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## WILLOW FLYCATCHER NONBREEDING TERRITORY DEFENSE BEHAVIOR IN COSTA RICA

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*Abstract.* We studied the intraspecific territorial defense behavior of wintering Willow Flycatchers (*Empidonax traillii*) in Costa Rica using a randomized playback experiment that exposed male and female birds to recordings of Willow Flycatcher songs and calls, Lesser Ground Cuckoo (*Morococcyx erythropygius*) vocalizations, and random noise. Flycatchers of both sexes responded most strongly to simulated conspecific territory intrusion, and the agonistic

behaviors that we observed were similar to those seen during natural intraspecific encounters in winter. Both males and females engaged in song and aggressive behaviors in defense of territories, and there was no significant difference between the sexes in scored agonistic responses. The similarity between the sexes in intraspecific territorial defense behaviors and aggressiveness may account for both sexes of flycatchers using the same habitats at our study sites in Costa Rica, and wintering females defending territories against males. The Willow Flycatcher, a sexually monomorphic species, differs in this way from a number of sexually dimorphic passerines, in which behaviorally dominant males occur in more optimal winter habitats.

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## Comportamiento de Defensa Territorial en la Época no Reproductiva de *Empidonax Traillii* en Costa Rica

*Resumen.* Estudiamos el comportamiento de defensa territorial intraespecífico de individuos invernantes de la especie *Empidonax traillii* en Costa Rica usando un experimento aleatorio de reproducción de vocalizaciones previamente grabadas que expuso a machos y hembras a grabaciones de cantos y llamadas de *Empidonax traillii*, a vocalizaciones de *Morococcyx erythropygius* y a ruidos al azar. Los individuos de *Empidonax traillii* de ambos sexos respondieron más fuertemente a las intrusiones estimuladas de aves coespecíficas, y los comportamientos agonísticos que observamos fueron similares a aquellos observados durante encuentros naturales intraespecíficos en el invierno. Tanto los machos como las hembras desplegaron cantos y comportamientos agresivos en defensa de los territorios, y no hubo una diferencia significativa entre los sexos en las respuestas agonísticas. La similitud entre los sexos en los comportamientos de defensa territorial intraespecíficos y la agresividad puede explicar el uso de los mismos ambientes en nuestros sitios de estudio en Costa Rica, y la defensa de los territorios ante los machos por parte de hembras invernantes. *Empidonax traillii*, una especie sexualmente monomórfica, difiere de este modo de otros paserinos con dimorfismo sexual, en los que los machos con comportamiento dominante se encuentran en ambientes más óptimos durante el invierno.

Studies investigating the behavioral ecology of Neotropical migrant passerines during the nonbreeding period have shown that some species exhibit stereotypical agonistic behaviors in defense of long-term, mutually exclusive (i.e., supporting only one individual) winter territories (Rappole and Warner 1980, Holmes et al. 1989, Rappole et al. 1992). Intraspecific territorial behavior in long-distance migrants that are sexually dimorphic has been shown to influence structuring patterns of habitat occupancy on the wintering grounds, with many species exhibiting sexual habitat segregation in both the New (Marra 2000, Latta and Faaborg 2001) and Old World (Nisbet and Medway 1972). It is generally hypothesized that the larger size and brighter coloration of males in these dimorphic species provides a competitive advantage over females in obtaining prime habitats and defending winter territories (Stutchbury et al. 2005). Based on this reasoning, one might hypothesize that monomorphic passerines would show fewer differences between the sexes in territorial behavior and habitat selection. Unfortunately, the wintering behavior of sexually monomorphic migrants has received little attention, with the exception of the Yellow-bellied Flycatcher (*Empidonax flaviventris*) and Least Flycatcher (*E.*

*minimus*; Rappole and Warner 1980, Rappole et al. 1992).

The Willow Flycatcher (*Empidonax traillii*) is a long-distance migrant passerine that winters throughout portions of Central America and northwestern South America. The species is sexually monomorphic, and both sexes maintain long-term, mutually exclusive winter territories for approximately three-quarters of the annual cycle (Koronkiewicz 2002, Koronkiewicz et al. 2006). This caused us to ask whether flycatchers use similar territorial defense behaviors on both the wintering and breeding grounds, and whether the sexes differ in the degree of exhibited territorial behavior. To answer these questions, we described and quantified intraspecific agonistic behaviors during the nonbreeding season, and exposed wintering Willow Flycatchers to a playback experiment that simulated a conspecific territory intrusion.

## METHODS

We conducted this study at two seasonal freshwater wetland sites in northwestern Costa Rica, where Willow Flycatchers are resident throughout the winter. Both sites, Chomes (Puntarenas Province) and Bolson (Guanacaste Province), are located in lowland areas (just above sea level) along the Pacific coast, between approximately 10° and 10°30'N latitude and from 85° to 85°30'W longitude. Vegetation structure and species composition are similar between sites, with patches and narrow strips of tropical deciduous forest bordering wetland vegetation (Koronkiewicz 2002).

To examine the intraspecific agonistic behaviors used by Willow Flycatchers in defense of winter territories, we conducted a series of simulated conspecific intrusions on territory-holding individuals. These intrusions consisted of randomized sound playbacks in conjunction with an *Empidonax* taxidermy decoy, placed near the center of each known Willow Flycatcher territory. Territory borders were determined by spot mapping the locations and movements of color-banded individuals on high-resolution aerial photographs and forming a minimum convex polygon that connected the outermost points of each individual's detections (Odum and Kuenzler 1955, Holmes et al. 1989); mean territory size was 0.5 ha at Chomes and 0.8 ha at Bolson (Koronkiewicz et al. 2006). All flycatchers that were exposed to simulated territory intrusions had been previously mist-netted (Sogge et al. 2001) and banded with unique combinations of colored metal bands (Koronkiewicz et al. 2005). The sex of each bird was determined with DNA-based assays exploiting intronic differences in W and Z chromosome copies of the CHD gene (Fridolfsson and Ellegren 1999).

Randomized playbacks consisted of a set of three standardized recordings: (1) Willow Flycatcher vocalizations from the breeding grounds (three individuals total, from Gila and Pima Counties, Arizona), including 'fitz-bew' and 'creet' advertising songs, 'whit' and 'chur/kitter' calls, and an array of flycatcher calls made during an aggressive encounter with a Brown-headed Cowbird (*Molothrus ater*); (2)

Lesser Ground Cuckoo (*Morococcyx erythropygius*; a common resident species at both winter study sites) vocalizations, including primary song and calls taped by B. Coffey and L. Coffey (ARA Records, Gainesville, Florida); and (3) random noise (a squeaker toy accompanied by digital beeps). The same vocalization and noise recordings were presented to all flycatchers throughout the study. The flycatcher vocalizations were the experimental treatment; cuckoo and random noise broadcasts were the controls. The Willow Flycatcher and random noise recordings were made with a Sony TCM-5000EV Cassette-Corder and Sennheiser ME20 microphone. We broadcast each of the three playback treatments for 4 min with a silent 4-min listening and observation period before and after each playback treatment (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 (Koronkiewicz 2002).

A Willow Flycatcher was randomly selected for the experiment (excluding any that were previously selected) the day before each simulated territorial intrusion (hereafter also "intrusion"), and the evening before each experiment we marked the playback area (a 20 m diameter circle) by hanging colored flagging 10 m from the approximate center of the selected bird's territory in each of the four cardinal directions. In all cases, the playback area was located in a part of the territory in which the flycatcher had been previously detected. An *Empidonax* decoy was mounted at 2 m on a camouflaged pole and placed in the center of the playback area. The decoy for each intrusion was selected randomly from among three *Empidonax* taxidermy mounts: Hammond's Flycatcher (*E. hammondi*), Dusky Flycatcher (*E. oberholseri*), and Cordilleran Flycatcher (*E. occidentalis*). We broadcast playback treatments at ca. 50–60 decibels (measured 6 m away) using a portable Memorex® (Cerritos, California) MD3015 CD player connected to two monaural RadioShack® (Fort Worth, Texas) AMX 9 amplified speakers via a monaural cable. The speakers were affixed back-to-back and mounted 0.5 m below the decoy.

All simulated territorial intrusions were conducted by a single observer (TJK), between 06:00 and 07:00 (EST), and only during calm and favorable weather. Not all birds were within the same distance of the playback area when playback began, but a flycatcher was assumed to be within its territory when the intrusion began, even if its exact location was not known. On mornings when more than one flycatcher was exposed to an intrusion, territories were at least 50 m apart to avoid habituation of future experimental birds to the playback broadcast. The observer remained stationary approximately 15 m from the experimental location, so the entire area could be clearly viewed. Flycatcher behaviors (visual displays, singing and calling rates, and movements) observed during each intrusion period were dictated into a handheld tape recorder and transcribed immediately following the experiment. Descriptions of Willow Flycatcher vocalizations and visual displays

follow the terminology in Stein (1963) and Sedgwick (2000).

We scored Willow Flycatcher agonistic responses separately for each of the three playback treatments and 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 the playback area; (2) vocalization rate; (3) aggressiveness toward the decoy; and (4) agonistic visual displays (Table 1). Individuals received one score per behavioral category, with a maximum possible score of 4 during any one treatment. We then compared the overall aggressiveness scores among the different treatments to determine whether flycatchers responded more strongly to the Willow Flycatcher vocalizations than to Lesser Ground Cuckoo vocalizations or random noise. The overwhelmingly strong response to the flycatcher vocalization treatment and the almost complete lack of response to the cuckoo and random noise treatments led to a response dataset with numerous "zero" values, which precluded the use of parametric tests. Therefore, we used a Friedman's test on the overall agonistic scores to test for differences among treatments. We tested for differences in response to conspecific playback between the sexes with a Mann-Whitney *U*-test. To test for an order effect we conducted a two-way ANOVA of order and treatment on rank-transformed agonistic scores. To better understand the basis of the order effects we conducted a Wilcoxon matched-pairs signed rank test on paired pretreatment and treatment scores for all three treatments. Statistical significance was accepted when  $P \leq 0.05$ . Values reported are means  $\pm$  SE.

## RESULTS

From 15 January to 22 February 2000, we exposed 30 Willow Flycatchers (17 female and 13 male; 20 at Chomes and 10 at Bolson) to simulated territory intrusions. The birds responded strongly to simulated intrusions by conspecifics (i.e., flycatcher vocalizations), and the aggressive responses to this treatment were significantly greater than to either the cuckoo or the random noise treatment ( $\chi_r^2 = 33.9$ ,  $P < 0.001$ ); responses to the latter two did not differ significantly (Fig. 1). There was no significant difference between females and males in the mean agonistic response toward the conspecific treatment ( $2.1 \pm 0.3$  and  $2.8 \pm 0.2$ , respectively;  $U = 146$ ,  $P = 0.12$ ).

We found no significant interaction between order and treatment ( $F_{4,81} = 1.4$ ,  $P = 0.25$ ), but there were higher agonistic scores for later treatments ( $F_{2,81} = 4.9$ ,  $P = 0.01$ ). However, we found no difference between the pretreatment and treatment scores for the random noise treatment ( $T = -4.5$ ,  $P = 0.83$ ), a greater pretreatment than treatment score for the Lesser Ground Cuckoo treatment ( $T = -64.5$ ,  $P < 0.001$ ), and greater treatment than pretreatment score for the conspecific treatment ( $T = 203$ ,  $P < 0.001$ ). Thus, while there was an order effect, this was simply due to "carryover" responses from the conspecific treatment; flycatchers did not specifically respond to the random noise or Lesser Ground Cuckoo treatments.

TABLE 1. The behavioral category index used for scoring the agonistic responses exhibited by Willow Flycatchers wintering in Costa Rica that were exposed to simulated territory intrusions (STI). The intrusions consisted of 4-min exposures to three randomized playback treatments—Willow Flycatcher vocalizations, Lesser Ground Cuckoo vocalizations, and random noise—separated by 4-min periods of no treatment. The STI area was a 20 m diameter circle located in the approximate center of each flycatcher's territory.

Behavioral category	Description of behavior	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 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 was 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 was greater than the total number of flycatcher vocalizations during the previous treatment	1
Aggressiveness to decoy	No observable flycatcher response to decoy during the treatment	0
	Flycatcher flew or perched within 1 m of decoy during the treatment	0.5
	Flycatcher made physical contact with decoy during the treatment	1
Agonistic visual displays <sup>a</sup>	No agonistic visual displays observed during the treatment	0
	Flycatcher displayed in the territory, but outside the STI area, during the treatment	0.5
	Flycatcher displayed within the STI area during the treatment	1

<sup>a</sup> Agonistic visual displays included rapid tail-flicking or pumping, crest-raising, wing-flicking, extension or puffing of the body feathers, bill snapping, and song flight.

Typical agonistic responses of both sexes 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) stereotypical agonistic visual displays; and (4) direct flights toward or physical contact with the taxidermy decoy. Willow Flycatchers responded with vocalizations almost immediately to the flycatcher treatment. Greatly increased calling rates (whits, wheeps, and chur/trills) were accompanied by rapid and direct movements toward the speaker location.

We recorded a total of six vocalizations given by both females and males in response to 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 vocalization described by Sogge et al. (2001) on the breeding grounds. The writ-tu/wee-oo call, heard commonly during the breeding season, was not noted during the experiment or during natural intraspecific interactions.

During the experiment we observed a total of six stereotyped agonistic visual displays given by both sexes. These included rapid tail-flicking or pumping, crest-raising, wing-flicking, wing-fluttering, spread (extension or puffing of the body feathers), and song flights accompanied by rapid bill-snapping. These displays, almost always accompanied by songs and calls, were given independently of each other as well as in a variety of combinations, and individuals often

perched in the open while displaying. The most common agonistic visual displays were crest-raising with simultaneous rapid tail-pumping or rapid wing-flicking. Highly agitated flycatchers displayed with wing-fluttering and spread accompanied by the chur/kitter vocalization, rapid wheep calls, or the 'squeaks and twitters' vocalization. Song flights, whereby flycatchers emitted both songs and calls while flying to perches, were accompanied by 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 contacted the taxidermy decoy. Another six flycatchers (four females and two males) made multiple direct flights that came within 1 m of the decoy.

## DISCUSSION

Resident wintering Willow Flycatchers at our Costa Rica study sites responded strongly to simulated intraspecific territory intrusions. The behaviors recorded in response to the conspecific playbacks were similar to those described by Gorski (1969) for wintering Willow Flycatchers in Panama, and to those noted by Koronkiewicz (2002) during natural intraspecific encounters. The same behaviors are used in defense of breeding territories (Sedgwick 2000), though writ-tu/wee-oo calls—a common breeding season vocalization—were not heard during our winter study.

Both male and female Willow Flycatchers vocalized during our simulated territory intrusions. This is

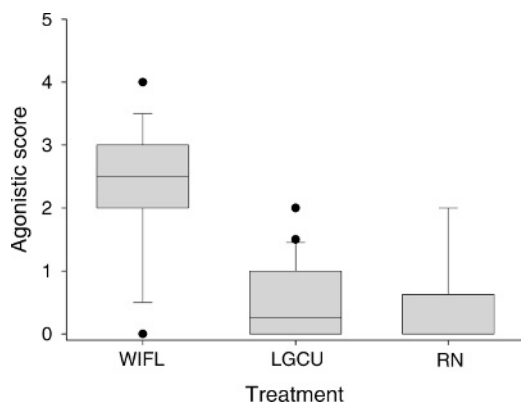


FIGURE 1. Box-plots of the agonistic scores of 30 wintering Willow Flycatchers in Costa Rica exposed to simulated territory intrusions, which consisted of three randomized playback treatments: WIFL = Willow Flycatcher vocalizations; LGCU = Lesser Ground Cuckoo vocalizations; and RN = random noise. Response to flycatcher vocalizations was significantly greater than to the other two treatments. Each box plot represents the 25th and 75th quartiles with the solid line indicating the median. The upper and lower whiskers indicate the 10th and 90th percentiles, respectively. Outliers are shown as black dots. The values of the median and 25th quartile for random noise were both zero, and therefore overlap.

consistent with the findings of Rappole (1995), who noted that both sexes sing in the few New World flycatcher species known to use advertising song on the wintering grounds (Yellow-bellied Flycatcher, Least Flycatcher, and Say's Phoebe [*Sayornis phoebe*]). This phenomenon of frequent singing by wintering females contrasts with behavior on the breeding grounds, where female song is thought to be uncommon in Willow Flycatchers (Sedgwick 2000). However, researchers using targeted mist-netting techniques during the breeding season have captured female Willow Flycatchers that sang and responded aggressively toward conspecific broadcasts (Sogge et al. 2001), and it may be that female song during the breeding season is more common than is currently believed.

The pattern of higher agonistic scores for later treatments during the intrusions demonstrates that the 4-min period between playback trials was not adequate to eliminate "carryover effects" from the conspecific treatment. Ideally, individuals would have received different treatments, such that no bird was exposed to more than one treatment, but this would have required more flycatchers than were present at the study sites. Another option would have been to conduct each treatment for an individual on different days. However, because the response to conspecific treatment was so much greater than to the controls, carryover effects did not mask the main effect of higher response to the flycatcher vocalizations.

Female and male responses to simulated conspecific territory intrusion were not significantly different. This may allow both sexes to occupy the same habitat type at our Costa Rica study sites (Kororkiewicz 2002, Koronkiewicz et al. 2006), and female flycatchers to supplant males and maintain and defend long-term winter territories in the presence of male territory holders and floaters. We believe that males do not have an inherent advantage in aggressive territorial encounters because male and female flycatchers are very similar in size and appearance. This differs from sexually dimorphic species, which exhibit sexual habitat segregation in winter, e.g., Prairie Warbler (*Dendroica discolor*; Latta and Faaborg 2001), American Redstart (*Setophaga ruticilla*; Parrish and Sherry 1994, Marra 2000), Hooded Warbler (*Wilsonia pusilla*; Stutchbury 1994), and Black-throated Blue Warbler (*Dendroica caerulescens*; Wunderle 1992, 1995). For these dimorphic species, the larger body size and brighter coloration of males may provide an agonistic advantage over females, such that males maintain territories in high-quality habitats while females are relegated to territories in suboptimal habitat.

Willow Flycatchers of both sexes responded almost immediately with songs and calls during the conspecific playback treatment. This suggests that vocalizations may be one of the primary behavioral mechanisms used to detect conspecific intruders and to defend winter territories. Furthermore, the aggressive response of flycatchers toward the experiment decoys, all of which were of other *Empidonax* species, may indicate that territorial birds cue primarily on vocalizations to determine if an "intruding" congener is a Willow Flycatcher. Although the conspecific vocalizations we used were recorded on the breeding grounds, they elicited strong responses from the wintering flycatchers. It is not known whether birds would respond differently, in the types of behaviors elicited or the magnitude of response, to vocalizations recorded on the wintering grounds.

Our experiment demonstrates that Willow Flycatchers use a wide array of behaviors in defense of their winter territories, and that the level of agonistic response to simulated intrusions is similar among females and males. However, it is possible that males and females may differ in their relative use of specific behaviors or vocalizations during winter territory defense; additional research could provide insights into such subtleties. In addition, the physiological mechanisms underlying the territorial behavior of female Willow Flycatchers in the nonbreeding season are unknown, and warrant further study. Additional studies of other Neotropical migrant passerines are needed to determine the degree to which sexual habitat segregation during winter is influenced by the degree of sexual dimorphism among wintering migrant species.

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