Willow Flycatcher (*Empidonax traillii*) Winter Ecology in Costa Rica: 1999/2000

Territorial mapping observation platform at Laguna Argentina, Chomes, Costa Rica. Photo by Phil Heavin.

Prepared by: Thomas J. Koronkiewicz and Mark K. Sogge
U.S.G.S. Forest and Rangeland Ecosystem Science Center, Colorado Plateau Field Station, Flagstaff, AZ

December 2000

Submitted to: U.S. Bureau of Reclamation, Phoenix, AZ
(Intra-agency Agreement No. 99-AA-32-002)

EXECUTIVE SUMMARY

The willow flycatcher (*Empidonax traillii*) is a neotropical migratory bird that is widely distributed as a breeding species across most of the United States and parts of extreme southern Canada. Willow flycatchers winter in portions of southern Mexico, Central America, and northern South America. Evidence from surveys in Costa Rica during the winter of 1997/1998 (Koronkiewicz et al. 1998) and 1998/1999 (Koronkiewicz and Whitfield 1999) suggested that wintering willow flycatchers are territorial, and that they may show some level of winter site fidelity. This study was undertaken to determine whether willow flycatchers exhibit within and between year site fidelity to wintering sites, and if they maintain and defend winter territories.

Between 17 December 1999 and 10 May 2000, we color-banded 69 willow flycatchers and conducted intensive territory mapping and behavioral experiments at two sites in northwest Costa Rica. Within-season site fidelity and survivorship averaged 85% (range = 80 – 88%). 1998/1999 to 1999/2000 between-year winter site fidelity was 77% at Chomes, and 43% at Bolsón. Preliminary values for winter 1999/2000 to 2000/20001 site fidelity were 52% (Chomes) and 47% (Bolsón), but these may increase based on additional surveys during winter 2000/2001 field work.

Spot-mapping and behavioral observations showed that individual willow flycatchers defended exclusive winter territories; males and females maintained separate territories. Over a given winter season, territorial flycatchers maintained the same territory in 97% of cases. Flycatchers also tended to occupy the same territory at a site in subsequent winter seasons; between-year territory fidelity ranged from 95% to 100%. Flycatcher territories, like flycatcher winter sites in general, included water and/or saturated soils, patches or stringers of trees, dense woody shrubs, and open areas. A simulated territorial intrusion experiment showed that flycatchers defended their territories with songs, calls, and aggressive interactions, and that they respond more strongly to conspecifics than to another species of bird and random noise. In addition to winter resident territory holders, non-territorial floaters were present; two floaters became territorial residents following the disappearance of another territorial flycatcher.

Migrant willow flycatchers began arriving at the study sites in the third week of April, and were subject to aggressive displacement by territorial winter residents. Most banded winter residents were still present on their territories at the end of April and in early May, when winter field work was terminated.

Observations suggest that flycatchers shift the location of their foraging activity over the course of the day; early mornings are spent primarily in the *laguna* (seasonal freshwater wetland) vegetation, moving into the adjacent tree line during the middle of the day, then returning to the *laguna* as darkness approaches. Wintering willow flycatchers were primarily insectivorous, commonly sally gleaning and hawking small insects. Fruit-eating was noted, and fruit may be an important diet component prior to and during migration.

TABLE OF CONTENTS

TABLES and FIGURES

INTRODUCTION

The willow flycatcher (*Empidonax traillii*) is a neotropical migratory bird that breeds in shrub and riparian habitats across most of the United States and parts of extreme southern Canada. As neotropical migrants, willow flycatchers spend less than half of each year on their breeding grounds in North America. The remainder of the year is spent south of the breeding range in the subtropical and tropical areas of southern Mexico, Central America and northern South America, south to eastern Ecuador and east to northwestern Venezuela (Stiles and Skutch 1989, Howell et al. 1995, Ridgely and Gwynne 1989, Ridgely and Tudor 1994, Unitt 1997, Meyer de Schauensee 1978).

The southwestern subspecies (*E. t. extimus*) is federally-listed as endangered (USFWS 1995), and breeds only in dense mesic riparian habitats in the southwestern United States and, at least historically, to extreme northwestern Mexico (Unitt 1987, Sogge et al. 1997). In California, *E.t. brewsteri* and *E. t. adastus* have also declined dramatically and are state-listed endangered species (Schlorff 1990). Thus, there is management concern for willow flycatcher populations over a substantial part of the species' breeding range. In addition to numerous threats identified on the flycatcher's breeding range (Unitt 1987, Marshall and Stoleson 2000), potential threats and negative impacts such as extensive habitat loss and use of agri-chemicals have been documented in willow flycatcher wintering areas (Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999, Lynn and Whitfield 2000).

Published literature on birds of Central and South America (Stiles and Skutch 1989, Howell and Webb 1995, Ridgely and Gwynne 1989, Ridgely and Tudor 1994, Meyer de Schauensee 1978) describes willow flycatcher wintering habitat as humid to semi-arid, partially open areas such as woodland borders. They also use brushy savanna edge, second growth, and scrubby fields with hedges and fences that are often associated with plantations, and favor areas near water. Gorski (1969) found wintering willow flycatchers using transitional areas from a wet, grassy field along the edge of a river to low-lying shrubs interspersed with tall grasses, and in vegetation consisting largely of shrubs with a number of trees present around an open, grassy area. In Costa Rica, Panama and El Salvador, Koronkiewicz et al. (1998), Koronkiewicz and Whitfield (1999) and Lynn and Whitfield (2000) found wintering willow flycatchers in lowland areas that are profoundly affected by seasonal inundation. Within these lowland areas, flycatchers inhabited sites comprised of patches or stringers of trees, dense woody shrubs, and open areas, in association with standing or slow moving water, and saturated soils.

During the breeding season, willow flycatchers are strongly territorial (Sogge 2000), with males defending specific areas against intrusions from other individuals (other than their mates). Based on willow flycatcher response to tape-playback during the winter, Gorski (1969), Koronkiewicz et al. (1998) and Koronkiewicz and Whitfield (1999) suggested that flycatchers are also territorial during the winter. However, winter territoriality was not yet proven by targeted research (which requires intense observations of individuals, preferably color-banded). Further, there were no data to show: (1) whether wintering flycatchers defended specific habitat areas (as opposed to defending a "zone" around themselves as they move among sites); (2) if they show strong fidelity to a particular wintering site and/or winter territory during a given season; and (3) whether they return to the same site or territory in subsequent winters.

Determining the nature and degree of winter territoriality 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, strong winter site fidelity could mean that flycatchers may be strongly negatively affected by the loss of particular wintering sites; movement to other suitable sites may be inhibited by the presence of winter resident individuals that will defend against intrusion by displaced flycatchers. Clearly, knowing more about willow flycatcher winter territoriality can help guide management and conservation strategies for this endangered neotropical migrant.

This study was undertaken to better our understanding of the willow flycatcher's winter ecology, especially with regard to winter territoriality and site fidelity. Our objectives were to determine if willow flycatchers:

- exhibit within- and between-year site fidelity on the wintering grounds;
- defend winter territories against con-specifics; and
- exhibit within- and between-year fidelity to particular territories within a site.

METHODS

Study Area

We conducted this study at two sites in northwest Costa Rica (Figure 1), where we had located willow flycatchers during previous surveys (Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999). Both sites are located in lowland areas (just above sea level) along the Pacific coast of Costa Rica, 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 of the year. During the dry season or *verano* (December to April/May), these coastal lowlands receive very little rain. In contrast, the rainy season or *invierno* (usually from May/June until the end of November) provides almost the total annual precipitation (Cohen 1983). Thus, wintering willow flycatchers arrive in this region during the rainy season, and depart near the end of the dry season.

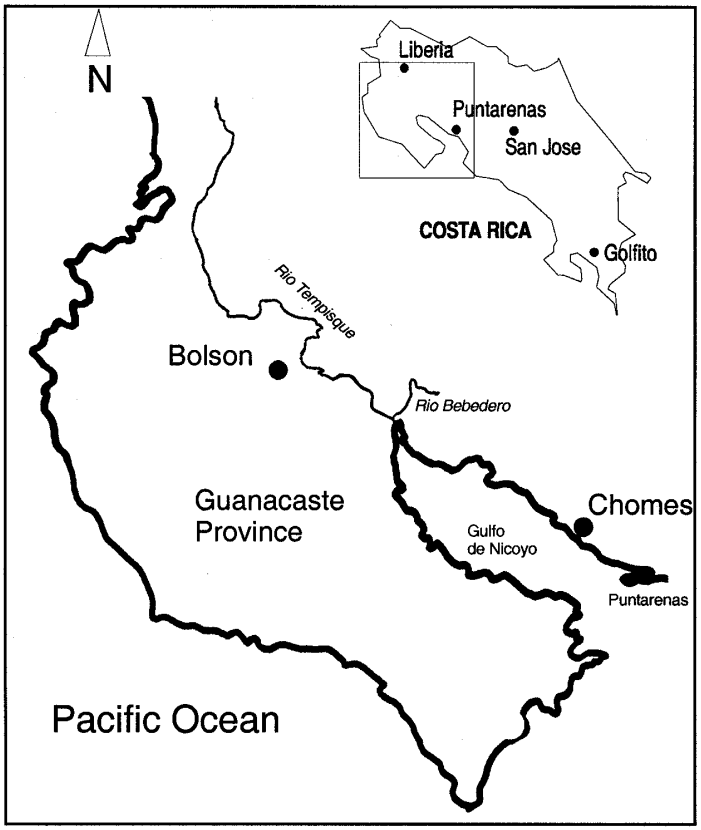

Figure 1. Location of Chomes and Bolsón winter ecology study sites in northwestern Costa Rica.

Study Sites

Chomes - located approximately 25 km northwest of the city of Puntarenas, along the Pacific coast of northwest Costa Rica. Habitat consists of a large, seasonal freshwater wetland bordered by patches and stringers of forest, dense woody shrubs and man-made savanna pastures. 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. Dry season begins in December and large areas of the wetland dry up as the season advances (Figure 2).

Figure 2. The Chomes study site, shortly following the end of rainy season (top photo; early January 1999), and at the height of dry season (bottom photo; March 1999). Both photos show the same northern portion of Laguna Argentina, though from different vantages. Note the pronounced drying (indicated by brown vegetation) during the dry season.

Bolsón - located approximately 25 km northeast of the city of Santa Cruz, within the Tempisque drainage of northwest Costa Rica. Habitat consists of a patchwork of large, seasonal freshwater wetlands, seasonally inundated man-made savanna pastures, meandering waterways and muddy seeps, all of which are bordered by patches and stringers of forest, dense woody shrubs and man-made savanna pastures (Figures 3 and 4).

Figure 3. Overview of the western area of the Bolsón study site. Occupied willow flycatcher habitat can be seen in the background.

Figure 4. Shrub, tree, and wetland components of willow flycatcher winter habitat at Bolsón.

The Bolsón site becomes totally inundated in October/November when the Rio Tempisque and its tributaries overflow their banks (Figure 5). The site dries up considerably starting in December, but retains some standing water and saturated soils year round.

Figure 5. The Bolsón study site (including this access road and nearby flycatcher habitat) becomes inundated during the rainy season. Photo taken during October 2000.

Field Work Schedule

We conducted field work for the 1999/2000 winter ecology study during the following six periods:

- 24 through 28 November 1999;
- 17 December 1999 through 5 January 2000;
- 12 January through 22 February 2000;
- 6 March through 11 April 2000;
- 20 April through 10 May 2000; and
- 28 September through 16 October 2000

We spent a total of 95 days at Chomes and 26 at Bolsón. More time was spent at the Chomes site, which was monitored more or less daily during each field session; Bolsón was monitored approximately once every 10-14 days during these sessions.

Capture and Color Banding

Determining willow flycatcher site fidelity and territoriality requires repeated observation of banded birds. Therefore, we captured and uniquely color banded individuals at both Chomes and Bolsón. To locate wintering flycatchers, we broadcast willow flycatcher vocalizations from hand-held tape players and listened for responding flycatchers (similar to the Sogge et al. 1997 survey protocol used on the breeding grounds). After an individual willow flycatcher was detected, we used additional broadcast of willow flycatcher vocalizations to lure willow flycatchers into a mist net (Figure 6). An *Empidonax* taxidermy mount ("decoy") was sometimes used to complement the broadcast. On several occasions we captured flycatchers via "passive netting", whereby a mist net was placed in an individual's territory, but no broadcast vocalizations were used. Each captured flycatcher was given a unique combination of colored leg bands (including a color-anodized and numbered USGS aluminum band). During handling of birds for color banding (Figure 7), we collected a drop of blood (by clipping a toenail per Busch et al. 2000) for later gender determination through genetic analysis (Kahn et al. 1998). Throughout the winter period, we periodically surveyed for and resighted these color-banded individuals. Most surveys and resighting were done during peak hours of avian activity (0600 hrs to 1100 hrs and 1500 hrs to 1730 hrs).

Figure 6. Willow flycatcher being extracted from a mist net.

Figure 7. Willow flycatcher being processed after capture. Note the color band on the flycatcher's right leg.

Documenting Territoriality and Site Fidelity

Site Fidelity and Over-winter Survivorship

Within-season site fidelity was calculated by determining (through resights) which of the color-banded flycatchers present in the middle of the winter (i.e., January and February) were still at the site at the end of winter (i.e., late April/May). To determine between-year site fidelity, we revisited both sites in subsequent winters and compared the number of color-banded flycatchers present during April/May of each year with the number that returned to the site during the following fall/winter.

Over-winter survivorship is an analog of within-season site fidelity, in that any banded birds not present by the end of winter season were assumed to have died, unless they were resighted the following year or at another site (per Holmes et al. 1989). It is impossible to know whether banded birds that disappear from a site during the winter have died, as opposed to moved elsewhere, unless they are detected again at a different place or time. This is an inescapable weakness in survival estimates. Therefore, it must be recognized that survivorship rates based on resights/recaptures provide conservative estimates, i.e., the *minimum* percent that survived.

Winter Territoriality

To determine whether willow flycatchers maintain winter territories, we mapped the locations, movements, and aggressive interactions of color-banded flycatchers onto high resolution, aerial photographs of each site. We then mapped the "use area" of each flycatcher by forming a polygon that connected the outermost points of each individual's detections (per IBCC 1970, Holmes et al. 1989). Non-overlapping or minimally-overlapping use areas, in combination with observations of aggressive interactions (especially along border areas), were considered evidence of territoriality.

Territorial Behavior

To document whether wintering willow flycatchers actively defend winter territories, and to note the vocalizations, agonistic behaviors, and displays used to do so, we conducted simulated territory intrusions (STIs) on flycatchers at both study sites. Each STI experiment consisted of randomized sound playbacks in conjunction with an *Empidonax* taxidermy decoy, placed near the center of a willow flycatcher's territory.

The randomized playbacks consisted of a set of three standardized recordings: (1) willow flycatcher vocalizations (*fitz-bews, breets, whitts, brrrr/kitters* and interaction calls); (2) lesser ground cuckoo (*Morococcyx erythropygius*; a common and vocal species at both study sites) vocalizations; and (3) random noise (a squeaky toy accompanied by digital beeps). We broadcast each of the three playback treatments for 4 minutes at a standardized volume (near that of a naturally singing bird), with a 4 minute listening and observation period/treatment before and after each treatment. 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.

The STI's were conducted by a single person (T.J. Koronkiewicz) from 0600 to 0700 hours in January and February 2000. Each day of the experiment, we randomly selected a willow flycatcher on which to conduct the STI (excluding any that were previously selected). The observer remained stationary and well hidden during the STI, situated so he could clearly view the STI area. The observer dictated all flycatcher behaviors (displays, song and calling rates, and movements) observed during the STI into a handheld tape recorder, and transcribed the tape immediately following the experiment.

We scored the agonistic responses of each willow flycatcher during each of the three playback treatments and for each of the four listening/observation periods. Individuals received a score ranging from 0 (lowest) to 1 (highest), for each of the following behavioral categories:

1. Proximity to STI area:

0 = the flycatcher not heard or seen within the STI area during the treatment
1 = the flycatcher heard or seen within the STI area during the treatment

2. Vocalization rate:

0 = no flycatcher vocalizations (songs and/or calls) heard during the treatment
0.5 = 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
1 = 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

3. Aggressiveness to decoy:

0 = no observable (non-vocal) flycatcher response to decoy during the treatment
0.5 = flycatcher flies or perches within 1 m of decoy during the treatment
1 = flycatcher makes physical contact with decoy during the treatment

4. Agonistic Displays/Behaviors:

Agonistic displays are defined as any one of the following:

a) *fitz-bew* (primary song) flight-songs
b) *brrrr/kitter* calls
c) bill snapping (when observed clearly and not part of a foraging attempt)
d) rapid wing flicking and/or rapid tail pumping with raised crest

0 = no agonistic displays/behaviors observed during the treatment
0.5 = flycatcher displays in the territory, but **outside** of the STI area during the treatment
1 = flycatcher displays **within** the STI area during the treatment

Individuals received one score per behavioral category, with the combined maximum possible score of 4 during any one treatment. We 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. Higher aggressiveness in response to flycatcher vocalizations is evidence of active territorial defense against conspecifics.

RESULTS

Within-Season Site Fidelity

Twenty-two of 25 (88 %) color-banded flycatchers monitored at Chomes remained at the site from 17 December 1999 through 4 May 2000. At Bolsón, 12 of 15 (80 %) monitored flycatchers remained there from 23 December 1999 through 28 April 2000. Thus, the combined within-year site fidelity from the approximate middle period of winter until the end of winter was 85%.

Over-winter Survivorship

No birds that disappeared from either site during the wintering period were located at other sites, or observed at a later date. Thus, the conservative (*minimum*) survivorship from the approximate middle winter to the beginning of the spring migratory period matched the within-season site fidelity values of 88% and 80% for Chomes and Bolsón, respectively (85% combined).

Between-Year Site Fidelity

Winter 1998/1999 to 1999/2000 (Table 1): Ten of 13 (77 %) willow flycatchers banded and monitored at Chomes during the winter of 1998/99 returned to the site during the winter of 1999/2000. At Bolsón, 3 of the 7 (43%) willow flycatchers banded during 1998/99 returned to the same territories during 1999/2000.

Winter 1999/2000 to 2000/2001 (Table 1): To date, we have conducted only the first of three winter 2000/01 site visits. During this field session, occurring from 28 September through 16 October 2000, we detected many banded birds that returned. However, fall migration was still underway and the site was far less populated than during winter 1999/2000. Therefore, we expect additional banded willow flycatchers to return during fall 2000, and the following return rates will likely increase as later-returning birds are located during subsequent field efforts. Through 16 October 2000, 13 of the 25 (52%) of willow flycatchers monitored in 1999/2000 returned at Chomes, and 7 of the 15 (47%) at Bolsón.

Table 1. Willow flycatcher between-year site fidelity for the Chomes and Bolsón study sites (** = % return rate is a preliminary estimate, subject to change with additional field work during 2000/01).

Site	Year	Number of Banded Flycatchers	Number of Returning Flycatchers	Return Rate
Chomes	winters 1998/1999 to 1999/2000	13	10	77%
	winters 1999/2000 to 2000/2001	25	13	52%**
Bolsón	winters 1998/1999 to 1999/2000	7	3	43%
	winters 1999/2000 to 2000/2001	15	7	47%**

Winter Territoriality

From 17 December 1999 to 10 May 2000, we conducted intensive territory mapping for 25 flycatchers at Chomes and 15 at Bolsón. Of the 25 Chomes birds, 14 were females, 10 were males, and 1 was undetermined. At, Bolsón, there were 7 females and 8 males.

Based on polygons generated by spot mapping, both male and female willow flycatchers maintained exclusive, well-defined territories that generally had little or no overlap with territories of adjacent individuals (Figures 8 and 9). Males and females did not share winter territories.

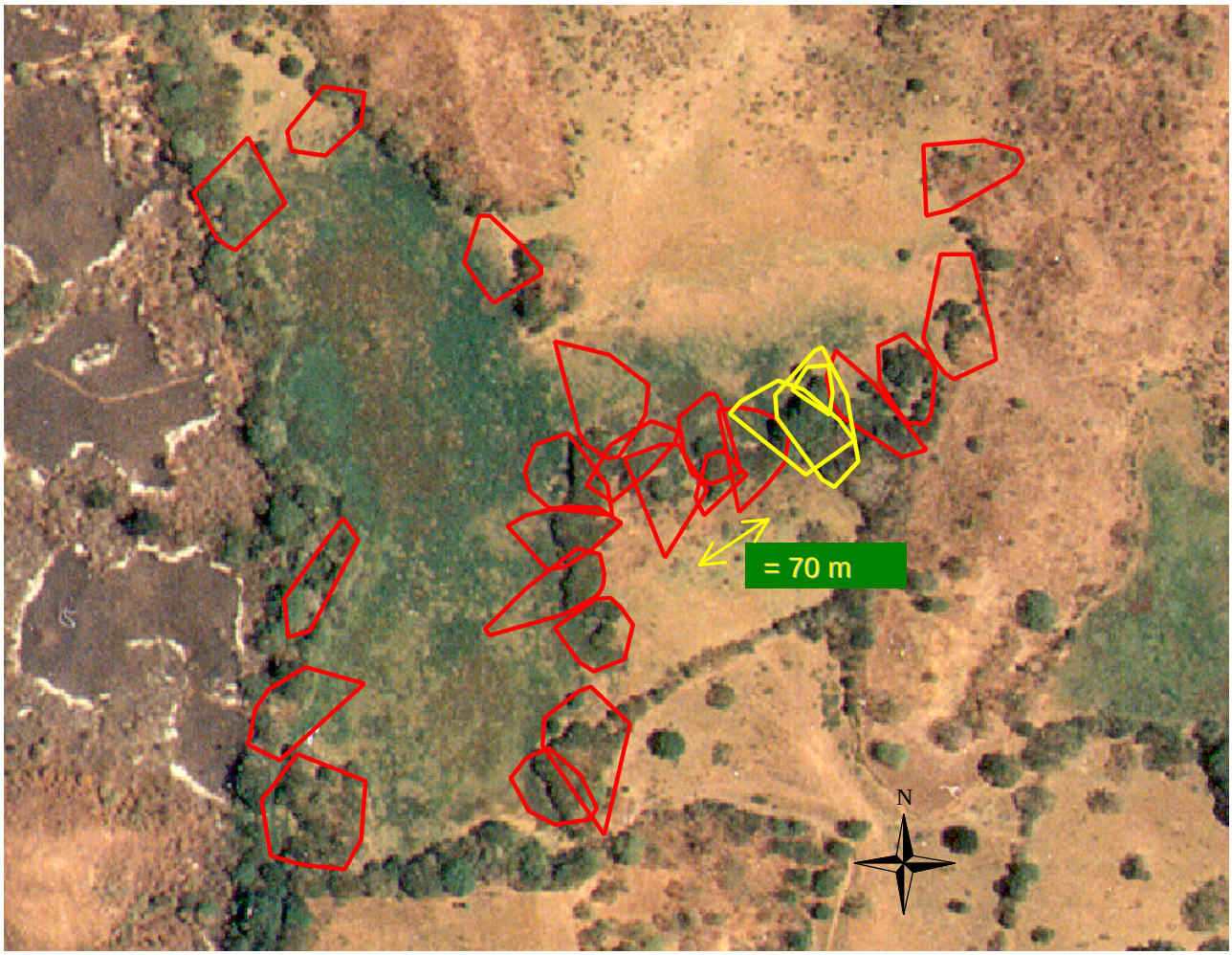

Figure 8. Willow flycatcher territories at the Chomes, Costa Rica study site. Polygons depict territories based on spot-mapping of *all* movements of 25 individuals that were monitored from 17 Dec 1999 to 10 May 2000. Red polygons are territories with boundaries that remained relatively constant during the winter. Yellow polygons are territories that shifted as territory ownership changed (see Figure 10 for a summary).

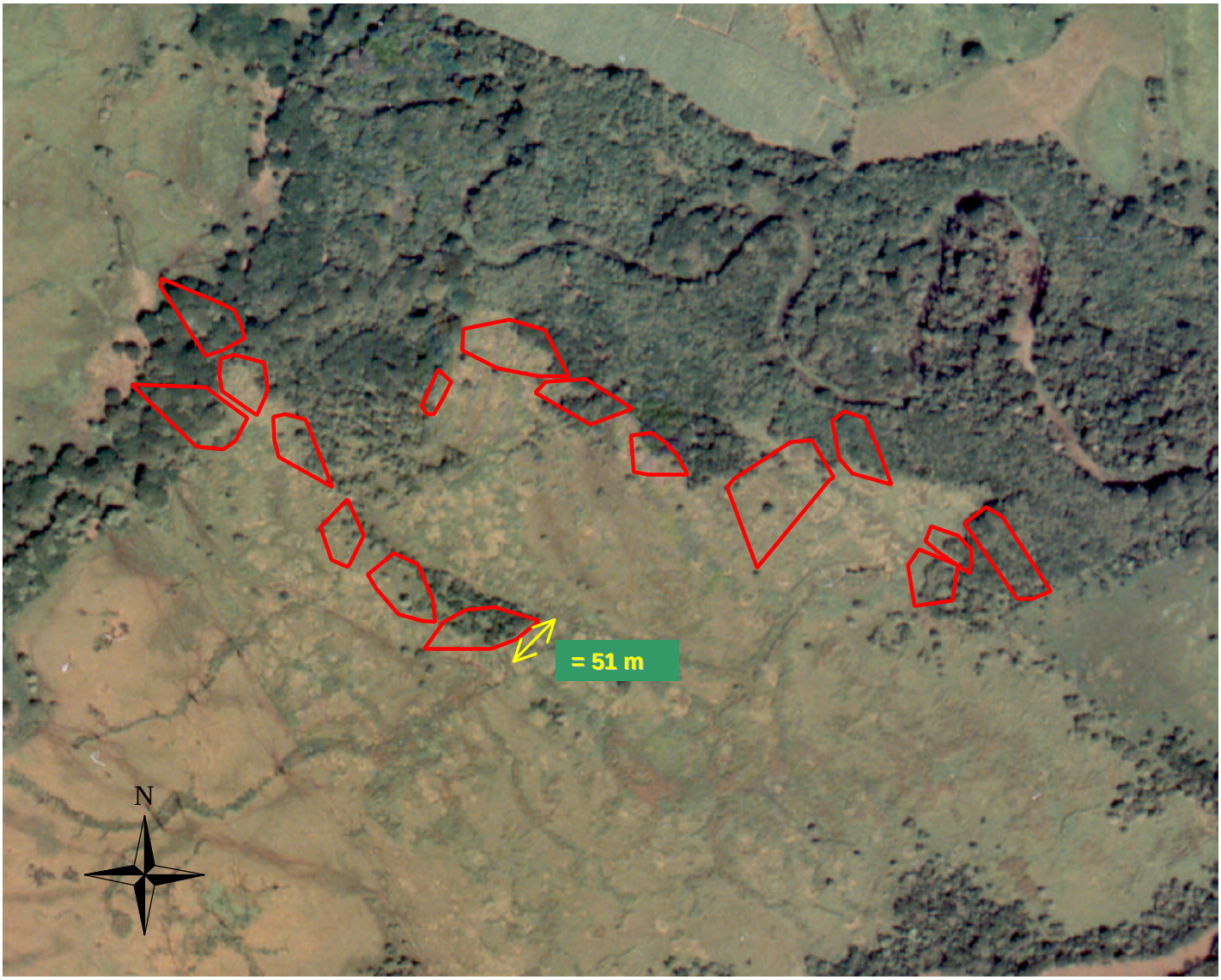

Figure 9. Willow flycatcher territories at the Bolsón, Costa Rica study site. Red polygons depict territories based on spot-mapping *all* movements of 15 individuals monitored from 23 Dec. 1999 to 28 April 2000.

Floaters

In addition to winter-resident territory holders, we detected and color-banded several floaters; i.e., flycatchers that were present at the site but were not defending distinct territories. We considered a bird to be a floater if: (a) it was seen only once, or very irregularly, throughout the field season; (b) typically observed in quiet, "skulking" behavior; (c) it did not display territorial behavior against other flycatchers; and/or (d) it did not respond aggressively to tape playback. In February 2000, two floaters (#40, #20B) became territory holders after they moved into an area from which the original resident (#20A) disappeared (Figure 10).

Within-season territory fidelity

Winter 1999/2000: At Chomes, all 21 flycatchers present throughout the winter held the same territories from December through May. At Bolsón, 11 of 12 individuals present at the site throughout the winter held the same territories from December through late April (the last date of field work). Thus, within-season territory fidelity was 100% and 92%, for Chomes and Bolsón, respectively (97% combined).

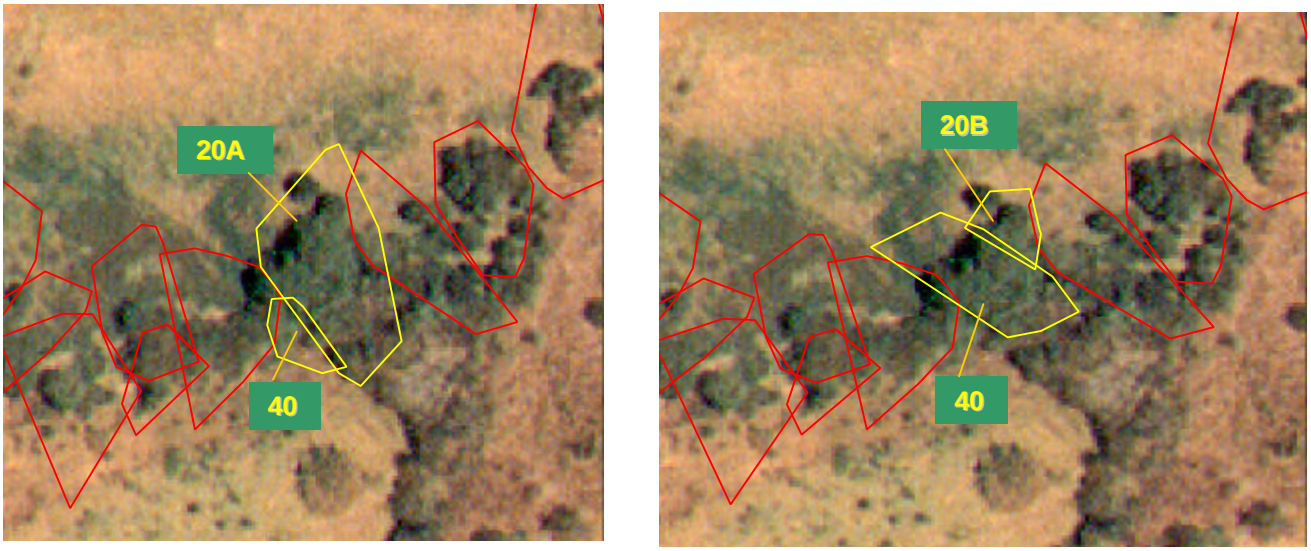

Figure 10. Shifts in territory boundaries and territory holders at the Chomes site. Colored polygons depict territories based on spot-mapping the movements of individuals during the 1999/2000 season. In the left figure, the yellow polygons depict the territory of flycatcher 20A and the use area of floater 40, prior to disappearance of flycatcher 20A on 7 February. In the right figure, the yellow polygons show the subsequent territorial boundaries established by flycatchers 40 and 20B, which moved into the area vacated by flycatcher 20A.

Between-year territory fidelity

Winter 1998/1999 to 1999/2000: All of the color-banded willow flycatchers that returned to Chomes and Bolsón (n=10 and 3, respectively) in the winter of 1999/2000 came back to their previous season's territory. Thus, between-year territory fidelity of birds known to have survived from one winter season to the next (n=13) was 100%.

Winter 1999/2000 to 2000/2001: To date, we have conducted only the first of three winter 2000/01 site visits. During this field session, occurring from 28 September through 16 October 2000, we detected many banded birds that returned. However, fall migration was still underway and the site was far less populated than during winter 1999/2000. Therefore, we expect additional banded willow flycatchers to return during fall 2000, and the following territory fidelity rates will likely change as later-returning birds are located during subsequent field efforts. Twelve of 13 (92%) flycatchers coming back to Chomes returned to the same territory. At Bolsón, all 7 (100%) returning flycatchers came back to their previous season's territory. Thus, between-year territory fidelity of birds known to have survived from one winter season to the next (n=20) was 95%.

Territorial Defense Behavior

Between 15 January to 22 March 2000, we exposed 30 willow flycatchers to simulated territory intrusions (STIs); 20 at Chomes and 10 at Bolsón. Male and female willow flycatchers responded to simulated intrusions, and were more aggressive toward simulated intrusion by another flycatcher than against another species of bird (lesser ground-cuckoo) or a control treatment (random noise) (Figure 11).

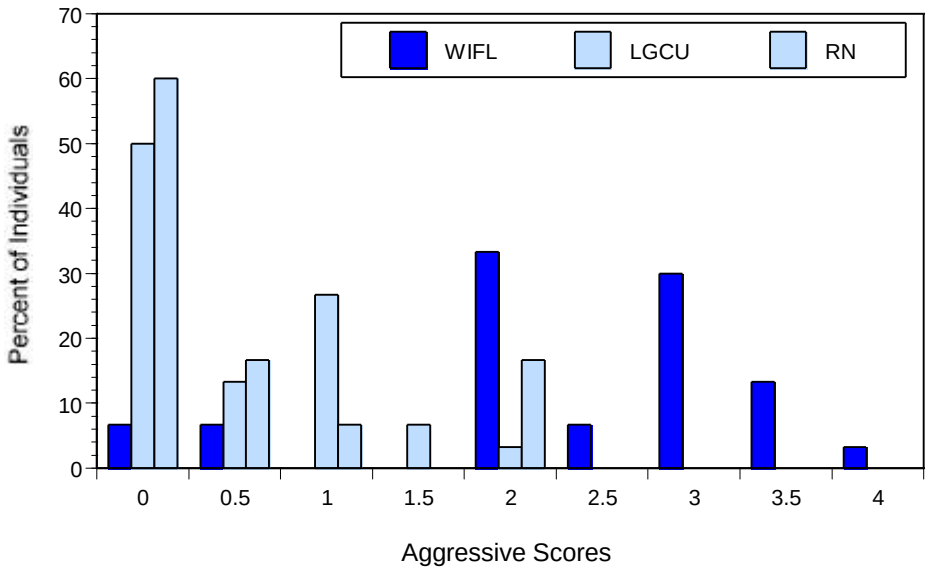

Figure 11. Aggressive scores of 30 willow flycatchers exposed to vocalizations of willow flycatcher (WIFL) and lesser ground cuckoo (LGCU), and random noise (RN = squeaky toy accompanied with digital beeps).

Based on aggressive scores ranging from 0 (lowest) to 4.0 (highest):

- 87% of individuals scored 2.0 or higher when exposed to the willow flycatcher playback treatment (47% scored 3.0 or higher);
- 97% of individuals scored 1.5 or less when exposed to the ground-cuckoo playback treatment (none scored 2.5 or higher); and
- 83% of individuals scored 1.0 or less when exposed to the random noise playback treatment; (none scored 2.5 or higher).

Often, individuals that were exposed to the willow flycatcher treatment continued to vocalize and display throughout (and sometimes well after) the remaining STI treatments. This frequently led to higher aggressive scores during subsequent cuckoo and random noise treatments. 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 (Figures 12 and 13). Thus, there was a clear treatment order effect.

Typical aggressive responses of individuals exposed to the willow flycatcher playback treatment included: (1) movements and flights toward the speaker location; (2) greatly increased singing and calling rates; and (3) direct flights and/or physical contact with the taxidermy mount. Flycatchers responded with song rates as high as 109 songs per 4 minute period. On one occasion a willow flycatcher made two direct flights at, and contacts with, the taxidermy mount. Another six flycatchers made multiple direct flights that came within 1 m of the mount. Other agonistic displays included raised crest with simultaneous rapid tailing pumping and/or rapid wing flicking, often accompanied by the *brrrr/kitter* vocalization and rapid *wheep* calls.

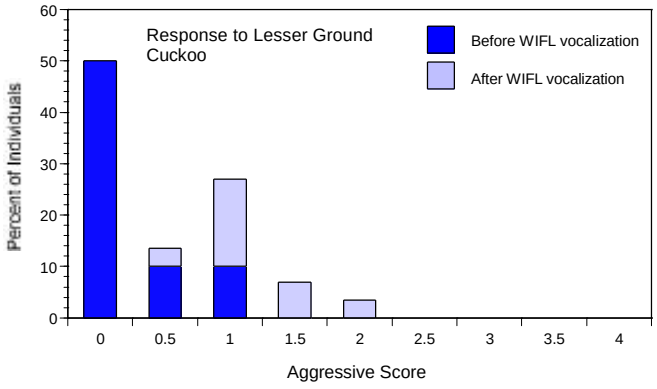

Figure 12. Aggressive response of 30 willow flycatchers exposed to lesser ground cuckoo playback treatment. Solid bars are individuals exposed to the cuckoo treatment before the willow flycatcher treatment; shaded bars are those exposed after the flycatcher treatment.

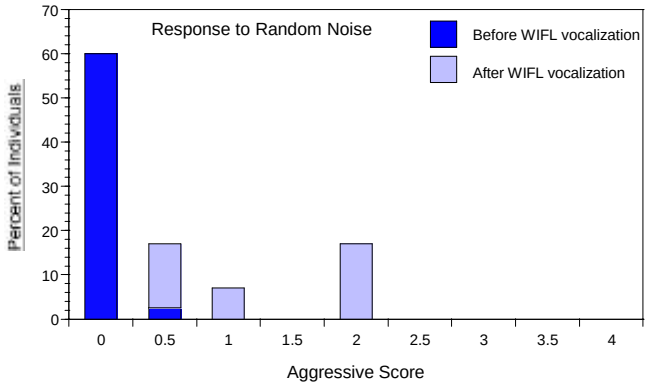

Figure 13. Aggressive responses of 30 willow flycatchers exposed to the random noise playback treatment. Solid bars are individuals exposed to the cuckoo treatment before the willow flycatcher treatment; shaded bars are those exposed after the flycatcher treatment.

Over the course of our territory mapping and resighting efforts, we also saw numerous spontaneous aggressive interactions among flycatchers, usually near territory boundaries of neighboring willow flycatchers. Aggressive interactions ranged from two individuals simultaneously perching in the open while displaying and vocalizing (Figure 14), to high speed chasing with actual physical tussling. Most chases resulted in the intruding flycatcher being displaced out of the defender's territory.

Timing of Migration and Departure

During the third week of April, migrant willow flycatchers began to arrive at both study sites. Based on repeated resights of non-banded flycatchers within the same general area, it appeared that migrants stayed at the sites from one to three days. We observed aggressive interactions between these migrants and the territorial winter residents, and noted a pronounced increase in spontaneous *fitz-bew* songs, usually just after first light. Migrants seen adjacent to or within the winter resident territories were quickly displaced. As a result, migrants were most often seen outside and adjacent to the winter resident's territories, though they sometimes foraged in the occupied tree lines and *laguna* (seasonal freshwater wetland).

Although we had expected that many of the winter residents would leave by late April, almost all were still present during our last field surveys in late April and early May. At Chomes, 21 of 25 monitored flycatchers were still present on 7 May. At Bolsón, 12 of 15 banded flycatchers were still present on 28 April. Funding constraints and on-going field work on the breeding grounds required us to stop the winter field work in early May. Thus, we have an approximate departure date for only one monitored flycatcher. This individual held a territory at Chomes territory from 19 December 1999 through 4 May 2000. Though not detected after 04 May 2000, it to Chomes in fall 2000.

Figure 14. Willow flycatchers perched in the open, vocalizing and displaying in response to conspecific tape playback. Photographs by Phil Heavin.

Habitat

Our previous characterization of willow flycatcher wintering sites (Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999) identified four major habitat components: (1) standing or slow moving water and/or saturated soils, (2) patches or stringers of trees, (3) dense woody shrubs, and (4) open areas. These four components also characterize the habitat within each individual willow flycatcher territory at both study sites. Flycatcher territories were distributed around the periphery of the *laguna* wetlands, and straddled the tree line and wetland interface (Figures 8 and 9). This interface - heavily used by flycatchers for foraging, preening and mid-day roosting - is characterized primarily by patches of dense woody shrubs (*Mimosa pigra*) which abruptly meet the relatively open under-stories of the tree lines.

Over the past three years, particular areas around the periphery of the *laguna* have not been occupied by wintering willow flycatchers. Interestingly, these unoccupied areas lack one or more of the four habitat components discussed above. For example, the unoccupied northwest side of the Chomes *laguna* (see Figure 8) completely lacks the dense woody shrub component along the wood line, with tall, herbaceous, aquatic vegetation being dominant. Also, the tree line in this area is structurally different, in that the understory is very dense and has few open areas.

Foraging

We noted a consistent temporal foraging pattern at both study sites. From first light to approximately 0730 hrs, willow flycatchers foraged primarily in the dense woody and herbaceous vegetation in the *lagunas*. From 0730 hrs (when the sun rises quickly off the horizon and light penetrates the tops of the tree lines) to approximately 1100 hrs, flycatchers shifted foraging to the tops of trees and on the tree line - *laguna* interface. Shortly thereafter, temperatures rise quickly and the prevailing northeasterly trade winds make resighting birds very difficult, so we have few foraging observations. During late afternoon (approximately 1600 hrs), when winds calm and observable foraging increases, flycatchers were still foraging primarily in the tree tops and along the tree line - *laguna* interface. Shortly before dark, willow flycatchers moved back to the dense woody and herbaceous shrubs in the *lagunas*. Flycatchers roosted in the woody shrubs within the *laguna*, and were first detected again there the following mornings.

Flycatchers primarily "sally gleaned" – flying upward and/or hovering briefly to pull small insects from the surface of leaves and branches - within moderately dense shrubs and somewhat open tree canopies. Flycatchers also perched near the tops of shrubs and trees and made aerial forays to capture small flying insects (i.e. "hawking"). This was most frequently seen early in mornings and later in the evenings, when winds were calm. Prey items were so small as to be seldom seen.

Based on foraging observations, wintering willow flycatchers feed almost exclusively on invertebrates at our Costa Rica study sites. However, we twice saw flycatchers feeding on fruit. On 19 March1999 (as noted in Koronkiewicz and Whitfield 1999), a resident willow flycatcher ate berries from a vine. The following year, on 27 April, an unbanded (and presumably migrant) willow flycatcher was seen eating numerous arilate fruits from a fruiting tree. This migrant spent at least 3 hrs feeding, eating approximately 20 fruits. The flycatcher chased away other willow flycatchers, and an alder flycatcher *(Empidonax alnorum*), that came to or near the tree.

DISCUSSION

Until quite recently, neotropical migrant passerines were generally thought of as being highly mobile generalists when on the winter grounds, moving about the landscape and exploiting only superabundant food resources (MacArthur 1972, Leck 1972, Karr 1976, Hutto 1980). Recent ecological studies (e.g., Holmes and Sherry 1992, Mabey and Morton 1992, Staicer 1992) have challenged these theories and shown that the behavior we found in wintering willow flycatchers (i.e., site fidelity, territorial behavior) are widespread among other long distance migrant species. Below we discuss the different aspects of our study, and relate our finding to those of other studies on wintering neotropical migrants. It is important to emphasize that even though our results were consistent between years and at our two study sites, we do not yet know if these results can be generalized across the wintering range, or to other sites that may differ in important ways such as size or habitat characteristics.

Within-year Site Fidelity and Over-winter Survivorship

Wintering willow flycatchers exhibited a high degree of within-year site fidelity and over-winter survivorship. These results are consistent with patterns seen in some other long distance neotropical migrants. In Venezuela, northern waterthushes (*Seiurus noveboracensis*) remained at a wintering site for an average of slightly over six months, with only one of 20 birds presumably succumbing to a predator (Schwartz 1964). Holmes et al. (1989) documented winter site fidelity/survivorship of 80% for American redstarts (*Setophaga ruticilla*) and 66% for black-throated blue warblers (*Dendroica caerulescens*) in Jamaica. Parrish and Sherry (1994) estimated fall to spring site fidelity/survivorship of American redstarts (also in Jamaica) at 66%. Our overall value of 85% within-year site fidelity and survivorship is the highest yet reported for a wintering neotropical migrant.

Between-year Site Fidelity

Reports of between-year return rates (i.e., between-year site fidelity) of neotropical migrants vary considerably among many different species. Values as low as 0% have been reported for common yellowthroat (*Geothlypis trichas*; Kricher and Davis 1986), and 3% for northern parula (*Parula Americana*; Faaborg and Arendt 1984). In contrast, Rappole and Warner (1980) found 49% site fidelity in yellow-bellied flycatchers (*Empidonax flaviventris*), and Holmes and Sherry (1992) reported 51% for American redstart (*Setophaga ruticilla).* Our value of 43 – 77% return rate for willow flycatchers is higher than generally reported for other species. However, we concur with Holmes and Sherry (1992) studies reporting very low return rates are based on general mist-netting activities; these undoubtedly underestimate between year site fidelity. Studies showing higher values of return and fidelity are based on color-banding birds and intensive subsequent searches, thereby producing more realistic estimates of between-year site fidelity.

Territoriality

Over a dozen papers have reported neotropical passerines, including hummingbirds, warblers, vireos, flycatchers, tanagers and orioles, defending winter territories against conspecifics (see Rappole 1995 for an excellent summary of literature and species involved). Many of the reports are based on single observations (i.e. one individual chasing a conspecific), and most do not incorporate color-banded individuals monitored over long periods of time. However, several long-term and/or experimental studies based on color-banded birds found that many wintering migrant passerines, in many different taxonomic groups, maintain and defend winter territories with vocalizations and agonistic displays (Rappole and Warner 1980, Holmes et al. 1989, Staicer 1992). Results from these more detailed studies are consistent with our findings that individual willow flycatchers maintain and defend winter territories, and that each sex excludes the other from its territories.

Brown (1964) and Kaufmann (1983) suggested that energy expenditure in territorial defense indicates that the resources defended are critical for survival. Because willow flycatchers are territorial on the wintering grounds, the number of flycatchers that can occupy a particular wintering site are limited and therefore access to critical resources may be limited. Movement of individuals into a site may be limited if other birds have already established territories there. This also implies that arrival date following fall migration may be important; early arriving individuals have first choice of high-quality site and/or territories, much as occurs on the breeding grounds. Late arriving birds may be forced into lower quality sites/territories, or be forced into the role of floater.

Floaters

We noted floaters at our study sites, and observed floaters replacing a territorial resident that disappeared mid-winter. Floaters have been documented in other studies of wintering neotropical migrants. Holmes et al. (1989) reported floater American redstarts and black-throated blue warblers. When territorial individuals disappeared, floater individuals moved in to replace the missing resident. Rappole and Warner (1980) also documented floaters in their banded populations of six species of neotropical migrants in Mexico. As we found for willow flycatchers, Rappole and Warner noted 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 floaters in wintering wood thrush (*Hylocichla mustelina*) in Mexico and found higher mortality for floaters than for territory holders. We do not know if there are survival differences between willow flycatcher floaters and territory holders.

Habitat Use

The Chomes and Bolsón study sites are wetland habitats which are affected by seasonal inundation. When the flycatchers arrive each fall, surface water covers most of the flycatcher habitat at each site. As dry season advances, most surface water dries up but both areas retain some surface water and saturated soils year-round. Although water levels change dramatically over the course of the flycatcher's residency each winter, the vegetation structure at both sites changes very little as compared to the surrounding non-wetland habitats. This persistence of wet conditions and relatively little vegetation change may be a key to wetland use by willow flycatchers, and may also influence

the high degree of site and territorial fidelity that we observed. Morton (1980) studied neotropical migrants in Panama and reported that territorial, obligatory insectivorous species were restricted to wet areas showing the least seasonal change. Habitat conditions during the dry season were critical, and restricted these insectivorous species to wetland habitats. He reported that seasonal changes constitute an important niche dimension for territorial species, as they occupy only the wettest and relatively "aseasonal" areas (such as the Chomes and Bolsón wetlands).

Research on insect movements in northwest Costa Rica suggests why wetland habitats may be critical for the willow flycatcher and other migrant and resident birds. In the Pacific lowlands of northwest Costa Rica, Janzen (1980) found that as the dry season intensifies large numbers of insects move from hillsides to nearby wetland riparian vegetation, and that many insect species pass the dry season in these "riparian refugium", resulting in high insect concentrations in wetland areas. Willow flycatchers are resident throughout the Pacific lowlands of Central America for the entire dry season, and the relatively abundant insects drawn to wetland habitats may be critical to their ability to survive during this period, and to accumulate the fat reserves needed to depart on their northward migration each spring.

Food and foraging

The predominantly insectivorous nature of willow flycatchers has been noted before on the breeding grounds (Beal 1912, Drost et al. 1998) and during the winter (Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999). The diet of willow flycatchers may have direct implications regarding winter territorial behavioral, in that social behavior during the nonbreeding season appears to be at least partly a function of a specie's diet (Rappole 1995). Frugivorous birds which exploit primarily temporally and spatially distributed fruits tend not to be territorial; rather, they usually join conspecific flocks to locate fruits more efficiently (Kricher 1997). In contrast, when food items are relatively evenly dispersed over space and time (such as insects in lowland wetland habitats), bird species which prey on them are often territorial and defend territories against conspecifics (Rappole 1995).

Most studies and general observations (Beal 1912, Drost et al. 1998) have described breeding willow flycatchers as almost exclusively insectivorous; as far as we can tell this is true for wintering flycatchers as well. However, the two winter observations of fruit-eating raise interesting questions regarding the role and importance of fruit during the late winter/early spring migration period. In the Pacific lowlands, most small-fruiting trees and shrubs produce their fruits toward the end of the dry season. This corresponds with the initiation of the flycatcher's migration, a period when nutritional state and energy reserves are particularly important. As fruits become more available at precisely that time during which flycatchers need more caloric and nutritional intake, consumption of fruits may increase greatly. This possibility is supported by observations during the fall migration, where many "Traill's flycatchers" mist-netted on the Caribbean side of Costa Rica had berry-stained mouth-linings, and flycatchers were frequently observed feeding gregariously on ripe berries (T. Koronkiewicz, *pers. observ*.).

Conservation Implications

Many aspects of flycatcher winter habitat use and behavior have substantial conservation and management implications. All recent survey and ecology work (Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999, Lynn and Whitfield 2000, this study) suggests that wintering flycatchers are not habitat generalists, and that suitable and/or high-quality wintering habitat is very rare on a landscape scale. Therefore, one can not assume that flycatchers can adapt to losses of their rare wetland habitats by simply dispersing into surrounding habitats. Clearly, continued loss of lowland Pacific wetland habitats will be detrimental to wintering willow flycatchers. Conservation of winter willow flycatcher populations requires maintaining and/or creating an adequate amount of suitable wintering habitat. Protection and/or enhancements of flycatcher wintering habitats must specifically target those sites with the habitat characteristics favored by flycatchers. General land or habitat conservation activities in the neotropics may be of little conservation value to the willow flycatcher unless appropriate habitat needs are explicitly considered and accounted for.

The fact that willow flycatchers have strong winter site fidelity implies that the persistence and quality of a particular wintering site has important consequences to the flycatchers that return there to overwinter each year. It may be difficult for flycatchers to move to alternative sites, in that (1) suitable wintering sites are uncommon, and (2) winter residents already occupying those sites may prevent displaced birds from settling. 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. Thus, maintaining and/or enhancing existing wintering sites should be a high-priority when developing plans for winter habitat protection or creation.

The high return rates for wintering willow flycatchers in our study may indicate that our study sites comprise relatively high-quality wintering habitat (Winker et al. 1995). High quality (e.g., larger, wetter) wintering sites may be able to better support larger, more stable local populations than many of the other smaller winter sites which have been recently located but not closely studied. This is a critical consideration in that we do not know whether small sites provide the same over-winter survival value as larger sites. The relative quality of large versus small sites can determine the types of conservation options to pursue; e.g., preserving fewer large patches as opposed to more but smaller ones. 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.

ACKNOWLEDGMENTS

This project would not have been possible without the work and support of numerous persons and many agencies. Funding was provided by the U.S. Bureau of Reclamation (Phoenix, AZ), the U.S. Fish and Wildlife Service, and the U.S. Geological Survey. Particular thanks to Susan Sferra (BoR) and Stuart Leon (USFWS) for their encouragement and assistance with funding and contracts. Particular thanks to the field crew who gave us their talent and many hours afield, and made our travel and field work a truly enjoyable experience. These persons include: Kristen Covert, Rebecca Davidson, Kristen Enos, and Phil Heavin. Additional thanks to Charles Drost and Eben Paxton with the USGS Colorado Plateau Field Station for assistance with many aspects of this project over the last four years. Special thanks to the Organization for Tropical Studies, which has proven invaluable in obtaining research and export permits in Costa Rica as well provided us with numerous contacts and logistical information. We would also like to thank the staff at the Colorado Plateau Field Station, particularly Margaret Rasmussen, for incredible administrative support in the face of many administrative challenges. A very special thanks goes to the wonderful and admirable people of Costa Rica. Alvaro Gonzáles and Nicola Bertoldi at Pensión de la Questa in San Jose provided us with charming accommodations as well as logistical support. Our deepest appreciation goes to the late Arturo Wolfe Fournier, Gerente General, Hacienda Chomes, for his invaluable logistical and moral support, and sharing with us his love of the land. We are grateful to the staff of the Pan American Health Organization, and most especially to Dr. Mira Leslie of the Arizona Department of Health Services, for assistance in obtaining rabies vaccine following an unexpected bat bite at Chomes. Last, but certainly not least, we offer heartfelt thanks to Lisa Koronkiewicz for putting up with her husband's work schedule.

LITERATURE CITED

Beal, F.E.L. 1912. Food of our more important flycatchers. U.S. Department of Agriculture, Biological Survey – Bulletin No. 44. Washington Government Printing Office.

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin 76:160– 169.

Busch, J.D., M.P. Miller, E.H. Paxton, M.K. Sogge and P. Keim. 2000. Genetic variation in the endangered southwestern willow flycatcher. Auk 117:586-595.

Coen, E. 1983. Climate. Pages 35-46 in Costa Rican Natural History (D.H. Janzen ed.) University of Chicago Press, Chicago.

Drost, C.A., M.K. Sogge and E.H. Paxton. 1999. Preliminary Diet Study of the Endangered Southwestern Willow Flycatcher. USGS Technical Report USGSFRESC/COPL/1998/15.

Faaborg, J. and W.J. Arendt. 1984. Population sizes and Philopatry of winter resident warblers in Puerto Rico. Journal of Field Ornithology 55:376-378.

Gorski, L.J. 1969. Traill's flycatchers of the "fitz-bew" songform wintering in Panama. Auk 88:745-747.

Holmes, R.T., Sherry, T.W. and Reitsma, L. 1989. Population Structure, Territoriality and Overwinter Survival of Two Migrant Warbler Species in Jamaica. Condor 91:545-561.

Holmes, R.T. and T.W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation. In Ecology and Conservation of Neotropical Migrant Landbirds, ed. J.M. Hagan III and D.W. Johnson, 563-575. Smithsonian Institution Press, Washington and London.

Howell, N.G. and S. Webb. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford University Press Inc., New York.

Hutto, R. 1980. Winter habitat distribution of migratory land birds in western Mexico, with special reference to small foliage-gleaning insectivores. *In* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation, ed. A. Keast and E.S. Morton, 181-203. Smithsonian Institution Press, Washington, D.C.

International Bird Census Committee. 1970. An International Standard for a mapping Method in Bird Census Work Recommended by the International Bird Census Committee. Audubon Field notes 24:722-726.

Janzen, D. 1980. Heterogeneity of Potential Food Abundance for Tropical Small Land Birds. *In* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation, ed. A. Keast and E.S. Morton, 181-203. Smithsonian Institution Press, Washington, D.C.

Kaufmann, J.H. 1983. On the definitions and functions of dominance and territoriality. Biological Review 58:1-20.

Karr, J. 1976. On the relative abundance of migrants from the north temperate zone in tropical habitats. Wilson Bulletin 88:433-458.

Kahn, N.W., St. John, J., and Quinn. 1998. Chromosome-specific intron size differences in the avian CHD gene provide an efficient method for sex identification in birds. Auk 115:1074-1078.

Koronkiewicz, T. J, M.K. Sogge and C.A. Drost. 1998. A preliminary survey for wintering Willow Flycatchers in Costa Rica. USGS, FRESC Colorado Plateau Research Station report. 47pp.

Koronkiewicz, T.J., and Whitfield M. 1999. Surveys for Wintering Willow Flycatchers (*Empidonax traillii*) in Costa Rica and Panama. San Diego Natural History Museum, Kern River Research Center, and USGS FRESC Colorado Plateau Research Station report. 91 pp.

Kricher, J. 1997. A Neotropical Companion: An introduction to the animals, plants, and ecosystems of the New World Tropics. Princeton University Press.

Kricher, J. and W.E. Davis Jr. 1986. Returns and winter-site fidelity of North American migrants banded in Belize, Central America. Journal of Field Ornithology 57:48-52.

Leck, C.F. 1972. The impact of some North American migrants at a fruiting tree in Panama. Auk 89:842-850.

Lynn, J.C., and Whitfield M. 2000. Winter Distribution of the Willow Flycatcher (*Empidonax traillii*) in Panama and El Salvador. Kern River Research Center report. 62 pp.

Mabey, S.E. and E.S. Morton. 1992. Demography and territorial behavior of wintering Kentucky Warblers in Panama. *In* Ecology and Conservation of Neotropical Migrant Landbirds, ed. J.M. Hagan III and D.W. Johnson, 329-336. Smithsonian Institution Press, Washington and London.

MacArthur, R.H. 1972. Geographical Ecology. New York: Harper and Row.

Marshall R.M and Stoleson S.H. 2000. Threats. Pages 13-24 *in* Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. USDA Forest Service Gen. Tech. Rep. RMRS-GTR-60.

Meyer de Schauensee, R.M. 1966. The Species of Birds of South America and Their Distribution. Livingston Pub. Co., Narberth, PA.

Meyer de Schauensee, R.M. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, New Jersey.

Morton, E.S. 1980. Adaptations to Seasonal Changes by Migrant Land Birds in the Panama Canal Zone. *In* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation, ed. A. Keast and E.S. Morton, 437-453. Smithsonian Institution Press, Washington, D.C.

Parrish, J.D. and T.W. Sherry. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: importance of resource seasonality. Auk 111:38-49.

Parrish, J.D. 1996. Dietary plasticity during migration: evolution and behavioral implications of diet shifts to frugivory in nearctic-neotropical landbird migrants. Ph.D. dissertation. Brown University, Providence, RI.

Rappole, J.H. 1995. The Ecology of Migrant Birds: A Neotropical Perspective. Smithsonian Institution Press, Washington and London.

Rappole, J.H. and D.W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. *In* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation, ed. A. Keast and E.S. Morton, 353-393. Smithsonian Institution Press, Washington, D.C.

Ridgely, R.S. and J. Gwynne. 1989. A Guide to the Birds of Panama with Costa Rica, Nicaragua and Honduras. Princeton Press, Princeton, NJ.

Ridgely, R.S. and G. Tudor. 1994. The Birds of South America; Volume II the Suboscine Passerines. University of Texas Press, Austin, Texas.

Schlorff, R.W. 1990. Report to the Fish and Game Commission: status review of the Willow Flycatcher (*Empidonax traillii*) in California. California Department of Game and Fish: Sacramento, California. Department Candidate Special Status Report 90-1.

Schwartz, P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3:169-184.

Sogge, M.K. 2000. Breeding Season Ecology. Pages 57-70 *in* Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. USDA Forest Service Gen. Tech. Rep. RMRS-GTR-60.

Sogge, M.K., R.M. Marshall, S.J. Sferra, and T.J. Tibbitts. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. National Park Service Technical Report USGS/NAUCPRS/NRTR-97/12.

Staicer, C.A. 1992. Social Behavior of the Northern Parula, Cape May Warbler, and Prairie Warbler Wintering in second-growth forest in southwestern Puerto Rico. *In* Ecology and Conservation of Neotropical Migrant Landbirds, ed. J.M. Hagar III and D.W. Johnson, 308-320. Smithsonian Institution Press, Washington and London.

Stiles, F.G. and Skutch, AF 1989. A Guide to the Birds of Costa Rica. Cornell University Press, New York.

Tibbitts, T.J., M.K. Sogge, and S.J. Sferra. 1994. A Survey Protocol for Southwestern Willow Flycatcher (*Empidonax traillii extimus*). National Park Service Technical Report NPS/NAUCPRS/NRTR-97/04.

Unitt, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. Western Birds 18:137-162.

Unitt, P. 1997. Winter range of *Empidonax traillii extimus* as documented by existing museum collections. Report to U.S. Bureau of Reclamation, Phoenix, AZ.

U.S. Fish and Wildlife Service. 1993. Proposed rule to list the Southwestern Willow Flycatcher as endangered with critical habitat. Federal Register 58:39495-39523.

U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. Federal Register 60:10694-10715.

Winker, K., J.H. Rappole, and M.A. Ramous. 1990. Population dynamics of the Wood Thrush (*Hylocichla mustelina*) on its wintering grounds in southern Veracruz, Mexico. Condor 92:444-460.

Winker, K., J.H. Rappole, and M.A. Ramos. 1995. The use of movement data as an assay of habitat quality. Oecologia 101:211-216.

Appendix 1. Willow flycatchers banded at the Chomes, Costa Rica study site. Table includes banding and return information. Individuals monitored in the main study area are in bold font.

USFWS Service Band Number	Color Band Combination	Date Captured/Banded	Years detected		
			1998/99	1999/2000	2000/01
1740-91831	**KY:N**	**12/18/98**	**X**	**X**	
1740-91832	**RW:N**	**12/18/98**	**X**	**X**	**X**
1740-91833	DW:N	12/18/98	X		
1740-81834	WW:N	1/2/99	X		
1740-91835	**RK:N**	**1/2/99**	**X**	**X**	**X**
1740-91836	**RD:N**	**1/2/99**	**X**	**X**	
1740-91837	**YV:N**	**1/2/99**	**X**	**X**	**X**
1740-91838	**WR:N**	**1/3/99**	**X**	**X**	**X**
1740-91839	**YR:N**	**1/6/99**	**X**	**X**	**X**
1740-91840	**WK:N**	**1/7/99**	**X**	**X**	**X**
1710-20358	X:KK	3/21/99	X		
1710-20359	**X:GG**	**3/21/99**	**X**	**X**	
1590-97505	**--:V**	**3/22/99**	**X**	**X**	
1710-46133	N:DK	3/29/00		X	
1740-91982	**N:YK**	**12/18/99**		**X**	**X**
1710-46116	N:KY	1/3/00		X	
1740-91984	**N:RW**	**12/20/99**		**X**	
1710-46106	N:WR	12/20/99		X	
1710-46105	N:WW	12/20/99		X	
1710-46118	N:KR	1/4/00		X	
1710-46119	N:RK	1/5/00		X	
1710-46107	N:DR	12/20/99		X	
1740-91994	**N:VY**	**1/2/00**		**X**	
1740-91985	**N:YR**	**12/20/99**		**X**	**X**
1710-46123	**RY:N**	**2/10/00**		**X**	
1710-46108	N:KW	12/21/99		X	
1740-91983	**N:RR**	**12/18/99**		**X**	**X**

Appendix 1 continued. Willow flycatchers banded at the Chomes, Costa Rica study site. Table includes banding and return information. Individuals monitored in the main study area are in bold font.

USFWS Service Band Number	Color Band Combination	Date Captured/Banded	Years detected		
			1998/99	1999/2000	2000/01
1740-91993	**N:YD**	**12/29/99**		**X**	**X**
1710-46117	N:DY	1/4/00		X	
1710-46124	**DY:N**	**2/10/00**		**X**	
1710-46115	**N:VK**	**1/3/00**		**X**	**X**
1740-91992	N:GR	12/29/99		X	
****** 1710-46132	GR:N	3/23/00		X	
1710-46103	**N:OO**	**12/19/99**		**X**	
1710-46104	**N:YY**	**12/19/99**		**X**	
1710-46134	**N:YW**	**4/1/00**		**X**	
1740-91986	**OD:N**	**12/28/99**		**X**	**X**
1710-46114	**N:GO**	**1/3/00**		**X**	**X**
1710-46109	KG:N	12/21/99		X	
1590-97479	KO:N	10/8/00			X
1740-91995	N:DO	10/9/00			X
****** 1740-91996	N:YG	10/10/00			X

N = bronze anodized USFWS service band; X = silver USFWS band; K = black; Y = yellow; R = red; W = white; D = blue; V = violet; G = green; O = orange; ****** = suspected migrant.

Appendix 2. Willow flycatchers banded at the Bolsón, Costa Rica study site. Table includes banding and return information. Individuals monitored in the main study area are in bold font.

USFWS Service Band Number	Color Band Combination	Date Captured/Banded	Years detected		
			1998/99	1999/2000	2000/01
1740-91806	**WD:N**	**1/16/99**	**X**	X	
1740-91807	KD:N	1/16/99	X		
1740-91808	**KW:N**	**1/17/99**	**X**	**X**	**X**
1740-91809	**DR:N**	**1/17/99**	**X**	**X**	**X**
1710-20355	RR:X	3/19/99	X		
1710-20356	DD:X	3/19/99	X		
1710-20357	X:ZZ	3/19/99	X		
1710-46121	**DK:N**	**1/28/99**		**X**	
1710-46131	N:KD	2/17/00		X	
1710-46113	YK:N	12/28/99		X	
1710-46111	**KR:N**	**12/23/99**		**X**	**X**
1710-46128	**N:RD**	**2/16/00**		**X**	
1740-91987	**N:WK**	**12/23/99**		**X**	
1710-46129	N:KG	2/16/00		X	
1710-46122	**YD:N**	**2/1/00**		**X**	
1710-46130	N:RG	2/16/00		X	
1710-46112	**RG:N**	**12/23/99**		**X**	**X**
1740-91990	OO:N	12/24/99		X	
1710-46110	**YY:N**	**12/23/99**		**X**	**X**
1710-46127	**YW:N**	**2/15/00**		**X**	**X**
1740-91991	WY:N	12/28/99		X	
1710-46125	N:WY	2/14/00		X	
1710-46120	**N:WG**	**1/28/00**		**X**	
1740-91988	**GW:N**	**12/23/99**		**X**	
1710-46126	**N:OR**	**2/14/00**		**X**	
1710-20561	**DO:V**	**1/29/00**		**X**	**X**