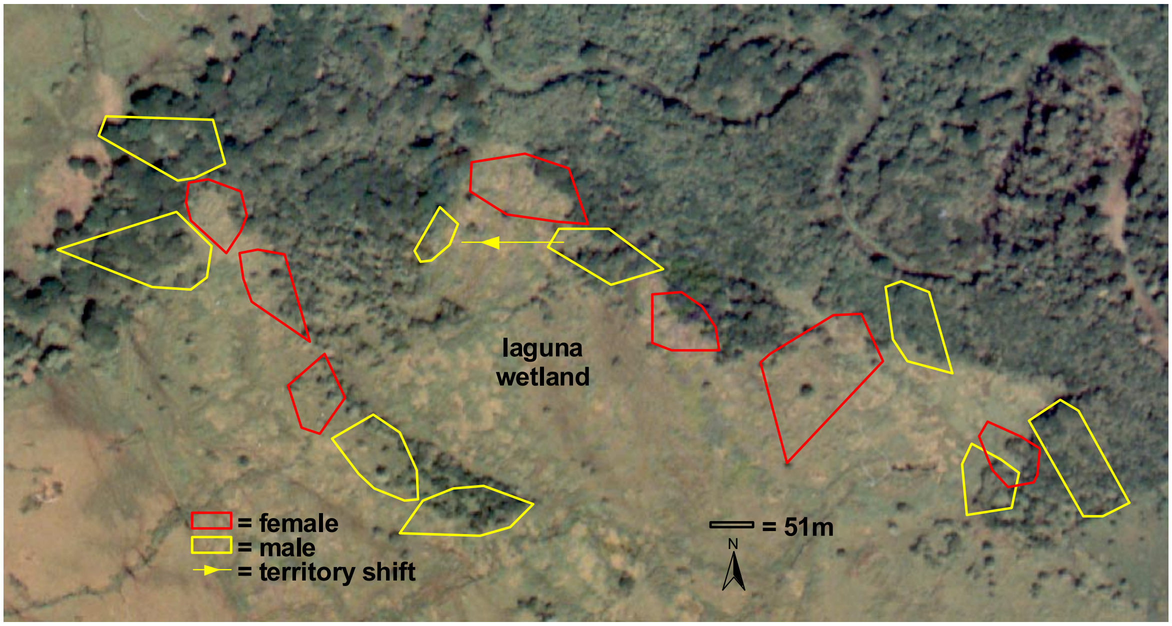

Figure 2.3. Willow flycatcher territories at the Bolsón, Costa Rica study site. Red and yellow polygons depict territories based on spot-mapping of *all* movements of 15 individuals that were monitored from 23 Dec 1999 to 28 April 2000 (arrow represents an abandoned territory).

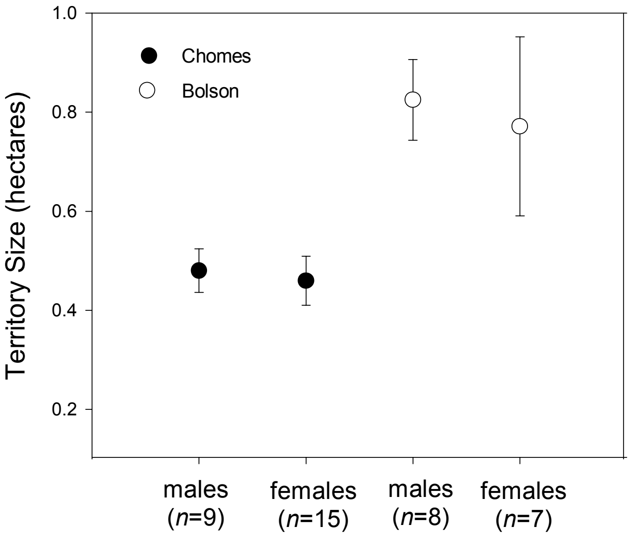

Figure 2.4. Mean territory size of males versus females at the Chomes (males = 0.48 ± 0.04; females = 0.46 ± 0.05) and Bolsón (males = 0.82 ± 0.08; females = 0.77 ±0.18) Costa Rica study sites.

Territoriality – At both study areas, I repeatedly observed stereotyped agonistic interactions between individuals of both sexes. From early winter until spring departure, sexes responded aggressively towards other individuals and to conspecific playbacks. Several ritualized aggressive visual displays in combination with advertising song and/or calls were used, and flycatchers chased and physically interacted with conspecifics. The agonistic behaviors that I observed were similar to those described by Gorski (1969) for wintering Willow Flycatchers in Panamá, and similar to behaviors used in defense of breeding territories (Sedgwick 2000, Sogge et al. 2001).

I observed a total of seven vocalization types and seven displays given by male and female Willow Flycatchers during aggressive intraspecific encounters (following the vocalization and display terminology of Sedgwick 2000). Vocalizations included the *fitz-bew* and *creet* advertising songs, and *whit*, *wheet*, *writ-tu* (*wee-oo* of Stein 1963), and *trill* (*churr call* of Stein 1963) calls. During the most intense confrontations (i.e. physical tussling), flycatchers gave a series of vocalizations "sounding roughly like a high-pitched squeaker-toy", the same vocalization described on the breeding grounds by Sogge et al. (2001). *Flight songs*, whereby a series of a vocalizations (rapid *fitz-bews* and/or *wheets*) are given during chases or during direct flights at other individuals, were also observed, and these *flight-songs* were often accompanied by rapid bill snapping. Ritualized visual displays included rapid *tail-flicking/pumping*, *crest-raising*, *wing-flicking*, *wing-fluttering*, *supplants* (replacement of another flycatcher in position), *chases* and rapid *bill-snapping*. These displays were given independently, as well as in a variety of combinations. During the most intense confrontations (i.e. prolonged intraspecific encounters with multiple *chases*), flycatchers combined several of these displays, while giving a combination of vocalizations. Typical agonistic displays during aggressive intraspecific encounters included *crest-raising* with simultaneous rapid *tailing-pumping* and/or *wing-fluttering*, often accompanied by the *churr* vocalization and rapid *wheep* calls. Agonistic displays and vocalizations were given most often from an exposed perch, in close proximity to the intraspecific territory intrusion.

The degree to which both sexes aggressively respond to intraspecific territory intrusion is illustrated by the efficacy of the target capture technique which simulates a conspecific intrusion (Sogge et al. 2001). An average 91% of the flycatchers detected at both Costa Rica sites over two winter seasons were captured and color banded, with the ratio of females to males approximately equal. Typical aggressive responses of individuals exposed to conspecific playbacks included almost immediate movements and flights toward the speaker location, greatly increased singing and calling rates (e.g. up to 109 *fitz-bew* songs per a 4 minute period), and direct flights and/or physical contact with the taxidermy mount/decoy. Furthermore, vocalizations from the first responding flycatcher initiated singing and/or calling from other, nearby Willow Flycatchers, and flycatchers could be heard responding up to 200m away from the point of broadcast.

Floaters and Territory Acquisition - In addition to winter-resident territory holders, I detected and color-banded two floaters that replaced a territory holding individual mid-winter 1999/2000 at Chomes. In February, two floaters (male #40 and female #20B) became territory holders after they moved into an area from which the original territory holding individual (female #20A) disappeared (Figure 2.5). Previous to territory acquisition, male #40 and female #20B were quiet and submissive to territory holding individuals' and did not respond to playback of conspecific vocalizations.

However, after territory acquisition male #40 and female #20B were no longer submissive to other flycatchers, vocalized regularly, responded strongly to playback of conspecific vocalizations, and defended territories until the end of winter.

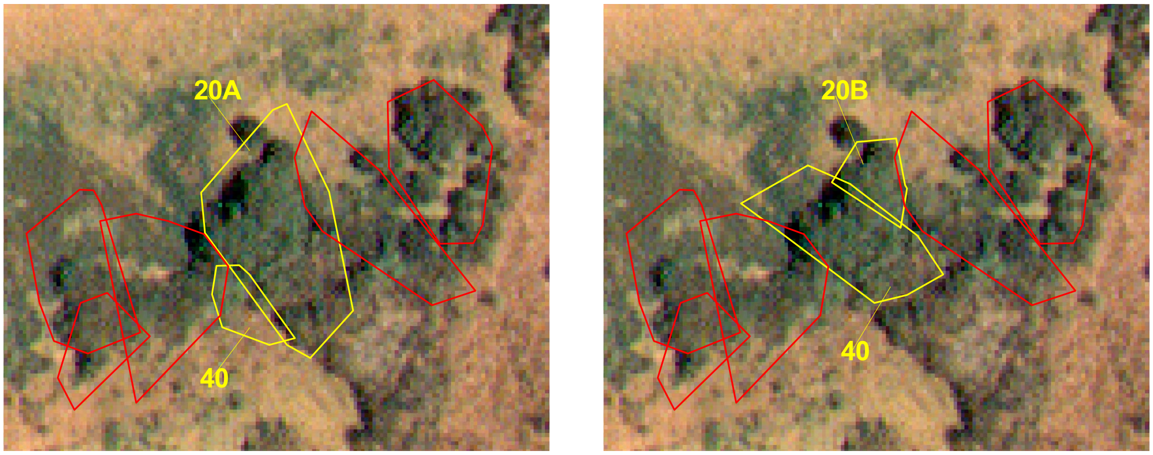

Figure 2.5. Shifts in territory boundaries and territory holders at the Chomes site. Colored polygons depict territories based on spot-mapping the movements of individuals during the 1999/2000 season. In the left panel, the yellow polygons depict the territory of flycatcher 20A and the use area of floater 40, prior to disappearance of flycatcher 20A on 7 February. In the right panel, the yellow polygons show the subsequent territorial boundaries established by flycatchers 40 and 20B, which moved into the area vacated by flycatcher 20A.

In addition to floaters replacing individuals that disappeared within a winter season, I also observed a floater which returned the following winter and acquired a territory. Late in the winter season of 1999/2000 at Chomes, floater male #42 was observed irregularly for 6 days prior to its capture on 23 March. Although submissive to chases and attacks by territory holder female #1, floater male #42 responded aggressively to conspecific playbacks during target capture. Male #42 was not seen again until the following winter, whereupon it returned to maintain and defend the area formerly held by female #1 (which was never again detected).

Replacement of Individuals That Disappeared - I also observed the replacement of two individuals that disappeared during winter seasons. At Bolsón, male #12 was observed regularly from 24 December 1999 to 31 January 2000, defending a territory in response to other flycatchers and playback of conspecific vocalizations. On 14 February male #30 was target netted in the same capture area as male #12. Male #12 was never seen again whereas male #30 remained to occupy and defend the territory until the end of winter. At Chomes, female #34 was seen regularly defending a territory from 28 September 2000 to 15 January 2001. From 6 to 10 January 2001, an unbanded flycatcher, not detected previously, and female #34 were observed engaging in multiple aggressive interactions within and adjacent to the boundaries of territory #34. On 10 January, the unbanded flycatcher (male #34B) was target captured. From 10 January through 19 May, only #34B was observed defending the territory in response to other flycatchers and playback of conspecific vocalizations; female #34 was never seen again.

Settlement and Territory Dynamics – During periods when Willow Flycatchers were still arriving at winter sites, I observed the territories of two individuals contract, as later arriving individuals established adjacent territories. From mid-December to early January in 1999/2000, female #3 was the only flycatcher detected defending a territory on the eastern boundary of the Bolsón study area. In late January male #4 arrived and settled immediately adjacent to female #3, resulting in a reduction of #3's "original" territory (Figure 2.6a). In early October in 2000/01, female #23 was observed defending a large cove and tree line at Bolsón. When the area was revisited in December and January, females #25 and #26B had established territories adjacent to #23, resulting in a fourfold decrease of #23's October territory (Figure 2.6b).

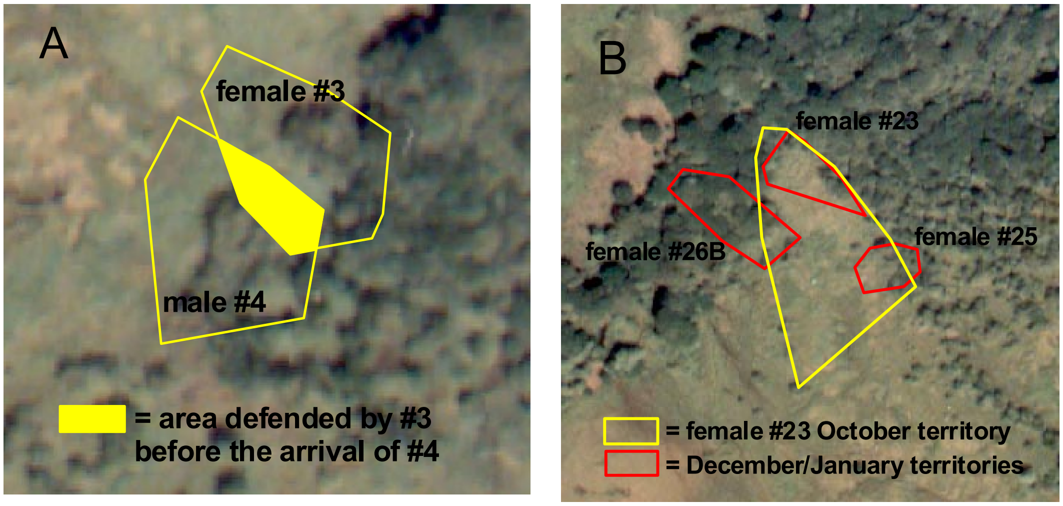

Figure 2.6. Willow flycatcher territories at the Bolsón, Costa Rica study site. (A) the reduction of a females' territory upon the arrival of an adjacent male (B) the reduction of a females' territory upon the arrival of two adjacent females

Noncontiguous Territories – By spot mapping within a selected portion of the Chomes *laguna*-wetland, I found two individuals (female #34 and male #40) that maintained and defended two noncontiguous territories. During early mornings, and from late afternoon until dark, both individuals were consistently detected defending a *laguna*-wetland area that was noncontiguous with the tree-line territories used throughout mid-day along the tree line (Figure 2.7). In this portion of the study site the habitat immediately adjacent to the tree-line territories is introduced, short grass cattle pasture for at least half of the winter season, rather than dense woody shrubs and swamp herbs found throughout the year in the noncontiguous laguna portions of their territories.

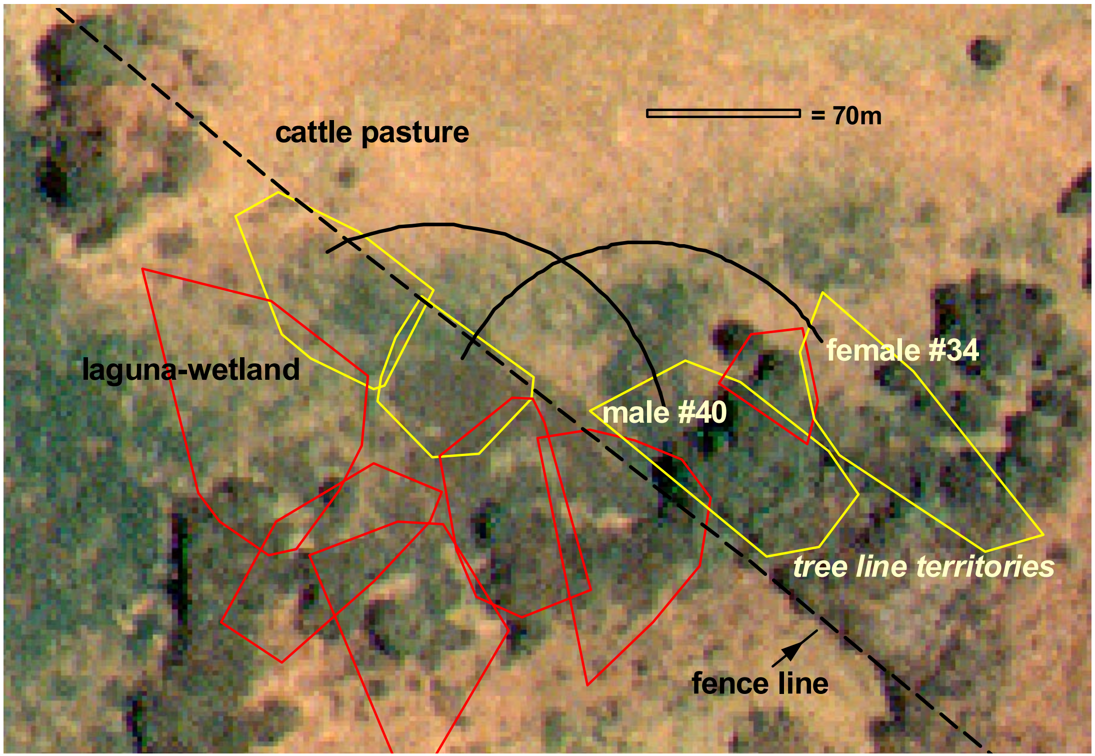

Figure 2.7. Selected spot mapping area within the *laguna*-wetland at the Chomes, Costa Rica study site. Yellow polygons depict territories of two individuals, female #34 and male #40; black arcs connect the noncontiguous territories defended by each individual. Habitat within the laguna-wetland, upper left of fence line, consists of dense woody shrubs and swamp herbs, whereas habitat upper right of fence line consists of short grass cattle pasture.

Seasonal Site Fidelity, Over Winter Survivorship, *Territory Fidelity and Movements* – A total of 40 Willow Flycatchers at both study areas acquired winter territories in 1999/2000, of which 38 were established by the middle period of winter (December/January) (Table 2.2). Thirty-four of these 38 individuals (89%); 18 females, 15 males, and one undetermined remained at both sites from the middle period of winter to late winter (April/May); 33 (97%) held the same territories for the entire period. During 2000/01, 42 Willow Flycatchers acquired winter territories, of which all were established by mid-winter. Thirty-five of these 42 individuals (83%); 17 females, 17 males and one undetermined remained at the sites from mid- to late winter; 32 (94%) held the same territories for the entire period. Thus, the seasonal site fidelity and survivorship from mid- to late winter, combined for both study areas over two consecutive winter seasons, was 86%, with approximate equal numbers of males (six) and females (five) disappearing over winter seasons. Combined seasonal territory fidelity from mid-to late winter for the two winter seasons was 95% (Table 2.2).

Table 2.2. 1999/2000 and 2000/01 Willow Flycatcher *seasonal* site and territory fidelity from mid-(December/January) to late (April/May) winter for the Chomes and Bolsón study areas in Costa Rica (numbers in parentheses represent numbers of individual flycatchers).

Site	**Winter Season**	**% Site Fidelity**	**% Territory Fidelity**
Chomes	1999/2000	91% (21 of 23)	100% (21 of 21)
	2000/01	85% (22 of 26)	86% (19 of 22)
Bolsón	1999/2000	87% (13 of 15)	92% (12 of 13)
	2000/01	81% (13 of 16)	100% (13 of 13)

In order to document early to mid-winter site fidelity, I visited both sites in September 2000. Willow flycatcher abundance was approximately half of what it was mid-winter in 1998/99 and in 1999/2000, with total of 16 and 7 color-banded flycatchers at the Chomes and Bolsón sites, respectively. At this time southbound passerine migration was well underway and Willow Flycatchers were still arriving. Twenty-two of these 23 individuals (96%); 10 females and 12 males remained at the sites until mid-winter; 19 (86%) held the same territories.

In 1999/2000 only one individual at Bolsón moved its territory over the winter season; in 2000/01 a total of three flycatchers at Chomes moved territories over the winter season (Table 2.3). All of these individuals moved to unoccupied areas and defended territories until spring departure.

Table 2.3. Willow Flycatcher *within* season movements at the Chomes and Bolsón study areas in Costa Rica.

Site	**Winter Season**	**Individual Flycatcher**	**Total # of Movements**	**Total Distance(s) Moved (meters)**
Bolsón	1999/2000	male #10	1	230
Chomes	2000/01	male #6B	1	475
		male #8	3	195, 225, 220
		male #44	2	325, 320

Between-Year Site Fidelity, Annual Survival, Between-Year Territory Fidelity and Movements – Twenty Willow Flycatchers were color-banded at both study sites in 1998/99. Thirteen of these individuals (65%); 7 females and 6 males returned to the sites in 1999/2000; all 13 returned to the same territories (Table 2.4). Approximately equal numbers of females (3) and males (4) did not return. During the winter of 1999/2000, a total of 35 territory holding Willow Flycatchers (19 females and 16 males) were known to have remained at both sites until late winter. Twenty-six of these 35 individuals (74%); 13 females and 13 males returned to the same sites in 2000/01 (Table 2.4). Twenty-three of these 26 individuals (88%) returned to the same territories (Figures 2.8 and 2.9). Thus, between-year site fidelity and minimal annual survival rate for two consecutive winter seasons combined was 71%. The combined between-year territory fidelity for two consecutive winter seasons was 92%.

Table 2.4. Willow flycatcher *between-year* site and territory fidelity over two winter seasons for the Chomes and Bolsón study areas in Costa Rica (numbers in parentheses represent numbers of returning flycatchers).

Site	Winter Seasons	% Site Fidelity	% Territory Fidelity
Chomes	1998/99 to 1999/2000	77% (10 of 13)^{aa}	100% (10 of 10)
	1999/2000 to 2000/01	68% (15 of 22)^{bb}	87% (13 of 15)
Bolsón	1998/99 to 1999/2000	43% (3 of 7)^{aa}	100% (3 of 3)
	1999/2000 to 2000/01	85% (11 of 13)^{bb}	91% (10 of 11)

( )^{aa} = includes all flycatchers banded in 1998/99

( )^{bb} = number of territory holding flycatchers known to have remained at sites/survived until late winter (April/May) 1999/2000

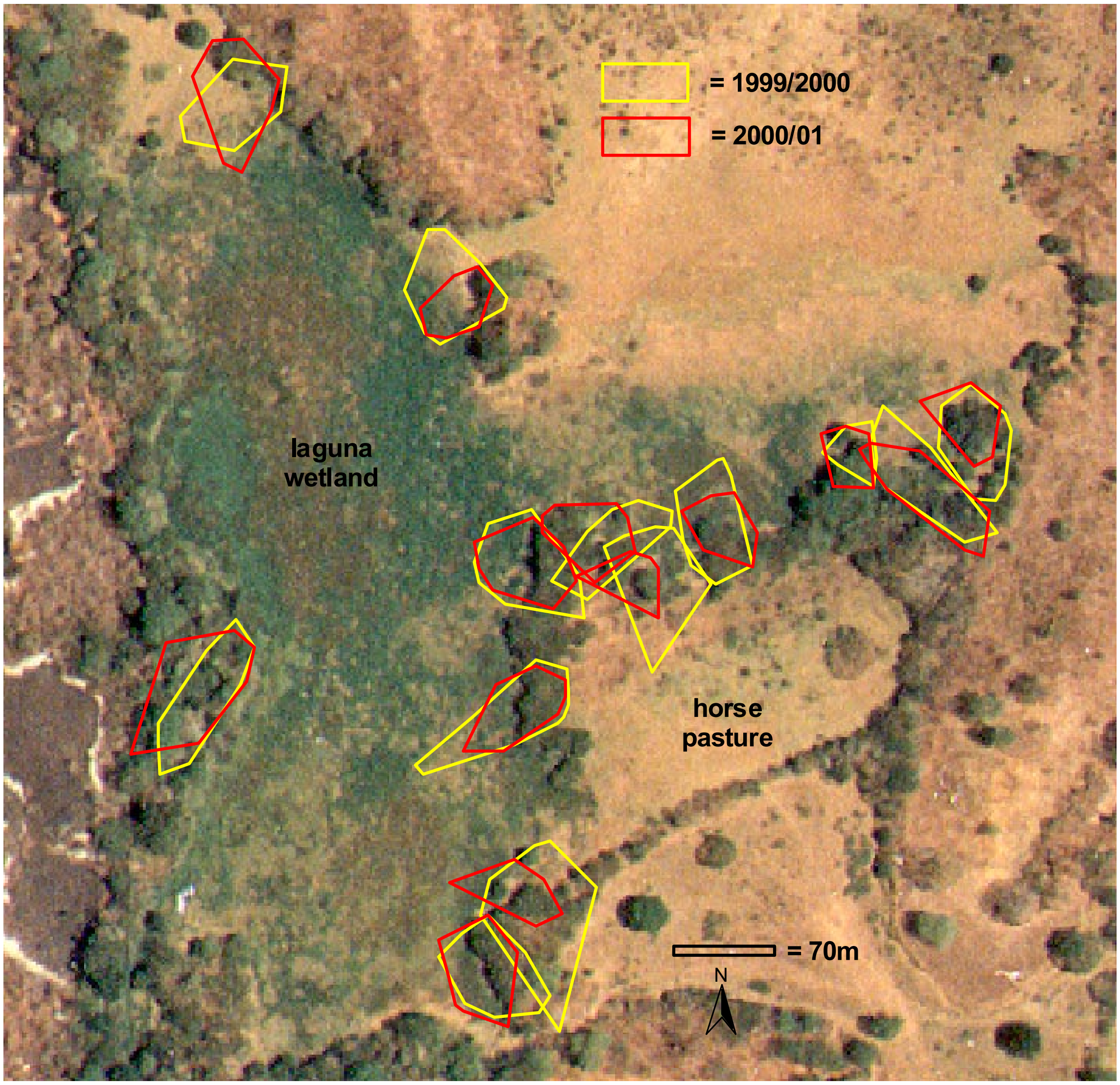

Figure 2.8. Willow flycatcher study site at Chomes, Costa Rica depicting the 13 individuals that held the same territories in 1999/2000 (yellow polygons) and 2000/01 (red polygons).

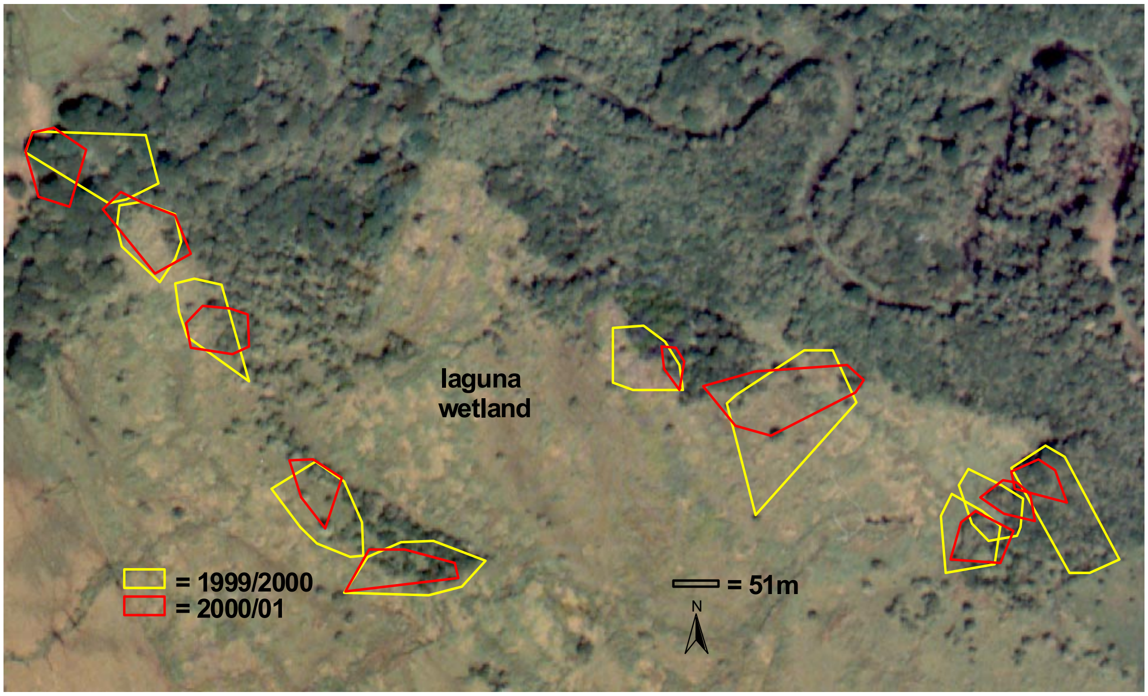

Figure 2.9. Willow flycatcher study site at Bolsón, Costa Rica depicting the 10 individuals that held the same territories in 1999/2000 (yellow polygons) and 2000/01 (red polygons).

A total of three Willow Flycatchers returned to different territories in 2000/01, two at Chomes and one at Bolsón. Males #6 and #8 at Chomes returned to the same territories in 1999/2000, but "switched" territories in 2000/01; #6 returned to #8's former territory and #8 returned to #6's former territory. At Bolsón male #26 returned and defended a territory 130m west of its 1999/2000 location, while female #26B occupied #26's former territory.

DISCUSSION

When examining population structure, intraspecific agonistic behavior, and site fidelity, it is evident that Willow Flycatchers exhibit territoriality during the non-breeding period. Unfortunately, the overall paucity of detailed ecological information on long-distance migrant Tyrannids in tropical regions limits quantitative comparison of many ecological parameters of wintering Willow Flycatchers in northwest Costa Rica. Comparative data are restricted primarily to the eastern U.S. wood warblers, which comprise the vast majority of long-term studies of marked individuals (Holmes et al. 1989, Holmes and Sherry 1992, Rappole et al. 1992, Staicer 1992, Latta and Faaborg 2001).

I observed no sexual habitat segregation for Willow Flycatchers wintering at my Costa Rica study sites, unlike that reported for the sexually dimorphic Prairie Warbler (*Dendroica discolor*) in the Dominican Republic (Latta and Faaborg 2001), American Redstart (*Setophaga ruticilla*) in Jamaica (Parrish and Sherry 1994, Marra 2000) and Mexico (Lopez Ornat and Greenberg 1990), Common Yellowthroat (*Geothlypis trichas*), Magnolia Warbler (*Dendroica magnolia*), and Northern Parula (*Parula americana*) in Mexico (Lopez Ornat and Greenberg 1990), Black-throated Blue Warbler (*Dendroica caerulescens*) in Puerto Rico (Wunderle 1992, 1995), and Hooded Warbler (*Wilsonia citrina*) in Mexico (Lynch et al. 1985, Morton et al. 1987). At the Costa Rica sites, female and male Willow Flycatchers were interspersed over study areas for two consecutive winter seasons and both sexes occurred in the same habitat type, with territories distributed along the homogenous peripheries of the *laguna*-wetlands (Figures 2.2 and 2.3). In addition, at neither of the Costa Rica wintering sites were there differences in territory size between the sexes, and both females and males defended territories using the same stereotyped displays and vocalizations. Rappole and Warner (1980) found both sexes of Yellow-bellied Flycatcher (*Empidonax flaviventris*) and Least Flycatcher (*E. minimus*) in Veracruz, Mexico in the same habitat types, and in both species the sexes defended separate territories using the same types of agonistic behavior. Thus, defense of mutually exclusive winter territories by both sexes and lack of sexual habitat segregation may be the rule in the monomorphic *Empidonax*; further study is needed of other migrant Tyrannids in tropical regions.

Song was used by both sexes of Willow Flycatcher in winter territory defense, consistent with Rappole and Warner's (1980) finding that advertising song acted as a mechanism in winter territory defense in Yellow-bellied and Least Flycatcher. It has been shown that 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 impossible to age most wintering Willow Flycatchers, at least one territorial female at Bolsón was a known juvenile (originally banded as a nesting in Arizona, U.S.A. five months prior). This juvenile responded strongly with advertising song and visual displays during target capture, and defended a territory for its entire first winter. Thus, all individuals, regardless of age and/or sex can potentially obtain and defend winter territories, and this may be due to the lack of sexual dimorphism and extremely subtle plumage differences (i.e. buff colored wing bars) among age classes (Pyle 1997).

Brown (1964) and Kaufmann (1983) suggested that energy expenditure in aggressive territorial defense indicates that defended resources may be critical for survival. The Willow Flycatcher's diet, predominantly insects during winter (Wetmore

1972) may have direct implications regarding the high degree of territoriality observed, in that "social behavior during the non-breeding season appears to be at least partly a function of the kinds of foods being used" (Rappole 1995). The Costa Rica sites are wetland habitats which are greatly affected by seasonal inundation. When the flycatchers arrive each fall, surface water covers most flycatcher habitat at each site. As dry season advances, surface water dries up, but the *laguna* retains surface water and saturated soils year-round. I observed vegetation structure changing very little in the flycatcher habitat as compared to the surrounding non-wetland habitats. In northwest Costa Rica, Janzen (1980) found as dry season intensifies, large numbers of insects move from dry hillsides to nearby wetland riparian vegetation, and that large concentrations of insects pass the dry season in these "riparian refugium." In conjunction with this, Morton (1980) reported that territorial, obligatory insectivorous migrant species in Panamá were restricted to wet areas showing the least seasonal change. Thus, the persistence of wet conditions, relatively little vegetation change and large concentrations of insects for the entire period Willow Flycatchers are resident at Costa Rica sites may contribute to the territorial behavior that I observed.

Wintering Willow Flycatchers exhibited a high degree of seasonal and between-year site fidelity in Costa Rica, with 96% of the birds remaining at the study sites from early to mid-winter, 86% remaining at sites from mid- to late winter, and 71% returning to the same sites between years. The high winter site fidelity recorded here for Willow Flycatcher is consistent with patterns seen in other long distance Neotropical migrant passerines. In Venezuela, Northern Waterthushes (*Seiurus noveboracensis*) remained at a wintering site for an average of slightly over six months (Schwartz 1964). Holmes et al.

(1989) documented over-winter fidelity of 80% for American Redstarts and 66% for Black-throated Blue Warblers in Jamaica, with birds remaining at winter sites for five to six months. Also in Jamaica, 51% of redstarts and 46% of Black-throated Blues returned to the same sites the next year (Holmes and Sherry 1992). In Puerto Rico, 54% of Northern Parulas (*Parula Americana*), 48% of Prairie Warblers (*Dendroica tigrina*) and 50% of Cape May Warblers (*D. discolor*) returned the year after banding (Staicer 1992). However, reported fidelity rates of Neotropical migrant passerines vary considerably among many different species and studies. Values as low as 0% have been reported for Common Yellowthroat (*Geothlypis trichas*; Kricher and Davis 1986), and 15% for American Redstart (Faaborg and Arendt 1984). In contrast, Rappole and Warner (1980) found 49% site fidelity in Yellow-bellied Flycatchers and Holmes and Sherry (1992) reported 51% for American Redstart. Although some variation in these parameters is expected among species, years, and study sites, I concur with Holmes and Sherry (1992) and Staicer (1992) that studies based on general mist-netting activities and reporting very low return rates undoubtedly underestimate between-year site fidelity. Studies based on color-banded birds and intensive re-sighting, show higher values of return and fidelity and most likely produce more realistic estimates of between-year site fidelity. It is also important to emphasize that even though my results were consistent between years and at both study sites, I do not know if these results can be generalized across the wintering range. For example, Staicer (1992) had shown flexibility in the winter social system of the Northern Parula 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 studies conducted at sites that differ in important ways (such as size or habitat characteristics) may yield different results than that reported above.

As reported above, non-territorial floater Willow Flycatchers were observed replacing individuals that disappeared over winter. In other studies of wintering Neotropical migrants, Holmes et al. (1989) reported floater American Redstarts and Black-throated Blue Warblers that moved in to replace territorial individuals that had disappeared. Rappole and Warner (1980) also documented floaters in their banded populations of six species of migrants in Mexico, noting that: (1) floaters were quiet, furtive, and submissive to the territory holders which chased and expelled intruding floaters; (2) floaters replaced territorial residents that disappeared; and (3) once they became territory holders, former floaters responded aggressively to conspecific intrusion. Winker et al. (1990) also documented "wanderers" in wintering Wood Thrush (*Hylocichla mustelina*) in Mexico and found higher mortality for wanderers than for territory holders. Whether there are survival differences between Willow Flycatcher floaters and territory holders requires special study.

Given that Willow Flycatcher site tenacity is very high and over-winter movements occur relatively infrequently (as noted above by the replacements of individuals who disappeared), site fidelity can be used as a *minimal* estimate of survival (as per Diamond and Smith 1973, Holmes et al. 1989, Mabey and Morton 1992, Staicer 1992). The overall fidelity values reported here for Willow Flycatcher are the highest yet reported for a wintering Neotropical migrant passerine and suggest that for both sexes of Willow Flycatcher, over-winter mortality is relatively low and annual survival is relatively high. Furthermore, Willow Flycatcher fidelity and survivorship estimates at the Costa Rica sites is higher than that reported on the breeding grounds, at least for this three year study. At two sites in Arizona, 40% (61 of 152) banded adults returned to the same breeding sites the following year (U.S.G.S. *unpublished data*). In southern California, 61.6% of adult males (*n* = 138) and 51.8% of adult females (*n* = 137) returned to the same breeding site the following year (Whitfield in Sedgwick 2000). Annual survivorship at two sites in Arizona was reported at 57%, with 86 of 152 adult banded Willow Flycatchers returning the following year (U.S.G.S. *unpublished data*). High site fidelity and survivorship on the wintering grounds suggests that disruptive events in tropical regions, such as habitat destruction, may have a profound effect on the population dynamics of wintering migrants with some species likely to show declines in recent years (Holmes et al. 1989, Holmes and Sherry 1992, Rappole et al. 1983, Rappole et al. 1992, Staicer 1992).

Recent surveys conducted at 122 sites throughout the Pacific lowlands of Costa Rica suggest that suitable and/or high-quality Willow Flycatcher wintering habitat is relatively rare on a landscape scale (Lynn et al. *in press*). 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 to the flycatchers that return to over-winter each year. It may be difficult for flycatchers to find alternative sites, in that 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 impacted sites, or attempting to find better quality sites, could be forced into the role of floaters, with unknown consequences to winter survivorship. Furthermore, the high fidelity and survivorship rates for wintering Willow Flycatchers at these Costa Rica sites may indicate that they comprise relatively high-quality wintering habitat (Winker et al. 1995). High quality wintering sites may be able to better support larger, more stable local populations. This is a critical consideration in that it is not presently known whether small sites provide the same over winter survival value as larger 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 survivorship.

Chapter III: Intraspecific Winter Territory Defense Behavior in The Willow Flycatcher (*Empidonax traillii*)

INTRODUCTION

Studies investigating the behavioral ecology of Neotropical migrant passerines in tropical regions have shown that several species exhibit agonistic behaviors in defense of long-term, mutually exclusive winter territories (Schwartz 1964, Rappole and Warner 1980, Holmes et al. 1989). Recorded aggressive winter territorial defense behaviors include vocalizations (advertising song and calls), stereotyped visual displays, chase, and/or attack. Brown (1964) and Kaufmann (1983) suggested that aggressive territorial defense behavior is associated with the acquisition of resources, and energy expenditure in territorial defense indicates that the resources defended may be critical for survival.

The Willow Flycatcher (*Empidonax traillii*), a sub-oscine in the family Tyrannidae, spends approximately three quarters of its annual cycle in subtropical and tropical regions (Stiles and Skutch 1989, Howell and Webb 1995). On the wintering grounds in Costa Rica, both sexes of Willow Flycatchers maintain long-term, mutually exclusive winter territories which are defended with vocalizations and stereotyped visual displays (see Chapter 2). This study was conducted to describe and quantify the agonistic behaviors used by Willow Flycatchers in intraspecific winter territory defense and to test whether there are behavioral differences between the sexes.

METHODS

Study Areas - I conducted this study at two sites in the Pacific lowlands of northwest Costa Rica, where Willow Flycatchers are winter residents from late September until May. Both study areas, Chomes (Puntarenas Province) and Bolsón (Guanacaste Province), are seasonal freshwater wetlands (*lagunas*) surrounded by areas intensively used for agriculture and human development. Vegetation structure and composition structure are similar between sites, with patches and stringers of forest bordering wetland vegetation (see Chapter 2).

Field Studies - To examine the agonistic behaviors used by Willow Flycatchers in defense of winter territories, I conducted a series of standardized, simulated conspecific intrusions on territory holding individuals. Starting in mid-December 1999, I determined territory boundaries by spot mapping locations and movements of color banded individuals onto high resolution, aerial photographs forming a minimum convex polygon that connected the outermost points of each individual's detections (per Odum and Kuenzler 1955, IBCC 1970, Holmes et al. 1989). Simulated territory intrusions consisted of randomized sound playbacks in conjunction with an *Empidonax* taxidermy decoy, placed near the center of each Willow Flycatcher territory. All flycatchers exposed to simulated territory intrusions (STIs) were color banded.

Randomized playbacks consisted of a set of three standardized recordings (descriptions of Willow Flycatcher vocalizations and visual displays follow the terminology in Stein 1963 and Sedgwick 2000): (1) Willow Flycatcher vocalizations recorded on the breeding grounds (Gila and Pima County, AZ) with a Sony TCM-5000EV Cassette-Corder and Sennheiser ME20 microphone; vocalizations included *fitz-*

bew and *creet* advertising songs, *whit* and *chur/kitter* calls, and array of flycatcher calls made during an aggressive encounter between a flycatcher and a Brown-headed Cowbird (*Molothrus ater)*; (2) Lesser Ground Cuckoo (*Morococcyx erythropygius,* a common and vocal species at both study sites), primary song and calls from Songs of Mexican Birds by Coffey and Coffey, 1990; and (3) random noise (a squeaker toy accompanied by digital beeps), recorded with a Sony TCM-5000EV Cassette-Corder and Sennheiser ME20 microphone microphone. Although the majority of flycatchers exposed to STIs were previously subject to conspecific playbacks (during target capture and resighting), the particular set of flycatcher vocalizations used for the treatment was unique, and individuals were exposed only once. In addition, I selected an array of flycatcher vocalizations (emphatic advertising songs and rapid calls) known to illicit agonistic behaviors on the breeding grounds (Sogge et al. 2001). I broadcast each of the three playback treatments for 4 minutes at a standardized volume (near that of a naturally singing bird), with a silent 4 minute listening and observation treatment before and after each playback treatment (*per* Smith 1996). The order of treatments was structured such that all possible order combinations (six total) were incorporated, and the treatment order for each individual flycatcher was chosen at random (Table 3.1).

Table 3.1. Playback treatments for the first six willow flycatchers exposed to simulated territory intrusions (**1** = willow flycatcher treatment **2** = lesser ground cuckoo treatment **3** = random noise treatment).

Individual #1	4 min. listen observation period	**3**	4 min. listen observation period	**2**	4 min. listen observation period	**1**	4 min. listen observation period
Individual #2	4 min. listen observation period	**2**	4 min. listen observation period	**3**	4 min. listen observation period	**1**	4 min. listen observation period
Individual #3	4 min. listen observation period	**1**	4 min. listen observation period	**2**	4 min. listen observation period	**3**	4 min. listen observation period
Individual #4	4 min. listen observation period	**2**	4 min. listen observation period	**1**	4 min. listen observation period	**3**	4 min. listen observation period
Individual #5	4 min. listen observation period	**1**	4 min. listen observation period	**3**	4 min. listen observation period	**2**	4 min. listen observation period
Individual #6	4 min. listen observation period	**3**	4 min. listen observation period	**1**	4 min. listen observation period	**2**	4 min. listen observation period

The day before each STI, I randomly selected a Willow Flycatcher for experimentation (including only individuals whose approximate territory center was determined and excluding any that were previously selected). The previous evening before each STI, flagging was hung 10 m from the approximate center of a territory in each of the four cardinal directions designating the STI area (a circular area with a 20 m diameter). An *Empidonax* decoy, chosen randomly from a selection of three for each STI, was mounted on the top of a camouflaged pole 2m in height and placed in the center of the STI area. The decoy was used for each of the three playback treatments. To broadcast playback treatments, I used a portable Memorex MD3015 CD player connected to two monaural Radio Shack AMX 9 amplified speakers via a monaural cable. The speakers were affixed back to back and mounted 0.5m below the decoy. The STI's were conducted only by myself, from 0600 to 0700 hours during January and February 2000, and only during calm and favorable weather (e.g. no rain, the undersides of vegetation could not be seen during windy periods). On mornings that more than one flycatcher was exposed to an STI, territories were at least 50 m apart to avoid habituation to broadcast. I remained as stationary and inconspicuous as possible, and situated approximately 15 m away from the STI area, so I could clearly view the area. I dictated flycatcher behaviors (visual displays, song and calling rates, and movements) observed during the STI period into a handheld tape recorder, and transcribed the tape immediately following the experiment.

I scored the agonistic responses of each Willow Flycatcher during each of the three playback treatments and for each of the four listening and observation treatments. Individuals received a score of 0 (lowest), 0.5, or 1 (highest) for each of four behavioral categories: (1) proximity to STI area; (2) vocalization rate; (3) aggressiveness to decoy; and (4) agonistic visual displays (Table 3.2). Individuals received one score per behavioral category, with the combined maximum possible score of 4 during any one treatment. I then compared the overall aggressive scores among the different treatments to determine whether flycatchers responded more strongly to other Willow Flycatcher vocalizations than to lesser ground cuckoo or random noise. Because the data were not normally distributed, I used a two-tailed Mann-Whitney *U*-test to test for differences among groups (agonistic scores for treatments, male versus female scores, and playback order effects). Statistical significance was accepted when probability was ≤ 0.05.

Table 3.2. Behavioral category index used for scoring the agonistic responses exhibited by wintering Willow Flycatchers exposed to simulated territory intrusions (STIs).

Behavioral Category	**Behavior Description**	**Score**
Proximity to STI area	flycatcher *not* heard or seen within the STI area during the treatment	0
	flycatcher heard or seen within the STI area during the treatment	1
Vocalization rate	*no* flycatcher vocalizations (songs and/or calls) heard during the treatment	0
	the total number of flycatcher vocalizations heard within the territory, but *outside* the STI area during the treatment, is greater than the total number of vocalizations during the previous treatment	0.5
	the total number of flycatcher vocalizations heard *within* the STI area during the treatment is greater than the total number of flycatcher vocalizations during the previous treatment	1
Aggressiveness to decoy	no observable (non-vocal) flycatcher response to decoy during the treatment	0
	flycatcher flies or perches within 1 m of decoy during the treatment	0.5
	flycatcher makes physical contact with decoy during the treatment	1
Agonistic visual displays [aa]	no agonistic visual displays observed during the treatment	0
	flycatcher displays in the territory, but *outside* of the STI area during the treatment	0.5
	flycatcher displays *within* the STI area during the treatment	1

[aa] = agonistic visual displays defined as any one of the following: *fitz-bew*, *whet* and/or *whee flight-song*; *churr* calls with ruffled/extended body feathers; bill snapping (when observed clearly and not part of a foraging attempt); rapid wing flicking and/or rapid tail pumping with raised crest

RESULTS

Between 15 January to 22 February 2000, I exposed 30 Willow Flycatchers to simulated territory intrusions; 20 at Chomes and 10 at Bolsón. Seventeen flycatchers were female and 13 male. Willow flycatchers responded strongly to simulated intrusions and were significantly more aggressive toward simulated intrusion by Willow Flycatcher than another species of bird (Mann-Whitney *U*-test, $U = 76$, $P < 0.001$) or a control treatment (Mann-Whitney *U*-test, $U = 86$, $P < 0.001$) (Figure 3.1). In addition, there was no significant difference in the mean agonistic response between females and males toward the flycatcher treatment (Mann-Whitney *U*-test, $U = 75$, $P = 0.15$) (Figure 3.2).

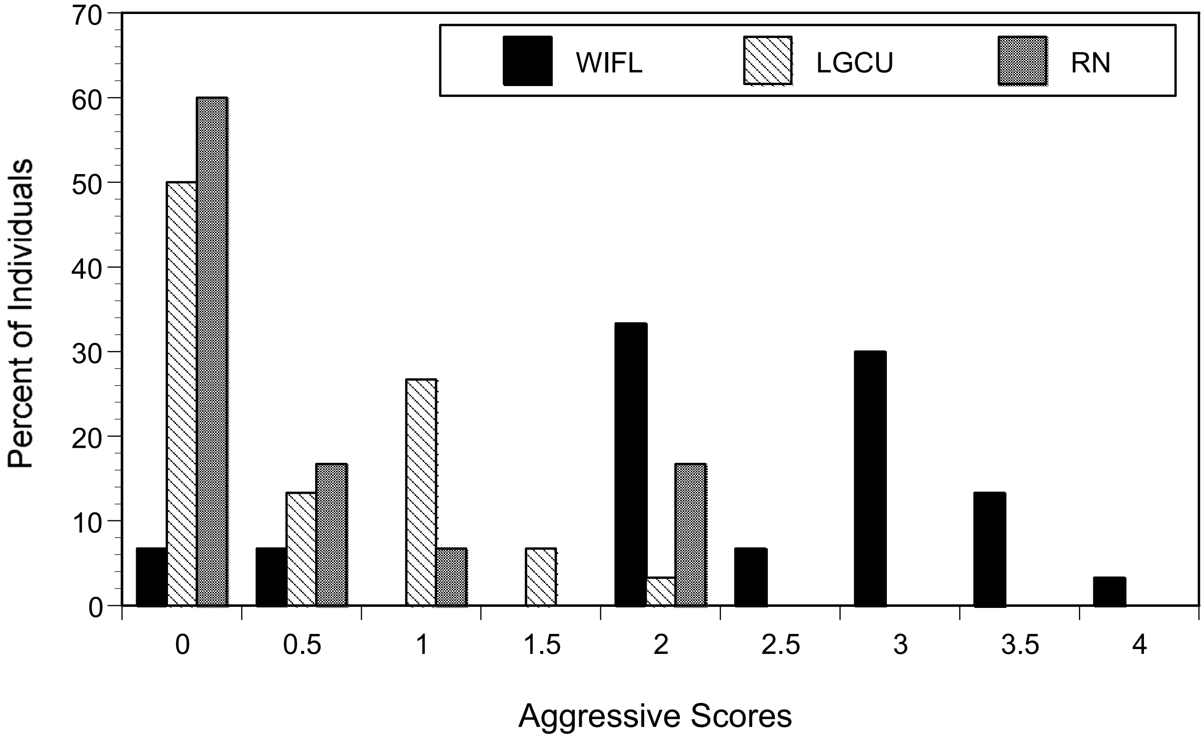

Figure 3.1. Agonistic scores of 30 Willow Flycatchers exposed to simulated territory intrusions which consisted of three randomized playback treatments: WIFL = Willow Flycatcher vocalizations; LGCU = lesser ground cuckoo vocalizations; RN = random noise.

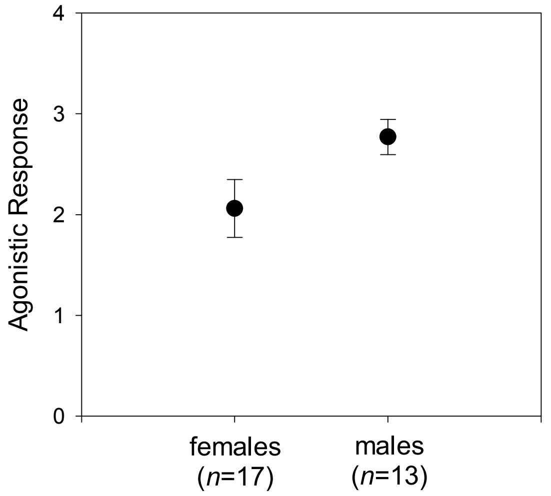

Figure 3.2. Mean agonistic responses of female (0 = 2.1, SE = 0.3) and male (0 = 2.8, SE = 0.2) Willow Flycatchers toward simulated conspecific territory intrusion: solid circles represent mean, bars represent standard error.

Often, individuals exposed to the Willow Flycatcher treatment early in the experiment continued to vocalize and display throughout (and sometimes well after) the remaining STI treatments. This frequently led to higher agonistic scores during subsequent cuckoo and random noise treatments. Thus, there was a clear treatment order effect (Figures 3.3 and 3.4). For example, 10 of 15 individuals (66.7 %) scoring higher than zero for the cuckoo treatment, and 11 of 12 individuals (92 %) scoring higher than zero for the random noise treatment, were *post* Willow Flycatcher treatment. To examine this treatment order effect, I hypothesized that individuals who received the Willow Flycatcher treatment *first* would attain higher scores across all subsequent treatments than individuals who received the flycatcher *last*. I then summed the scores across all treatments, including the four listening and observation treatments, for the individuals who received the Willow Flycatcher treatment first (*n*=10) and last (*n*=10), and then tested the null hypothesis that there was no difference in the total scores across all treatments. Total scores across all treatments for individuals who received the Willow Flycatcher treatment first, were significantly higher than for individuals who received the flycatcher treatment last (Mann-Whitney *U*-test, *U*= 23.5, *P* = 0.04), rejecting the null hypothesis and supporting the hypothesis that individuals that received the conspecific playback first would attain higher scores across all subsequent treatments.

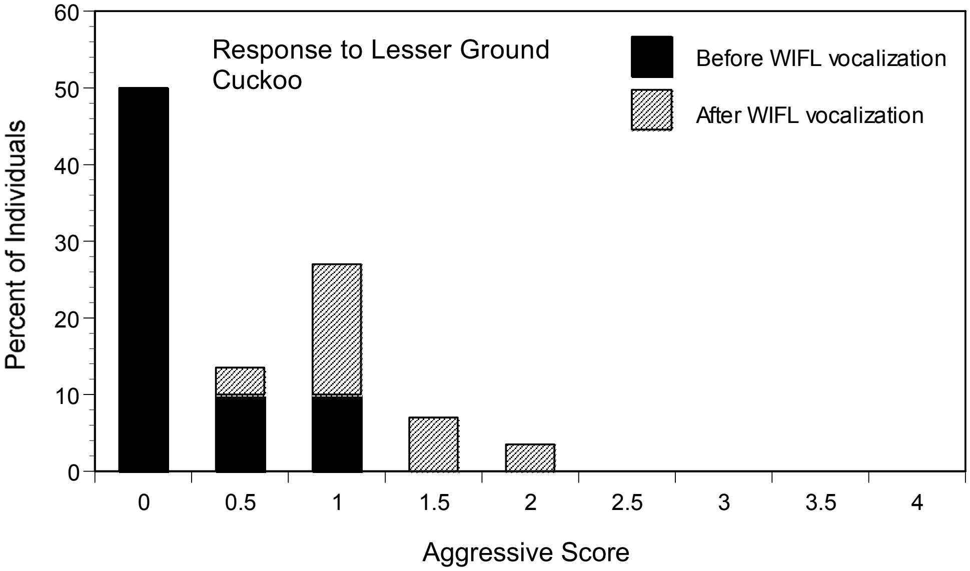

Figure 3.3. Aggressive response of 30 Willow Flycatchers exposed to lesser ground cuckoo playback treatment. Solid bars are individuals exposed to the cuckoo treatment before the Willow Flycatcher treatment; shaded bars are those exposed after the flycatcher treatment.

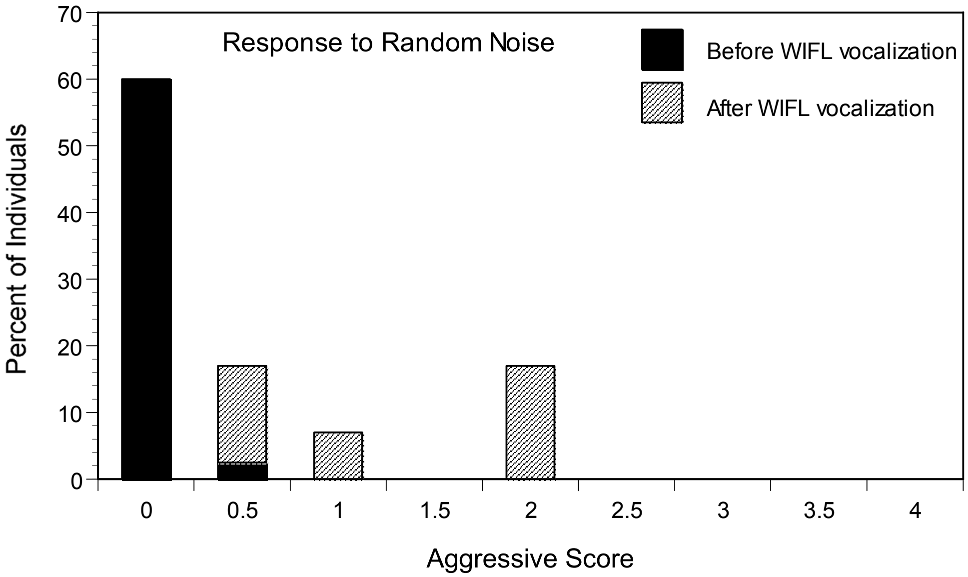

Figure 3.4. Aggressive responses of 30 Willow Flycatchers exposed to the random noise playback treatment. Solid bars are individuals exposed to the cuckoo treatment before the Willow Flycatcher treatment; shaded bars are those exposed after the flycatcher treatment.

The agonistic behaviors that I observed during the STIs were similar to those described by Gorski (1969) for wintering Willow Flycatchers in Panama. The same behaviors are used in defense of breeding territories (Sedgwick 2000). In addition, the agonistic responses toward conspecific playback were similar to those I observed during natural intraspecific encounters throughout the winter period (see Chapter 2). Typical agonistic responses of both sexes exposed to the Willow Flycatcher playback treatment included: (1) rapid and direct movements and flights toward the speaker location; (2) greatly increased singing and calling rates as playback continued; (3) stereotyped agonistic visual displays; and (4) direct flights and/or physical contact with the taxidermy decoy.

I recorded a total of six vocalizations given by both females and males in response toward the flycatcher treatment. These included the *fitz-bew* and *creet* advertising songs, and *whit, wheet,* and *chur/trill* calls. Highly agitated flycatchers combined these into a series of high-pitched squeaks and twitters, similar to the "high-pitched squeaker toy" vocalization described by Sogge et al. (2001) on the breeding grounds. Willow flycatchers of both sexes responded with emphatic vocalizations almost immediately to the flycatcher treatment only, and I recorded song rates as high as 109 *fitz-bew* songs per 4 minute period. Eleven individuals continued to vocalize up to 30 minutes after playback ceased and this often resulted in simultaneous singing and calling by other nearby flycatchers up to 200 m away. Greatly increased calling rates (*whits*, *wheeps* and *chur/trills*) were accompanied by rapid and direct movements toward the speaker location. One noteworthy point was that the *writ-tu/wee-oo* call, heard commonly throughout much of the breeding season, was not recorded during the experiment or during natural intraspecific encounters, and may be associated only with defense of breeding territories (Koronkiewicz *pers*. *obs*.).

During the experiment I observed a total of six stereotyped agonistic visual displays given by both sexes. These included rapid *tail-flicking/pumping*, *crest-raising*, *wing-flicking*, *wing-fluttering*, *spread* (extension or puffing of the body feathers) and *flight songs* accompanied with rapid *bill-snapping*. These displays, almost always accompanied by vocalizations including songs and calls, were given independently of each other as well as in a variety of combinations, and individuals often perched out in the open while displaying. The most common agonistic visual displays were *crest-raising* with simultaneous rapid *tail-pumping* and/or rapid *wing-flicking*. Highly agitated flycatchers displayed with *wing-fluttering* and *spread* accompanied by the *chur/kitter* vocalization, rapid *wheep* calls and/or the *squeaker-toy* vocalization. One particular set of playback vocalizations, flycatcher calls made during an aggressive encounter with a brown-headed cowbird, elicited the most agonistic behavior. When the cowbird encounter vocalization was broadcast, flycatchers moved toward the speaker location and/or displayed from multiple perches, and it appeared that flycatchers were visually searching for the conspecific intrusion. *Flight songs*, whereby flycatchers emitted both songs and calls while flying to perches, were accompanied with rapid *bill-snapping* and movements were directed toward the decoy and speaker location. On one occasion a male Willow Flycatcher made two direct flights at, and contacts with, the taxidermy decoy. Another six flycatchers, four female and two male, made multiple direct flights that came within 1 m of the mount.

DISCUSSION

Winter resident Willow Flycatchers at the Costa Rica sites responded strongly to simulated intraspecific territory intrusions, and behaviors recorded in response to the conspecific playbacks were similar to those I observed during natural intraspecific encounters (see Chapter 2). Both sexes of Willow Flycatchers used vocalizations (including advertising songs and calls) and stereotyped agonistic visual displays toward simulated intraspecific territory intrusions. Although female advertising song is thought to be uncommon on the breeding grounds (Sedgwick 2000), advertising song is repeatedly used as a winter territory defense mechanism by both sexes. This is consistent with the findings of Rappole (1995) in that for the few New World flycatcher species known to use advertising song on the wintering grounds (*Empidonax flaviventris*, *E. minimus*, *Sayornis phoebe*), both sexes sing. Rappole (1995) also reported the use of similar agonistic visual displays in defense of breeding and wintering territories for two species of long-distance migrant passerines (Wood Thrush (*Hylocichla mustelina*) and American Redstart (*Setophaga ruticilla*)). For the Willow Flycatcher, the same agonistic visual displays used in defense of breeding territories are used by both sexes as a winter territory defense mechanism.

Female and male responses to simulated conspecific territory intrusion were not significantly different; this similarity in aggressiveness may account for the observed pattern of the sexes interspersed throughout study areas (see Chapter 2). At the Costa Rica sites, both sexes occupied the same habitat type, and I observed females supplanting males in natural aggressive encounters. In addition, females were able to maintain and defend long-term winter territories in the presence of male territory holders and floaters, and there was no indication of sexual habitat segregation as has been recorded for a number of wintering sexually dimorphic passerines, including Prairie Warbler, *Dendroica discolor* (Latta and Faaborg 2001); American Redstart, *Setophaga ruticilla* (Parrish and Sherry 1994, Marra 2000); and Black-throated Blue Warbler, *Dendroica caerulescens* (Wunderle 1992, 1995).

During the experiment, rapid agonistic responses from flycatchers were recorded only for the conspecific treatment. Willow flycatchers of both sexes responded with emphatic songs and calls almost immediately in response to the conspecific playback treatment, and movements were rapid and directed toward the speaker location. This suggests that vocalizations may be one of the primary behavioral mechanisms used to detect conspecific intruders and defend winter territories. In addition to vocalizations, Willow Flycatchers can use visual cues in the recognition of conspecific territory intrusion. During the winter of 1999/2000, a known territory holding individual was observed intruding on an adjacent territory. This individual was observed moving about silently for approximately two minutes before the territory holder supplanted this individual with a direct, approximately 30 m downward flight and physical blow. Furthermore, although not exposed to the simulated territory intrusion experiment, one of the territory holding females at Bolsón was a known juvenile that responded strongly with advertising song and visual displays during target capture, and defended a territory for its entire first winter. Thus, vocalizations and visual displays are behavioral mechanisms used in winter territory defense by all individuals, regardless of age and/or sex.

Standardized simulated territory intrusions conducted on wintering Willow Flycatchers enabled a detailed description of the behaviors used in winter territory defense, and generated the behavioral information necessary to help explain a critical aspect of the species' non-breeding ecology. Sexual habitat segregation may occur only in wintering sexually dimorphic species, but additional studies of behavioral ecology, conducted on other monomorphic migrant passerines is needed.

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Appendix 1. Documentation of intraspecific territoriality and philopatry in wintering Neotropical migrant passerines (complete citations of sources at end of appendix).

Species	**Source**	**Locality**
Great Crested Flycatcher (*Myiarchus crinitus*)	Hespenhide (1980)	Panama
Eastern Wood Pewee (*Conotopus cinereus*)	Fitzpatrick (1980)	Peru
Least Flycatcher (*Empidonax minimus*)	Ely (1973)	Mexico
Acadian Flycatcher (*Empidonax virescens*)	Hespenhide (1980)	Panama
	Willis (1966)	Panama
Alder Flycatcher (*Empidonax alnorum*)	Gorski (1971)	Peru
Willow Flycatcher (*Empidonax traillii*)	Gorski (1969)	Panama
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
Bank Swallow (*Riparia riparia*)	Nickell (1968)	Honduras
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	Nickell (1968)	Honduras
Wood Thrush (*Hylocichla mustelina*)	Rappole, Morton and Ramos (1992)	Mexico
	Kricher and Davis (1986)	Belize
	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Willis (1966)	Panama

Appendix 1 continued.

Gray Catbird	Kricher and Davis (1986)	Belize
(*Dumetella carolinensis*)	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Nickell (1968)	Honduras
	Galindo and Mendez (1966)	Panama
	Loftin (1963)	Panama
White-eyed Vireo	Rappole and Warner (1980)	Mexico
(*Vireo griseus*)	Ely, Latas, and Lohoenfoner (1977)	Mexico
Yellow-throated Vireo	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
(*Vireo flavifrons*)	Barlow (1980)	Mexico
	Hespenhide (1980)	Panama
	Nickell (1968)	Honduras
Solitary Vireo	Barlow (1980)	Mexico
(*Vireo solitarius*)	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
Red-eyed Vireo	Loftin, Rogers, and Hicks (1966)	Panama
(*Vireo olivaceus*)		
Philidelphia Vireo	Loftin (1977)	Panama
(*Vireo philadelphicus*)	Woods (1973)	Haiti
Prothonotary Warbler	Faaborg and Arendt (1984)	Puerto Rico
(*Protonotaria citrea*)	McNeil (1982)	Venezuela
	Faaborg and Winters (1980)	Puerto Rico
	Faaborg and Winters (1979)	Puerto Rico
	Loftin, Rogers, and Hicks (1966)	Panama
Tennessee Warbler	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
(*Vermivora peregrina*)	Tramer and Kemp (1979)	Costa Rica
	Loftin (1977)	Panama
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Loftin, Child and Bongiorno (1967)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
	Loftin (1963)	Panama

Appendix 1 continued.

Orange Crowned Warbler (*Vermivora celata*)	Rappole and Warner (1980)	Mexico
Northern Parula (*Parula americana*)	Staicer (1992)	Puerto Rico
	Faaborg and Arendt (1984)	Puerto Rico
	Diamond and Smith (1973)	Jamaica
Black and White Warbler (*Mniotilta varia*)	Rappole, Morton and Ramos (1992)	Mexico
	Faaborg and Arendt (1984)	Puerto Rico
	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Faaborg and Winters (1980)	Puerto Rico
	Rappole and Warner (1980)	Mexico
	Faaborg and Winters (1979)	Puerto Rico
	Loftin (1977)	Panama
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Diamond and Smith (1973)	Jamaica
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Loftin, Rogers, and Hicks (1966)	Panama
Black-throated Blue Warbler (*Dendroica caerulescens*)	Holmes and Sherry (1992)	Jamaica
	Wunderle (1992, 1995)	Puerto Rico
	Holmes, Sherry and Reitsma (1989)	Jamaica
	Woods (1973)	Haiti
	Diamond and Smith (1973)	Jamaica
Chesnut-sided Warbler (*Dendroica pensylvanica*)	Rogers, Hicks, Wischusen, and Parrish (1982)	Guatemala
	Loftin (1977)	Panama
	Loftin, Child and Bongiorno (1967)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
Cape May Warbler (*Dendroica tigrina*)	Staicer (1992)	Puerto Rico
	Emlen (1973)	Bahamas
Magnolia Warbler (*Dendroica magnolia*)	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Nickell (1968)	Honduras
	Loftin (1963)	Panama

Appendix 1 continued.

Townsend's Warbler (*Dendroica townsendi*)	Thurber and Villeda (1972, 1974, 1976)	El Salvador
Black-throated Green Warbler (*Dendroica virens*)	Rappole and Warner (1980)	Mexico
	Loftin (1977)	Panama
	Ely, Latas, and Lohoenfoner (1977)	Mexico
Yellow-throated Warbler (*Dendroica dominica*)	Nickell (1968)	Honduras
Kirtland's Warbler (*Dendroica kirtlandii*)	Radabaugh (1974)	Bahamas
Prairie Warbler (*Dendroica discolor*)	Latta and Faaborg (2001)	Dominican Republic
	Staicer (1992)	Puerto Rico
	Faaborg and Winters (1979)	Puerto Rico
	Diamond and Smith (1973)	Jamaica
Palm Warbler (*Dendroica palmarum*)	Emlen (1973)	Bahamas
Yellow Warbler (*Dendroica petechia*)	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Rappole and Warner (1980)	Mexico
	Morton (1976)	Panama
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Nickell (1968)	Honduras
	Loftin, Rogers, and Hicks (1966)	Panama
	Loftin (1963)	Panama
	Skutch in Bent (1953)	Costa Rica
Mourning Warbler (*Oporornis philidelphia*)	Loftin (1977)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
MacGillivray's Warbler (*Oporornis tolmiei*)	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Thurber and Villeda (1972, 1974, 1976)	El Salvador

Appendix 1 continued.

Kentucky Warbler (*Oporornis formosus*)	Mabey and Morton (1992)	Panama
	Rappole, Morton and Ramos (1992)	Mexico
	Kricher and Davis (1986)	Belize
	Rappole and Warner (1980)	Mexico
	Loftin (1977)	Panama
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Karr (1971)	Panama
	Loftin, Child and Bongiorno (1967)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
Canada Warbler (*Wilsonia canadensis*)	Loftin, Rogers, and Hicks (1966)	Panama
Wilson's Warbler (*Wilsonia pusilla*)	Rappole, Morton and Ramos (1992)	Mexico
	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Loftin (1977)	Panama
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Nickell (1968)	Honduras
	Moynihan (1962)	Panama
	Skutch in Bent (1953)	Costa Rica and Guatemala
Hooded Warbler (*Wilsonia citrina*)	Stutchbury (1994)	Mexico
	Rappole, Morton and Ramos (1992)	Mexico
	Kricher and Davis (1986)	Belize
	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Nickell (1968)	Honduras
Worm-eating Warbler (*Helmitheros vermivorus*)	Rappole, Morton and Ramos (1992)	Mexico
	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Diamond and Smith (1973)	Jamaica
	Loftin, Rogers, and Hicks (1966)	Panama
Swainson's Warbler (*Limnothlypis swainsonii*)	Diamond and Smith (1973)	Jamaica

Appendix 1 continued.

Ovenbird (*Seiurus aurocapillus*)	Rappole, Morton and Ramos (1992)	Mexico
	Kricher and Davis (1986)	Belize
	Faaborg and Arendt (1984)	Puerto Rico
	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Rappole and Warner (1980)	Mexico
	Faaborg and Winters (1980)	Puerto Rico
	Faaborg and Winters (1979)	Puerto Rico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Diamond and Smith (1973)	Jamaica
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Nickell (1968)	Honduras
	Loftin, Child and Bongiorno (1967)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
	Loftin (1963)	Panama
Louisiana Waterthrush (*Seiurus motacilla*)	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Rappole and Warner (1980)	Mexico
	Loftin (1977)	Panama
	Eaton (1953)	Cuba
Northern Waterthrush (*Seiurus novaboracensis*)	Kricher and Davis (1986)	Belize
	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	McNeil (1982)	Venezuela
	Rappole and Warner (1980)	Mexico
	Diamond and Smith (1973)	Jamaica
	Nickell (1968)	Honduras
	Loftin, Rogers, and Hicks (1966)	Panama
	Schwartz (1964)	Venezuela
	Slud (1964)	Costa Rica
	Loftin (1963)	Panama
	Schwartz (1960)	Trinidad
	Snow and Snow (1960)	Trinidad
Common Yellowthroat (*Geothlypis trichas*)	Rappole and Warner (1980)	Mexico
	Woods (1973)	Haiti
	Diamond and Smith (1973)	Jamaica
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Nickell (1968)	Honduras

Appendix 1 continued.

Yellow-breasted chat	Rappole and Warner (1980)	Mexico
(*Icteria virens*)	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Nickell (1968)	Honduras
	Loftin, Child and Bongiorno (1967)	Panama
	Loftin (1963)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
American Redstart	Marra (2000)	Jamaica
(*Setophaga ruticilla*)	Marra, Sherry, and Holmes (1993)	Jamaica
	Holmes and Sherry (1992)	Jamaica
	Winker, Rappole, and Ramos (1990)	Mexico
	Holmes, Sherry and Reitsma (1989)	Jamaica
	Faaborg and Arendt (1984)	Puerto Rico
	McNeil (1982)	Venezuela
	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Rappole and Warner (1980)	Mexico
	Faaborg and Winters (1979)	Puerto Rico
	Diamond and Smith (1973)	Jamaica
	Nickell (1968)	Honduras
	Loftin, Child and Bongiorno (1967)	Panama
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	Loftin (1977)	Panama
Blue Grosbeak (*Guiraca caerulea*)	Nickell (1968)	Honduras
Indigo Bunting	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
(*Passerina cyanea*)	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Rappole and Warner (1980)	Mexico
	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Downer (1972)	Jamaica
	Nickell (1968)	Honduras
	Johnston and Downer (1968)	Jamaica
	Loftin, Child and Bongiorno (1967)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
	Van Tyne (1931)	Guatemala

Appendix 1 continued.

Painted Bunting (*Passerina ciris*)	Ely, Latas, and Lohoenfoner (1977)	Mexico
	Ely (1973)	Mexico
	Thurber and Villeda (1972, 1974, 1976)	El Salvador
	Nickell (1968)	Honduras
Dickcissel (*Spiza americana*)	ffrench (1960)	Trinidad
Northern Oriole (*Icterus galbula*)	Loftin, Rogers, and Hicks (1966)	Panama
Orchard Oriole (*Icterus spurius*)	Nickell (1968)	Honduras
Summer Tanager (*Piranga rubra*)	Rogers, Hicks, Wischusen and Parrish (1982)	Guatemala
	Hespenhide (1980)	Panama
	Rappole and Warner (1980)	Mexico
	Loftin (1977)	Panama
	Karr (1971)	Panama
	Loftin, Rogers, and Hicks (1966)	Panama
	Loftin (1963)	Panama

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Appendix 2. Field schedule/field effort at the Chomes and Bolsón, Costa Rica study sites.

Winter Season	**Dates**
1998/99	17-18 December 1-3, 6-11, 13, 16-17, and 25 January 11-12 February 17, 19 and 21 March
1999/2000	17 December-5 January 12 January-22 February 6 March-11 April 20 April-10 May
2000/01	28 September-16 October 27 December-16 January 6-13 April 10-26 May 2001