Conservation Implications of Golden-winged Warbler Social and Foraging Behaviors during the Nonbreeding Season*

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Abstract. We used radiotelemetry and observations of color-banded birds in Costa Rica and Nicaragua to characterize the social system and foraging behavior of Golden-winged Warblers (*Vermivora chrysoptera*) at the nonbreeding grounds, and we assessed how these behaviors affected intraspecific spacing and home-range size. Golden-winged Warblers spent the majority of their time associating with mixed-species flocks composed of migrant and resident species. Males were territorial, responding aggressively to broadcast vocalizations and exhibiting a high degree of within- and among-season site fidelity. We rarely observed males flocking with other male Golden-winged Warblers, and there was little overlap of neighboring male home ranges. In contrast, female home ranges overlapped extensively with neighboring male home ranges. Home-range sizes did not differ between sexes but were larger in Costa Rica (8.77 ± 0.92 ha) than in Nicaragua (4.09 ± 1.30 ha). Home ranges were larger than reports of most other migratory parulids, and we hypothesize that large home-range size and high propensity to join mixed-species flocks result from the species' specialized foraging behaviors. The predominant foraging behavior involved probing hanging dead leaves and epiphytes for arthropods. Although this foraging strategy can be highly effective, it is noisy and reduces vigilance, which may explain the propensity for joining mixed-species flocks because group living can reduce predation risk. Our results indicate that the nonbreeding season behaviors of Golden-winged Warbler have important conservation implications because mixed-species flocks can be disrupted by habitat loss and fragmentation, and because specialized foraging requirements, large home ranges, and territorial behavior reduce the potential density at which the species can occur.

Key Words: behavioral ecology, mixed-species flocks, site fidelity, social system.

Little is known about the social and foraging behaviors of long-distance migratory birds during the nonbreeding season, yet these behaviors have important conservation implications because they affect space use, energy expenditure, susceptibility to predation, habitat

requirements, and hence population density and survival (Crook 1970, Rappole and Morton 1985, Sutherland 1998, Rappole et al. 2003, Morton and Stutchbury 2005). A lack of information on basic behavioral ecology limits efforts to conserve these species, many of which are declining, possibly due to events occurring on the nonbreeding grounds (Rappole et al. 2003, Sherry et al. 2005, King et al. 2006, Sauer et al. 2008, Calvert et al. 2009).

Greenberg and Salewski (2005) summarized the literature on Neotropical–Nearctic migrant social systems during the nonbreeding season and classified species according to the following aspects of sociality: regional movements, local tenacity, territoriality, group size, and tendency to occur in mixed-species flocks. High variability exists among species with respect to each of these components, and within species, variation exists among populations and between sexes. Important factors thought to explain variation in social systems include foraging behavior and predator avoidance behavior (Buskirk 1976, Pulliam and Millikan 1982).

Research on the influences of foraging behavior on sociality has revealed several common patterns in migratory birds during the nonbreeding season. In general, most studies support hypotheses predicting that species exploiting rapidly renewing, defensible resources should have smaller home ranges and be more territorial than species exploiting ephemeral resources (Brown 1969, Pulliam and Millikan 1982). For example, many frugivorous migrants such as Swainson's Thrushes (*Catharus ustulatus*) and Eastern Kingbirds (*Tyrannus tyrannus*) move over large regions in search of preferred fruit (Rappole and Morton 1985). In contrast, many insectivorous migrants such as Black-throated Blue Warblers (*Setophaga caerulescens*) and Ovenbirds (*Seiurus aurocapilla*) maintain small territories within seasons and exhibit high site fidelity among seasons (Rappole and Warner 1980, Wunderle 1992, Sherry and Holmes 1996). Several frugivores also maintain territories (Latta and Faaborg 2002; Brown and Sherry 2008; Townsend et al. 2010, 2012), which suggests that social behavior is influenced less by resource type than it is by the abundance and temporal variability of resources. In addition, most published evidence supports theory predicting that species exploiting pulsed resources should occur in larger groups than species that rely on stable resources (Zahavi 1971, Greenberg and Salewski 2005).

Predation risk may be at least as important as resource exploitation strategies in influencing group size and propensity to occur in mixed-species flocks (Morse 1977, King and Rappole 2000). Survival probability can be lower for solitary individuals than for individuals in flocks (Page and Whitacre 1975), and it has been noted that flock formation is rare on islands lacking predators (Willis 1972). However, the importance of predation pressure does not diminish other benefits of flocking such as increased food intake via social enhancement (Krebs et al. 1972, Sridhar et al. 2012), and it seems likely that many migrant birds that participate in mixed-species flocks do so for multiple reasons.

Golden-winged Warblers (*Vermivora chrysoptera*) are one of the most rapidly declining Neotropical–Nearctic migrants (Chapter 1, this volume), yet little is known about its nonbreeding season ecology. Recent studies suggest that Golden-winged Warblers are patchily distributed and occur at low densities throughout their nonbreeding range (Chapter 1, this volume). Golden-winged Warblers can occur in multiple forest types, but they are strongly associated with specific microhabitat characteristics such as hanging dead leaves and epiphytes (Chandler and King 2011). Prior anecdotal observations suggested that Golden-winged Warblers forage by probing these substrates while in mixed-species flocks (Buskirk et al. 1972, Morton 1980, Tramer and Kemp 1980); however, until now no quantitative studies of Golden-winged Warbler nonbreeding season foraging and social behaviors have been conducted. Without this information, it is impossible to understand the mechanisms governing spatial variation in density during the nonbreeding season, which is necessary for effective conservation planning (Sutherland 1998). The objectives of this study were to (1) quantify Golden-winged Warbler social system and foraging behavior in terms of within- and among-season site fidelity, territoriality, and mixed-species flock participation; and (2) assess how these behaviors are related to home-range size and overlap, which are important determinants of population density. When possible, we assessed whether males and females differed with respect to each of these behaviors because such differences could influence sexual segregation among habitats (Marra 2000).

METHODS

Field Methods

We studied social and foraging behaviors of Golden-winged Warblers in Costa Rica during three nonbreeding seasons: December 2006–March 2007, October 2007–March 2008, and January–March 2009, and during two nonbreeding seasons in Nicaragua: January–March 2012 and February–March 2013. We used radiotelemetry to collect data on site fidelity, home-range size, and foraging behavior. Telemetry was necessary because Golden-winged Warblers are generally too silent and move too rapidly to track without telemetry in the structurally complex habitats in which they occur, as can also be true on the breeding grounds (Streby et al. 2012; Chapter 5, this volume). We captured individuals using mist nets, broadcast vocalizations, and decoys. We banded each individual with a unique U.S. Geological Survey metal band and two or three unique combinations of color bands. We determined sex and age using plumage characteristics, but we could not reliably age several individuals, and we therefore excluded age from our analyses.

We began tracking each bird one day after attaching a VHF radio transmitter using the backpack harness design of Rappole and Tipton (1991). Most transmitters weighed 0.43 g (Holohil Systems Ltd., Ontario, Canada) with an expected battery life of 21 days, although we used some 0.27-g Holohil units and 0.35-g Blackburn units (Blackburn Transmitters, Nacogdoches, TX) in Nicaragua. All transmitters weighed <5% of body mass, which averaged 8.7 g in both countries. We relocated birds every 1–2 days, and we tracked individuals for 2–4 hr per day. During our first season in Costa Rica, we recorded bird locations with a GPS unit (Garmin Ltd., Olathe, KS) every 30 min, but only when we saw the bird. However, the resulting data did not adequately reflect space use because some birds were difficult to see while in dense vegetation or high in the canopy. Therefore, in the latter two seasons, we recorded locations every 30 min regardless of whether we saw the bird. When we did not see birds, we determined approximate locations by triangulation or signal strength, which we calibrated from visual observations. We stayed >5 m from birds in an effort to avoid influencing their behavior. In Nicaragua, we initially recorded locations every hour, but after the first four birds removed

their transmitters after four days, we recorded locations ≥20 min apart. At both study sites, we continued tracking each individual until battery failure or bird mortality. The only mortality event we observed in Costa Rica involved depredation by a striped palm pit viper (*Bothriechis lateralis*) that consumed a bird with an active transmitter. In Nicaragua, we recovered one dead individual, but the cause of mortality was unknown.

Home-Range Size and Overlap

We estimated home-range size using bivariate normal kernel density estimators (Worton 1989). Kernel density estimators yield utilization distributions, which are the relative probability of an individual occurring at each location in its home range. We characterized home-range size using 50% and 95% intensity levels. We regarded 50% kernels as core areas (Townsend et al. 2010). We excluded individuals for which we recorded <15 locations because it was not possible to estimate the kernel bandwidth for those individuals.

As a measure of territoriality and social tolerance, we computed the overlap of 50% kernel home ranges using the volume intersection index described in Fieberg and Kochanny (2005) and implemented in the R package `adehabitat` (Calenge 2006). For 50% kernels, the index ranges from 0.0 (no overlap) to 0.5 (complete overlap). We used 2 × 2 factorial ANOVAs to test if home-range size differed between sexes and between Costa Rica and Nicaragua. We used a similar approach to test for differences in home-range overlap between male–male and male–female neighbors.

Social System

We assessed site fidelity using our telemetry data and by monitoring color-banded individuals over multiple nonbreeding seasons. We considered an individual to exhibit high within-season site fidelity if it maintained a home range during the course of tracking and resighting. We considered individuals located during multiple seasons to exhibit high among-season site fidelity if they were located ≤100 m from their previous home range. In Costa Rica, we searched for birds that had been color banded in previous years by making monthly visits to three locations within each home range, and we broadcast Golden-winged Warbler songs and chip notes for 30 min or until

we encountered the marked bird. We did not conduct resighting efforts in Nicaragua.

We assessed territoriality by observing the response of birds to broadcast vocalizations and decoys (clay mounts) of conspecifics used to capture birds. Birds that attacked the mount were considered to be territorial. Other behaviors in response to call broadcast and decoys that we considered to reflect territoriality, as opposed to mere curiosity, included chipping and singing, rapid position switching, and feather raising (Rappole and Warner 1980). Chipping and singing were never heard without the call broadcast stimuli.

In Costa Rica, we recorded data on mixed-species flock participation and composition at 30-min intervals while radio-tracking. We classified Golden-winged Warblers as flocking, not flocking, or associating with mixed-species flocks. Following Hutto (1987), we classified individuals as flocking if they were ≤25 m from groups of other species and moving in the same direction. We classified Golden-winged Warblers as "associating" with mixed-species flocks if they occurred ≤25 m from groups of other species but were not moving with the flock. For instance, we occasionally observed Golden-winged Warblers associating with large flocks of frugivores that spent >20 min in a single tree. We collected mixed-species flock composition data continuously during each tracking period, and we compiled a list of all species that were observed flocking with Golden-winged Warblers.

Foraging Behavior

We recorded foraging observations exclusively on radiomarked individuals in Costa Rica and Nicaragua. In Costa Rica, we recorded data on the first foraging maneuver we observed during each 30-min interval. Foraging data included the height that the bird was above the ground; the height of the tree; the foraging maneuver, including glean, probe, sally, hawk, or flush; and the substrate on which the maneuver occurred: open live leaf, rolled live leaf, dead leaf, flower, bark, moss or lichen, bromeliad, or miscellaneous epiphyte. We were unable to adequately measure foraging rate because it was difficult to watch radiomarked birds for prolonged periods due to their rapid movements within dense vegetation. In Nicaragua, we recorded the height that the bird was above the ground but not the other foraging variables.

To determine if foraging behavior differed between sexes or among the three flocking states, we used mixed-effects models that allowed for inference about variation within and among individuals. We modeled height at which birds foraged and tree height as normally distributed response variables and treated variation among individuals as a random effect. Models were equivalent to two-way ANOVA models with an additional error term for random variation among individuals. Foraging maneuver is a categorical variable, but because 99% of observations were probes or gleans, we modeled maneuver as a binomial response variable. Models were fit in Program R (ver. 3.0.1; R Development Core Team 2013) using the lme4 package (Bates et al. 2013). We tested the effects of sex and flocking state using likelihood ratio tests applied to models with and without each effect. We used a two-sample t-test to test for differences between sexes.

RESULTS

Home-Range Size and Overlap

We radio-tracked a total of 39 Golden-winged Warblers in Costa Rica (n = 26) and Nicaragua (n = 13, Figure 11.1). In Costa Rica, the battery life of transmitters ranged from two to 26 days (median = 12 days). Premature battery failure prevented us from acquiring >15 location points to calculate kernel-based utilization distributions for six individuals. Of the 20 individuals with a sufficient number of locations for home-range analysis, 17 were males and three were females, and we recorded an average of 31.6 locations for each of these individuals. In Nicaragua, 10 of the 13 radiomarked individuals had sufficient data for analysis, and we recorded an average of 30.1 locations for each of eight males and two females.

Home-range size was similar between sexes in both countries (Figure 11.2); however, our sample size was small, with only five females included in the analysis. Estimates of 50% home-range size were 0.44–2.52 ha, and we found no effect of sex ($F_{1,26}$ = 0.49, P = 0.49) or of the interaction of sex and country ($F_{1,26}$ = 0.041, P = 0.84). However, there was an effect of country alone ($F_{1,26}$ = 8.78, P < 0.01), with home-range sizes in Nicaragua averaging less than half of those in Costa Rica (Table 11.1).
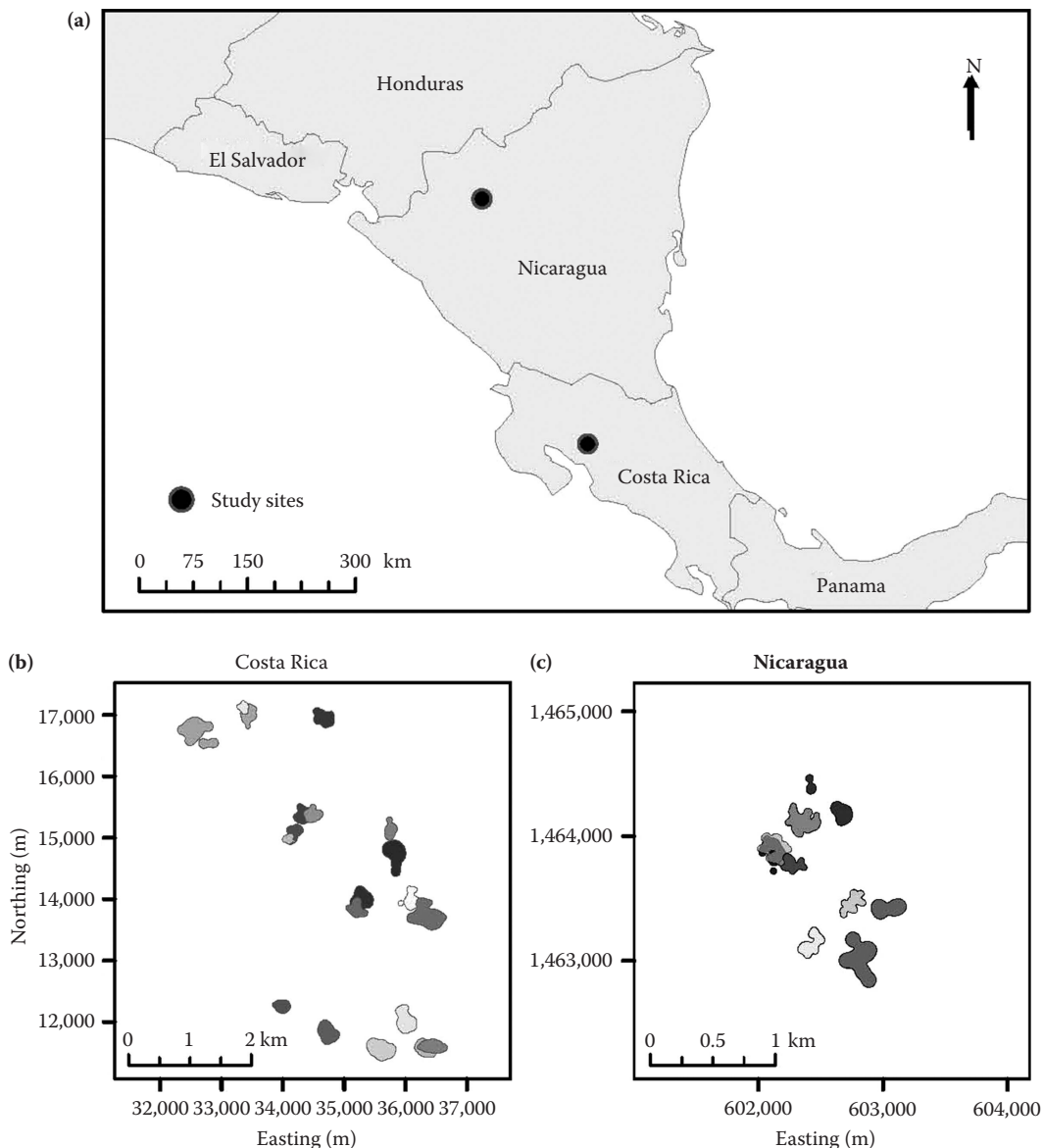
Figure 11.1. The two study sites (a), and the distribution of Golden-winged Warbler home ranges during the nonbreeding season in Costa Rica (b) and Nicaragua (c).

We obtained similar results for 95% home-range sizes with an area of 2.3–19.5 ha in Costa Rica and 2.48–10.82 ha in Nicaragua (Table 11.1).

Home ranges of neighboring males did not overlap extensively (Figure 11.3). The overlap of 50% core areas was higher for male–female neighbors than for male–male neighbors. Even with a sample of only three male–female neighbors and two male–male neighbors in Costa Rica, home-range overlap was different between the two groups ($t_2 = 3.78$,

P = 0.031). For the male–male neighbors, overlap occurred only in the outer extremes of the home range, and not in the core areas. We found similar results in Nicaragua. Core areas did not overlap in one set of neighboring males, but as in Costa Rica, male–female home-range overlap was extensive, ranging from 21.7% to 51.3% (Figure 11.3). In Nicaragua, we observed one instance of female–female home-range overlap, but one of the individuals was not radiomarked. Relying on resighting data
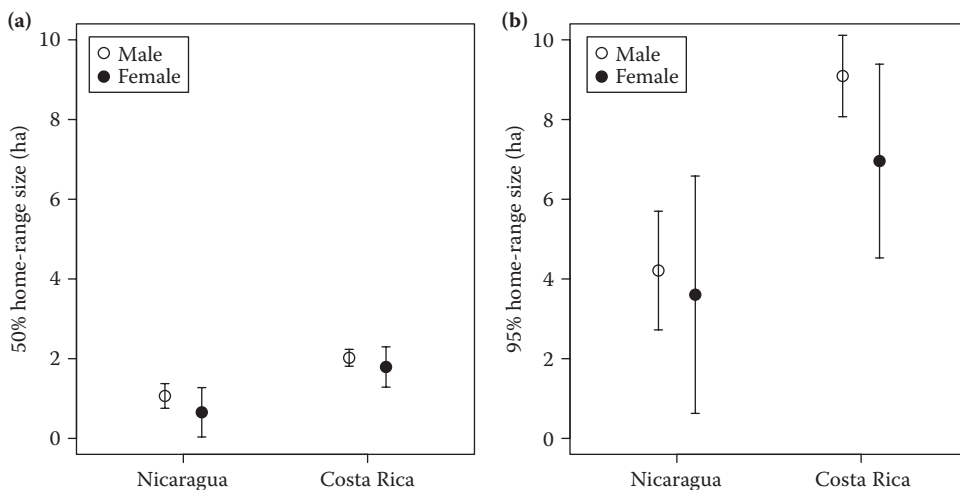
Figure 11.2. Home-range size (±1 SE) for 50% contour (a) and 95% contour (b) by sex and country of Golden-winged Warblers during the nonbreeding season.

TABLE 11.1
Summary statistics (mean, standard deviation, minimum, and maximum) of Golden-winged Warbler home-range sizes (50% and 95% kernel home-range percentiles).

Country	Percentile (%)	Mean	SD	Min	Max
Costa Rica	50	1.99	0.95	0.44	4.00
	95	8.77	4.69	2.31	19.50
Nicaragua	50	0.98	0.60	0.49	2.52
	95	4.09	2.48	2.22	10.82

Twenty individuals were tracked during three nonbreeding seasons 2006–2009 in Costa Rica, and 10 individuals were tracked during two seasons in Nicaragua. Home-range size units are hectares.

from a nonradiomarked individual for home-range delineation is problematic due to potentially low detection probability, but we include the overlap information in Figure 11.3 as anecdotal information.

Site Fidelity and Territoriality

In both Costa Rica and Nicaragua, male and female Golden-winged Warblers maintained home ranges characterized by one or two core areas where most activity was concentrated (Figure 11.4). In some instances, activity centers shifted slightly among days, with extensive interday overlap (Figure 11.5). Patterns were consistent for birds tracked both early and late in the season, suggesting that Golden-winged Warblers exhibit high site fidelity throughout the entire season.

In Costa Rica, three Golden-winged Warblers exhibited movement patterns inconsistent with the general patterns described earlier. We relocated one individual, a male, the day following capture and then never saw it again despite three days of searching the surrounding area using radiotelemetry and broadcast vocalizations. Probability of detection with playback is extremely high (0.97; Chandler and King 2011), and it is unlikely that this individual remained within the study area. If the bird moved to another location within the study area, the radio must have been defective because we were able to detect transmitter signals at distances >1 km and the entire study area was included within that range. Alternatively, the individual may have been depredated and the transmitter destroyed.
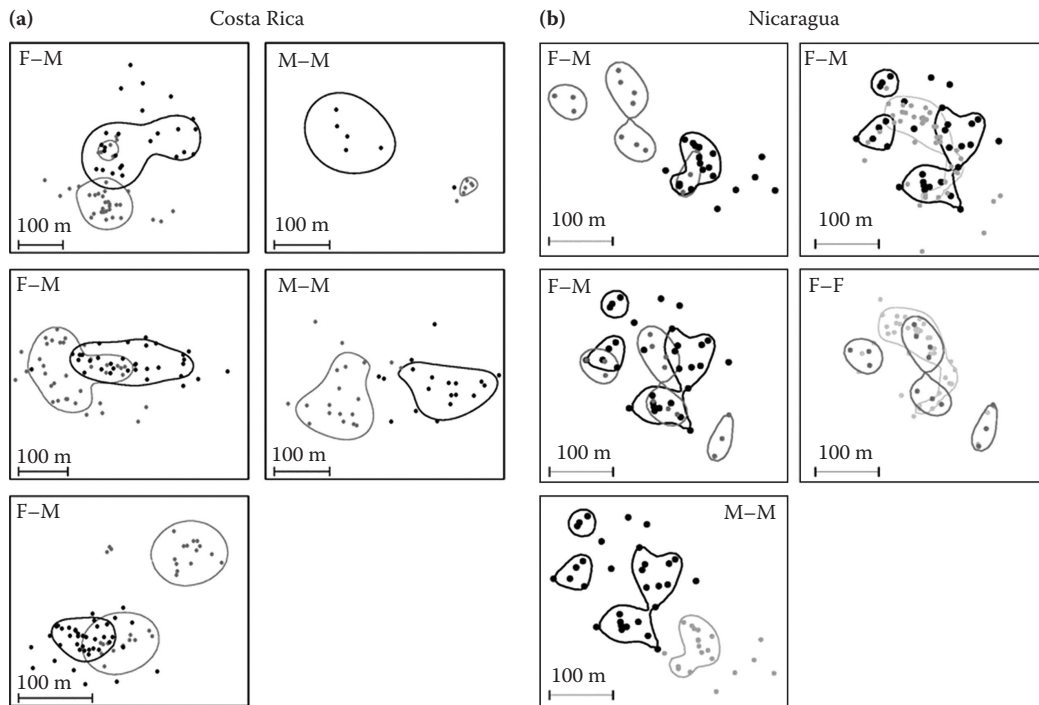
Figure 11.3. Overlap of 50% home ranges for neighboring Golden-winged Warblers during the nonbreeding season in Costa Rica and Nicaragua. The sex of members of neighboring pairs is indicated by F–F, M–F, or M–M. Only neighbors that were radio-tracked simultaneously and had ≥5 recorded locations are shown.

Two other males made brief long-distance forays. In each case, the bird moved from patches of secondary forest to contiguous forest ~2 km away and then returned to its home range within 24 hr. Foray locations were not included in home-range size calculations. In Nicaragua, three Golden-winged Warblers exhibited similarly uncharacteristic movement patterns. One male traveled 369 m and one female 478 m but returned to their respective home ranges within 24 hr. The other male may have been an early passage migrant or a floater that covered an area much larger than the size of an average home range (Brown and Long 2007). The male was captured at the end of March and frequently moved >150 m between sequential locations and was often difficult to locate. After two days of tracking, we were no longer able to detect the signal from that individual's transmitter in the study area.

Systematic visits to home ranges of color-banded birds throughout all three field seasons in Costa Rica indicated that all relocated individuals remained on their home ranges until the onset of migration. Furthermore, we found all five individuals that we

were able to relocate in subsequent years ≤200 m from their original capture location, including three individuals that we observed during three consecutive nonbreeding seasons. During our two field seasons in Nicaragua, we encountered four of 28 individuals that had been banded prior to our study. Two of the radiomarked males in Nicaragua were originally banded two and four years before, and we recaptured them ≤100 m from their initial capture locations.

Both male and female Golden-winged Warblers showed aggressive responses to broadcast vocalizations and decoys. In Costa Rica, we captured 23 of 26 birds as part of our radiotelemetry study using these stimuli. Each of these individuals flew at the decoy, occasionally making direct contact. We caught the other three individuals (two males and one female) during constant-effort mist netting as part of a separate study (Chandler et al. 2013). Warblers captured without stimuli in systematic mist netting also maintained home ranges suggesting that our sample was not biased toward territorial individuals. In Nicaragua, we captured all birds using broadcast vocalizations, often without decoys.
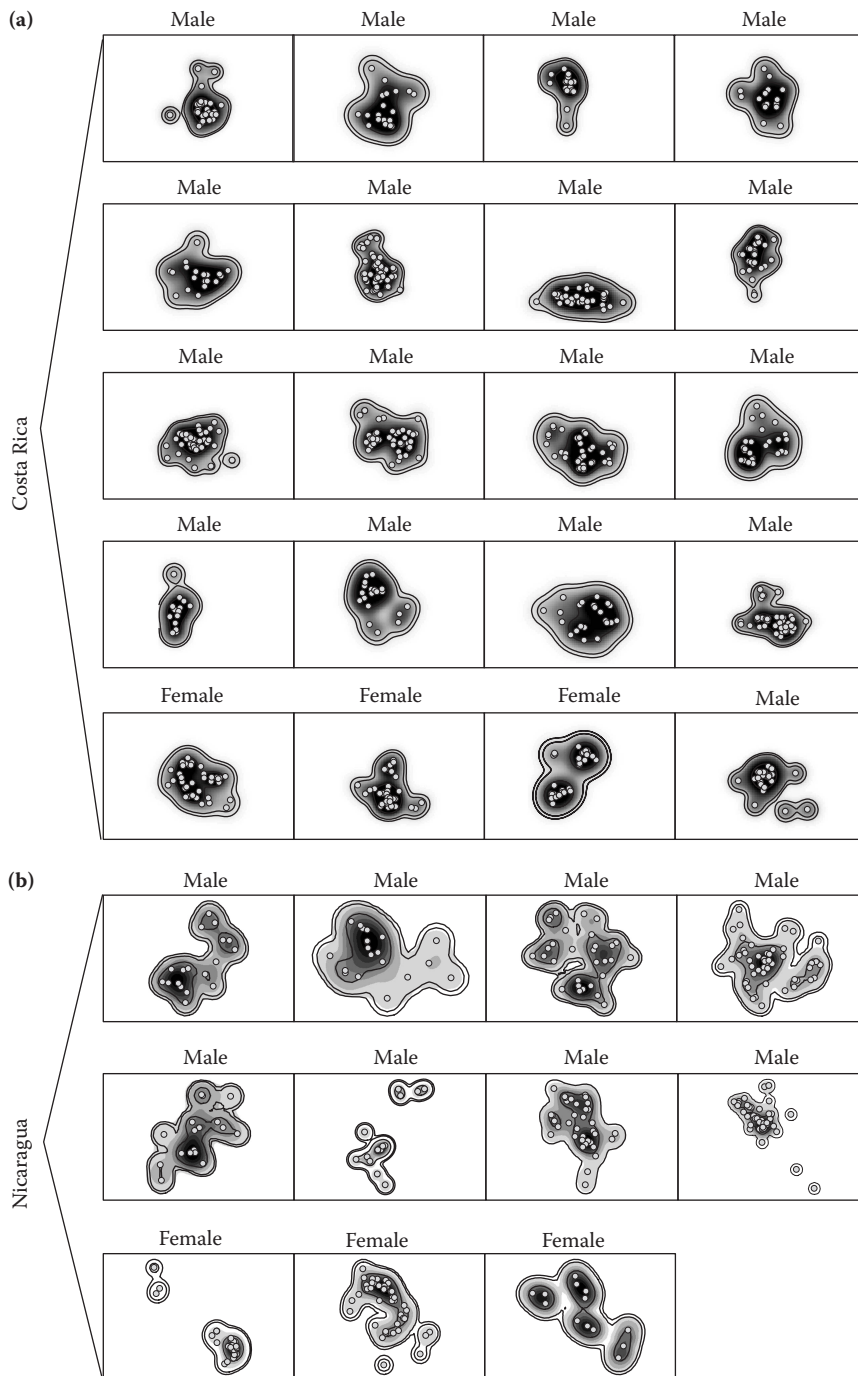
Figure 11.4. Kernel utilization distributions and location points for Golden-winged Warblers during the nonbreeding season in (a) Costa Rica and (b) Nicaragua. Contour lines represent kernel home-range percentiles.
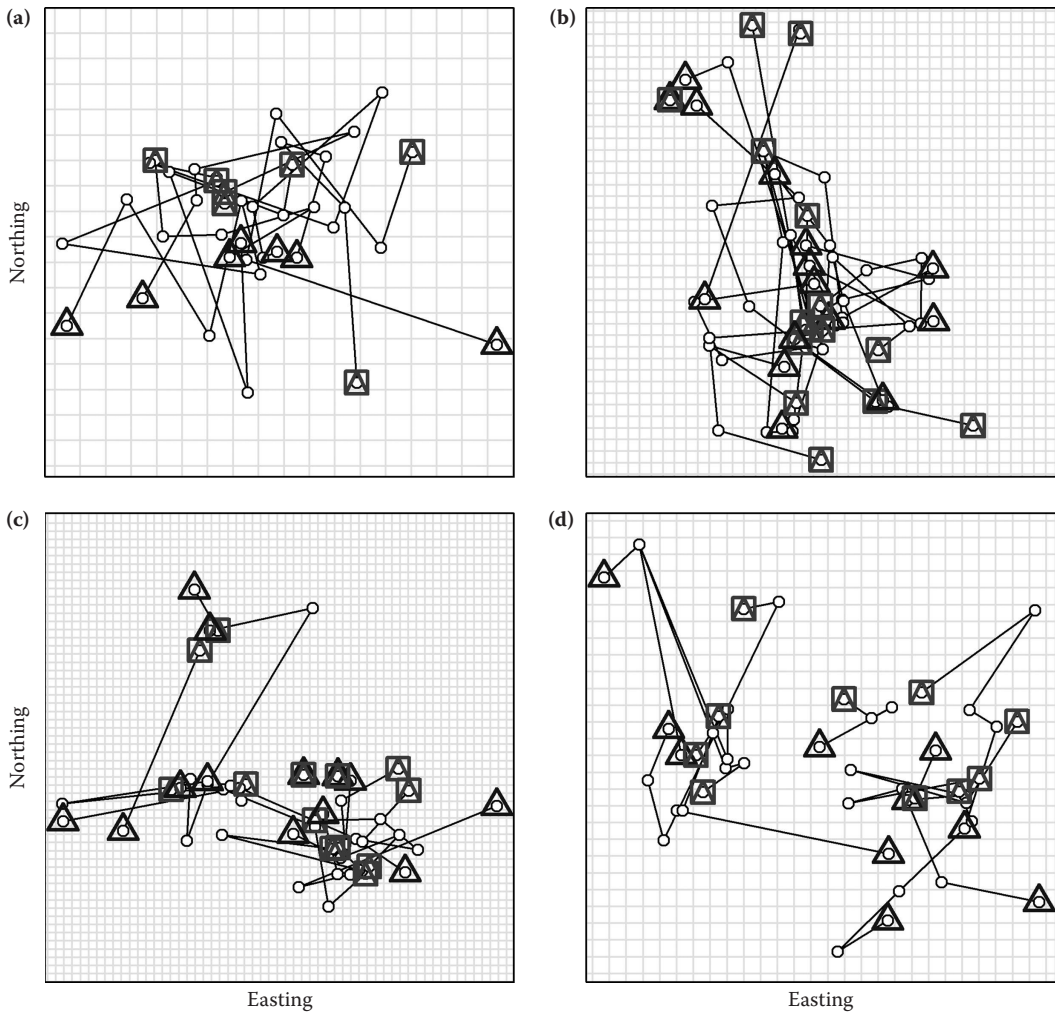
Figure 11.5. Examples of movement patterns for four Golden-winged Warblers (a–d) during the nonbreeding season in Costa Rica. Each tracking episode is represented by segments starting from a triangle and ending at a triangle within a square. Segments represent 30-min intervals. A 10-m grid is provided for scale.

Mixed-Species Flock Participation

We collected mixed-species flock data for 26 Golden-winged Warblers observed on 214 occasions totaling 562 hr. These individuals spent an average of 59% of their time with mixed-species flocks (Figure 11.6), which typically included Common Bush-Tanagers (*Chlorospingus ophthalmicus*) as the nuclear species (Table 11.2). Marked Golden-winged Warblers spent an additional 26% of their time associated with other species in loose flocks without obvious movement cohesion or nuclear species. Thus, we only observed marked Golden-winged Warblers away from flocks 15% of the time. We observed 88 species flocking with Golden-winged Warblers in cohesive flocks. No species was ubiquitously present in these flocks, and both resident and migratory species were common participants (Table 11.2). Flock participation was not related to sex of warblers ($t_9 = 0.148$, $P = 0.89$), although only three females were included in our sample.

Foraging Behavior

Of 293 foraging maneuvers we recorded for 24 color-banded Golden-winged Warblers, 72% were
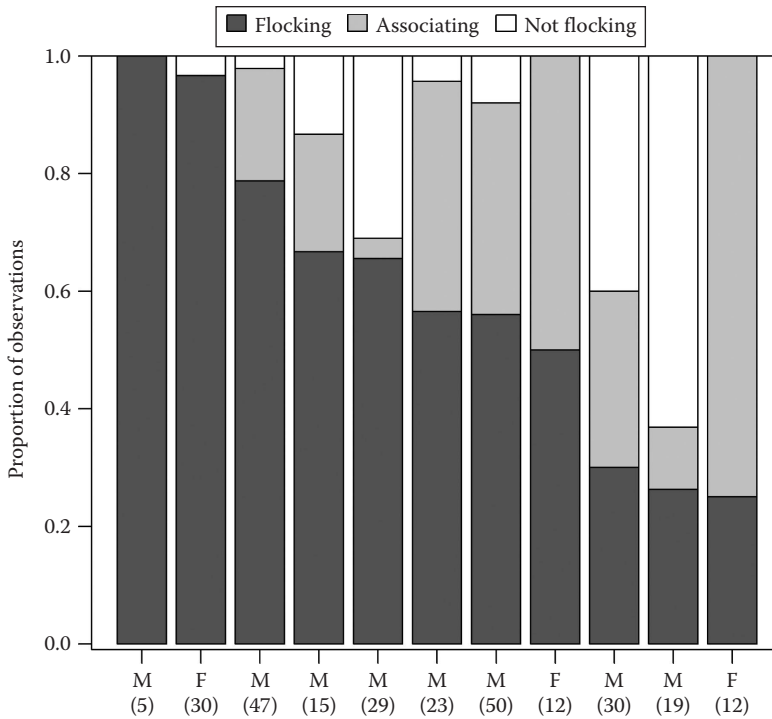
Figure 11.6. Proportion of observations in which 11 individual Golden-winged Warblers were flocking in Costa Rica during the nonbreeding season. Associating refers to cases where an individual occurred with other species but was not moving together in concert. Individuals are ranked by propensity for flocking and referenced by sex (M, male; F, female) with sample size of observations in parentheses.

probes and 27% were gleans (Figure 11.7). Sallies, hawks, hover-gleans, and flush-dives constituted <2% of observations. The most commonly probed substrate was hanging dead leaves (40%), although moss, bark, rolled leaves, bromeliads, and flowers were used to a lesser extent (Figure 11.7). Golden-winged Warblers probe in a specialized fashion that involves inserting the beak and opening it to pry open the leaf or flake off bark. Most of the bark foraging we observed occurred in *Psidium guajava*, which like many other members of Myrtaceae has thin flaking bark. Golden-winged Warblers were the only bird species observed using this resource. The longest foraging maneuvers (>1 min) occurred on individual *Cecropia* sp. leaves. Although *Cecropia* sp. was never a dominant plant species in home ranges of marked Golden-winged Warblers, the large leaves with hooked petioles are easily caught in the canopy. The leaves form tight curls upon desiccation and often host diverse arthropod assemblages (Rosenberg 1997). The only marked warbler that regularly foraged ≥20 m above the ground almost exclusively used *Ocotea* sp. It was not possible to closely observe the foraging behavior of this individual due to the height above the ground at which it foraged.

We found no evidence that any of the foraging variables, including foraging height, tree height, and maneuver differed between sexes or among the three flocking states of flocking, associating, or solitary in Costa Rica (all P-values from mixed effects models >0.05). However, in Nicaragua male foraging height (13.1 ± 1.5 m) was higher than female foraging height (4.2 ± 2.4 m; t_9 = 3.19, P = 0.01). In addition to differences between sexes, we found substantial variation in foraging heights within and among individuals in Costa Rica and Nicaragua (Figure 11.8).

DISCUSSION

We documented the aspects of behavioral ecology during the nonbreeding season, which have important conservation implications for Golden-winged

TABLE 11.2
Co-occurrence probabilities for bird species observed flocking with 26 Golden-winged Warblers on >5% of observation days in Costa Rica.

Species	Resident/ migrant	Co-occurrence probability
Myioborus miniatus	R	0.37
Chlorospingus ophthalmicus	R	0.36
Cardellina pusilla	M	0.36
Setophaga virens	M	0.36
Setophaga pensylvanica	M	0.35
Mniotilta varia	M	0.34
Oreothlypis peregrina	M	0.29
Tangara icterocephala	R	0.18
Vireo philadelphicus	M	0.16
Myiarchus tuberculifer	R	0.16
Mionectes olivacea	R	0.14
Vireo flavifrons	M	0.12
Basileuterus culcivorous	R	0.10
Saltator maximus	R	0.09
Hylophilus decurtatus	R	0.08
Turdus grayi	R	0.08
Basileuterus tristriatus	R	0.08
Elaenia frantzii	R	0.07
Basileuterus rufifrons	R	0.07
Ramphocelus passerinii	R	0.07
Thraupis episcopus	R	0.06
Xiphorhynchus erythropygius	R	0.06
Euphonia hirundinacea	R	0.06
Phlogothraupis sanguinolenta	R	0.05
Piranga rubra	M	0.05
Premnoplex brunnescens	R	0.05

Probabilities represent the mean proportion of telemetry occasions during which a species was observed in flocks with radiomarked Golden-winged Warblers. Anecdotal observations from Nicaragua suggest that flocks there contained similar species.

Warblers. Golden-winged Warblers appear to have larger nonbreeding season area requirements than other long-distance migratory passerines, which may limit their ability to persist in small forest fragments. In Costa Rica, home-range size averaged 8.8 ha, almost 10 times larger than the average of 0.78 ha for Ovenbirds studied by Brown and Sherry (2008). Similarly, Rappole and Warner (1980) reported home-range sizes <1 ha

for 10 species of wintering long-distance migrants. Wood Thrushes (*Hylocichla mustelina*) and Bicknell's Thrushes (*Catharus bicknelli*), both larger-bodied migrant species, maintained smaller nonbreeding season territories (0.44 and 1.41 ha, respectively) than those of Golden-winged Warblers in either Costa Rica or Nicaragua (Winker et al. 1990, Townsend et al. 2010). Golden-winged Warbler home ranges were smaller in Nicaragua than in Costa Rica, and additional research is needed to determine the causes of geographic variation in home-range size.

In addition to large area requirements, male Golden-winged Warblers appeared to be highly territorial during the nonbreeding season. We rarely observed more than one male in mixed-species flocks, and neighboring male home ranges had little overlap. Males also responded aggressively to playback and decoys. Large home-range size and territorial behavior may explain why Golden-winged Warblers are not reported to be abundant anywhere throughout their known nonbreeding range (Johnson 1980, Morton 1980, Orejuela et al. 1980, Powell et al. 1992, Komar 1998, Blake and Loiselle 2000; Chapter 1, this volume).

Territoriality may also affect how Golden-winged Warblers respond to habitat loss because limited habitat can lead to competitive interactions resulting in losers that cannot defend territories. For Ovenbirds in Jamaica, where predation pressure is low, costs and benefits appear to be associated with territorial and nonterritorial social systems (Brown and Sherry 2008). Territorial individuals can access stable resources and minimize space use and energy expenditure, whereas nonterritorial individuals can exploit temporary resources more effectively. Wood Thrushes, in contrast, conform to an ideal despotic population model in which territory owners occur in primary forest whereas floaters occur in lower quality areas (Fretwell and Lucas 1969, Winker et al. 1990). Floaters wander over large areas and incur higher mortality costs (Rappole et al. 1989). We encountered only one Golden-winged Warbler that could have been described as a floater, suggesting that few individuals adopt this strategy at our study sites.

We found some evidence that tolerance of sharing space was higher between sexes than within sexes. Home-range overlap was higher for male–female neighbors than for male–male neighbors. Generally, within zones of
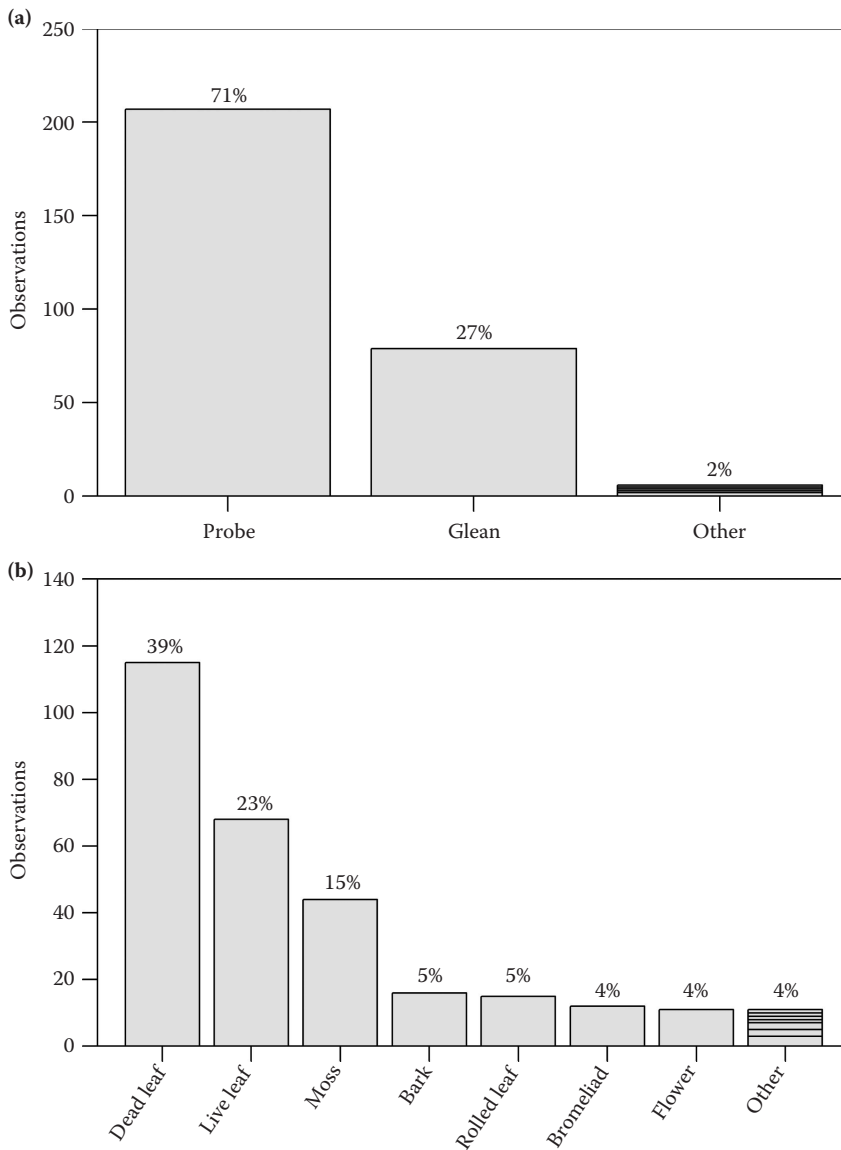
(a)

(b)

Figure 11.7. Bar plots of foraging maneuvers (a) and foraging substrates (b) of Golden-winged Warblers during the non-breeding season. Data are from Costa Rica, 2006–2009.

home-range overlap, male–female neighbors did not occur near each other, although one male in Costa Rica consistently foraged ≤5m from an unbanded female without displaying aggressive behaviors. In one area in Nicaragua, we identified four Golden-winged Warblers (two males and two females) with varying levels of home-range overlap. We resighted one female, which was not radiomarked, multiple times, typically ≤10 m from one of the other radiomarked individuals.

We found no evidence of sexual differences in the foraging behavior of Golden-winged Warblers in Costa Rica. However, males tended to forage higher above the ground than females in Nicaragua. With data on only five females in Costa Rica and two females in Nicaragua, a larger sample is necessary before conclusive statements can be made regarding sex-specific foraging behavior. Furthermore, even with the use of transmitters, it was difficult to record behavioral observations when Golden-winged Warblers were
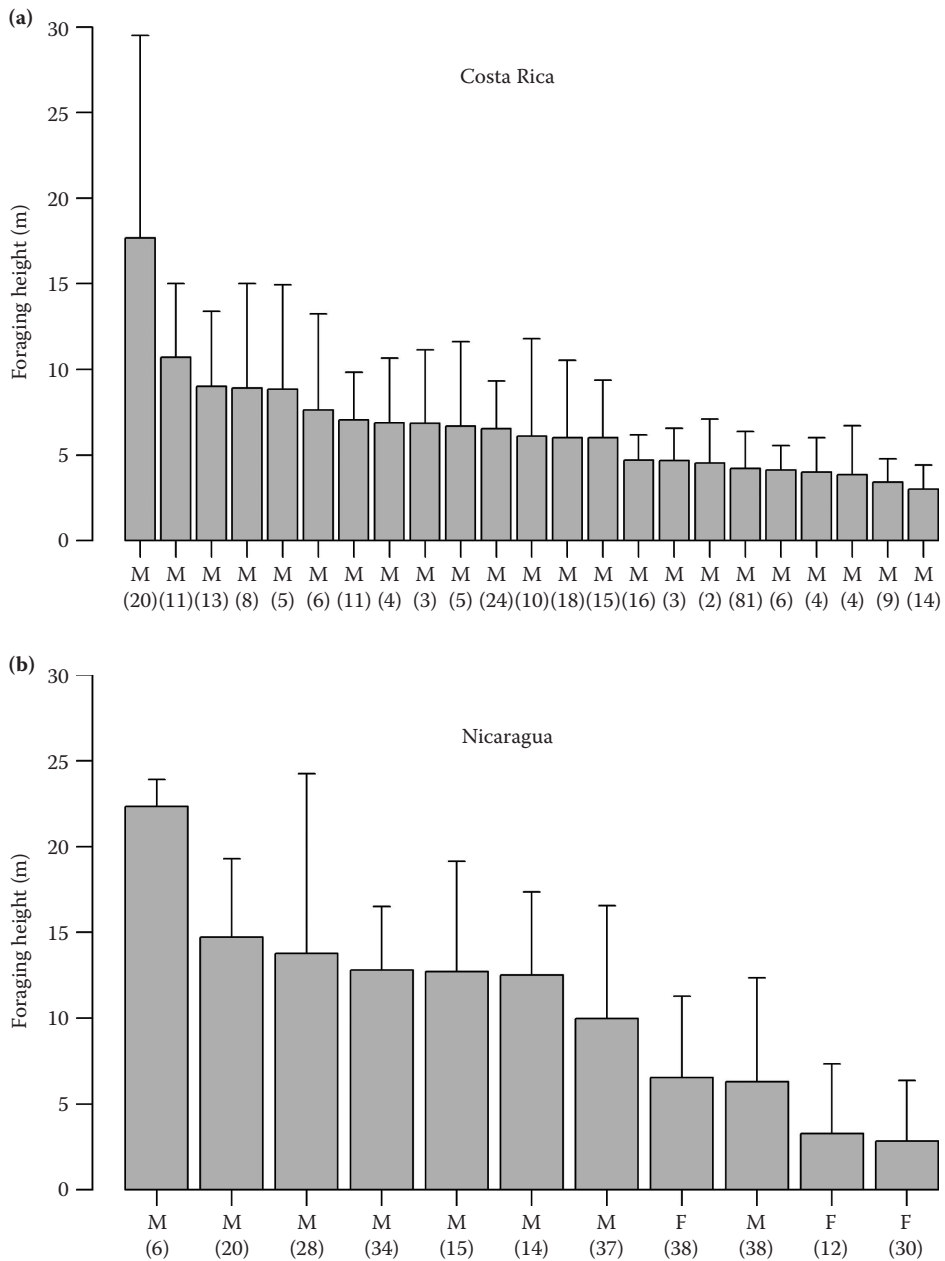
Figure 11.8. Mean foraging heights (+1 SE) for (a) 20 male and three female Golden-winged Warblers in Costa Rica and (b) eight males and three females in Nicaragua monitored using radiotelemetry during the nonbreeding season. Sample size and sex are indicated below each individual's bar.

high in the canopy or in low thickets. Low detectability may have introduced bias because two of the three females we studied in Costa Rica and all three of the females we studied in Nicaragua used dense understory vegetation, and we were only able to record foraging behavior when birds emerged from thickets. Future work could overcome this problem by estimating the probability of detecting individuals in different types of cover as a function of the height of foraging locations in the canopy. Corrections for detectability would shed light on whether males tend to forage higher

in the canopy than females, as has been observed in several other Nearctic migrants (Rappole 1988, Wunderle 1992).

Our finding that male–female tolerance was higher than male–male tolerance differs from studies demonstrating sexual habitat segregation and dominance (Morton et al. 1987, Marra 2000, Latta and Faaborg 2002, Studds and Marra 2005, Townsend et al. 2012). However, male–female tolerance during the nonbreeding season has been observed for many Neotropical–Nearctic migrants, including Prothonotary Warblers (*Protonotaria citrea*), Canada Warblers (*Cardellina canadensis*), and Golden-cheeked Warblers (*Setophaga chrysoparia*; Morton 1980, Rappole et al. 1999). In addition, observations of pairs of Philadelphia Vireos (*Vireo philadelphicus*), Blue-headed Vireos (*Vireo solitarius*), and Gray Vireos (*Vireo vicinior*) suggest that some species may exhibit pair territoriality, as do Stonechats (*Saxicola torquata*) and White Wagtails (*Motacilla alba*; Zahavi 1971, Tramer and Kemp 1982, Gwinner et al. 1994, E. Morton, unpubl. data). In other species, males and females may be randomly distributed within a forest type (Brown and Sherry 2008), or may have horizontally overlapping home ranges, but stratify vertically (Rappole 1988, Wunderle 1992). The reason for higher intersexual tolerance in Golden-winged Warblers is unclear, but we found some evidence that males foraged higher above the ground than females in Nicaragua. However, given our small sample sizes, more research is needed to assess the possibility of vertical resource partitioning. The primary conservation implication of the absence of sexual habitat segregation is that differential rates of habitat loss would not lead to biased sex ratios, an important concern with species such as American Redstarts (*Setophaga ruticilla*) and Bicknell's Thrushes (Marra 2000, Townsend et al. 2012). In spite of high tolerance and overlapping home ranges, an apparent sex ratio bias was observed within our Costa Rica study area (Chandler and King 2011), indicating that males and females may segregate geographically.

Golden-winged Warblers occurred in mixed-species flocks 85% the time and were highly territorial. Many Neotropical resident species that regularly join mixed-species flocks are also territorial and may either defend the flock against conspecifics (Munn and Terborgh 1979) or have distinct territory boundaries and drop out of the flock when these boundaries are crossed (Powell 1979, Munn 1985, King and Rappole 2001).

Territorial flock participants often occur as lone individuals or pairs and will attack conspecifics that attempt to enter the flock (Buskirk 1976, Hutto 1987). Other species, such as Cerulean Warblers (*Setophaga cerulea*), occur with conspecifics within mixed-species flocks and show little conspecific aggression (Bakermans 2008). Such species should be able to occur at higher densities than species that defend flocks against conspecifics. More generally, reliance on mixed-species flocks may increase a species' vulnerability to deforestation and fragmentation because anthropogenic processes can disrupt flocks (Rappole and Morton 1985, Stouffer and Bierregaard 1995, Stratford and Stouffer 1999, Stouffer et al. 2006). Dependence on mixed-species flocks might also suggest that nuclear species, around which flocks are formed, need to be considered in conservation plans; however, the low co-occurrence probabilities we observed in our study suggest that Golden-winged Warblers are not reliant on particular nuclear species.

Our results support the hypothesis that social systems develop as an outcome of resource availability and foraging behavior. Golden-winged Warblers exhibit a specialized foraging strategy during the nonbreeding season in which they primarily probe hanging dead leaves and epiphytes. A gleaning or probing foraging strategy is shared by many resident Neotropical species from several families (Capitonidae, Formicaridae, Furnariidae, Troglodytidae) and some Neotropical–Nearctic migrants (Morton 1980, Remsen and Parker 1984, Greenberg 1987, Rosenberg 1993). Dead leaves provide habitat for numerous large-bodied arthropods, especially roaches (Blattaria), spiders (Araneae), and Orthopterans (Gradwohl and Greenberg 1982, Rosenberg 1993, R.B. Chandler, unpubl. data). Prey density and biomass can be much higher in dead leaves than in live leaves, due to the larger body size and different taxonomic compositions among arthropods (fewer Hymenopterans and Dipterans, Rosenberg 1997). Accessing these food resources, however, requires behaviors and morphological traits that nonspecialized species do not possess (Rosenberg 1993). For example, many dead-leaf foragers, including Golden-winged Warblers, lack rictal bristles that could interfere with probing.

The benefits of accessing abundant food resources in dead leaves are associated with two

important costs. First, dead leaves are much less abundant than live leaves and are patchily distributed (Remsen and Parker 1984). Dead-leaf foragers might therefore be required to travel farther than live-leaf foragers, which may partially explain the large home ranges of Golden-winged Warblers during the nonbreeding season. Second, dead-leaf foraging may increase predation risk because it is a noisy process and precludes vigilance because the entire head of a foraging bird is often inside a curled leaf (Morton 1980). The predator avoidance benefits of mixed-species flocks might therefore explain why virtually all regular dead-leaf foragers participate in mixed-species flocks (Remsen and Parker 1984, Rosenberg 1997).

The reliance on a high-quality, patchily distributed food resource may also explain Golden-winged Warbler territoriality during the nonbreeding season. Arthropod populations in dead leaves can be quickly diminished by avian insectivores, but colonization rate is also high (Gradwohl and Greenberg 1982, Rosenberg 1993). Therefore, successfully defending an area with many dead-leaf clusters could ensure an adequate food supply throughout the nonbreeding season. In accordance with this hypothesis, most dead-leaf-foraging resident species occur as single individuals or pairs in mixed-species foraging flocks and actively defend territories against conspecifics during the nonbreeding season (Munn and Terborgh 1979, Powell 1979).

Our results suggest that the distinctive social and foraging behaviors of Golden-winged Warblers explain why the species exhibits a patchy distribution and low density during the nonbreeding season. These behaviors may also make Golden-winged Warblers vulnerable to habitat loss and fragmentation because they have relatively large area requirements and depend on flocks, which are more common in contiguous forest. However, Golden-winged Warblers use forest fragments and advanced secondary forests that contain vine tangles and hanging dead leaves (Chandler and King 2011). Future research is needed to compare nonbreeding season behavior and survival between fragmented and contiguous forests to assess the quality of these landscapes. Direct energetic measurements and their influences on body condition would also be helpful in identifying suitable areas for targeted conservation and management.

LITERATURE CITED

Bakermans, M. H. 2008. Demography and habitat use of Cerulean Warblers on breeding and wintering grounds. Ph.D. dissertation, Ohio State University, Columbus, OH.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. Lme4: linear mixed-effects models using Eigen and S4, R package version 1.0-5. <http://CRAN.R-project.org/package=lme4> (1 February 2013).

Blake, J. G., and B. A. Loiselle. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. Auk 117:663–686.

Brown, D. R., and J. A. Long. 2007. What is a winter floater? Causes, consequences, and implications for habitat selection. Condor 109:548–565.

Brown, D. R., and T. W. Sherry. 2008. Alternative strategies of space use and response to resource change in a wintering migrant songbird. Behavioral Ecology 19:1314–1325.

Brown, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bulletin 81:293–329.

Buskirk, W. H. 1976. Social systems in a tropical forest avifauna. American Naturalist 110:293–310.

Buskirk, W. H., G. V. N. Powell, J. F. Wittenberger, R. E. Buskirk, and T. U. Powell. 1972. Interspecific bird flocks in tropical highland Panama. Auk 89:612–624.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Calvert, A. M., S. J. Walde, and P. D. Taylor. 2009. Nonbreeding-season drivers of population dynamics in seasonal migrants: conservation parallels across taxa. Avian Conservation and Ecology 4:5.

Chandler, R. B., and D. I. King. 2011. Habitat quality and habitat selection of Golden-winged Warblers in Costa Rica: an application of hierarchical models for open populations. Journal of Applied Ecology 48:1038–1047.

Chandler, R. B., D. I. King, C. C. Chandler, R. Raudales, R. Trubey, and V. J. Arce Chavez. 2013. A small-scale land-sparing approach to conserving biodiversity in tropical agricultural landscapes. Conservation Biology 27:785–795.

Crook, J. H. 1970. Social organization and the environment: aspects of contemporary social ethology. Animal Behavior 18:197–209.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Gradwohl, J., and R. Greenberg. 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. Ecology 63:581–583.

Greenberg, R. 1987. Seasonal foraging specialization in the Worm-eating Warbler. Condor 89:158–168.

Greenberg, R., and V. Salewski. 2005. Ecological correlates of wintering social systems in New World and Old World migratory passerines. Pp 336–358 in R. Greenberg and P. P. Marra (editors), Birds of two worlds: the ecology and evolution of migration. John Hopkins University Press, Baltimore, MD.

Gwinner, E., T. Rödl, and H. Schwabl. 1994. Pair territoriality of wintering Stonechats: behaviour, function and hormones. Behavioral Ecology and Sociobiology 34:321–327.

Hutto, R. L. 1987. A description of mixed-species insectivorous bird flocks in western Mexico. Condor 89:282–292.

Johnson, T. B. 1980. Resident and North American migrant bird interactions in the Santa Marta highlands, northern Colombia. Pp. 239–247 in A. Keast and E. S. Morton (editors), Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC.

King D. I., and J. H. Rappole. 2000. Winter flocking of insectivorous birds in montane pine-oak forests in Middle America. Condor 102:664–672.

King, D. I., and J. H. Rappole. 2001. Mixed-species bird flocks in dipterocarp forests of north-central Burma (Myanmar). Ibis 143:380–390.

King, D. I., J. H. Rappole, and J. P. Buonaccorsi. 2006. Long-term population trends of forest-dwelling Nearctic-Neotropical migrant birds: a question of temporal scale. Bird Populations 7:1–9.

Komar, O. 1998. Avian diversity in El Salvador. Wilson Bulletin 110:511–533.

Krebs, J. R., M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the Great Tit *Parus major* L.—an experimental study. Ibis 114:507–530.

Latta, S. C., and J. Faaborg. 2002. Demographic and population responses of Cape May Warblers wintering in multiple habitats. Ecology 83:2502–2515.

Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. Behavioral Ecology 11:299–308.

Morse, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. Bioscience 27:332–339.

Morton, E. S. 1980. Adaptations to seasonal change by migrant land birds in the Panama Canal zone. Pp. 437–453 in A. Keast and E. S. Morton (editors), Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC.

Morton, E. S., J. F. Lynch, K. Young, and P. Mehlhop. 1987. Do male Hooded Warblers exclude females from nonbreeding territories in tropical forest? Auk 104:133–135.

Morton E. S., and B. J. Stutchbury. 2005. The significance of mating system and nonbreeding behavior to population and forest patch use by migrant birds. Pp. 285–289 in C. J. Ralph and T. D. Rich (editors), Bird conservation implementation and integration in the Americas. U.S. Department of Agriculture, Pacific Southwest Research Station, Albany CA.

Munn, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Ornithological Monographs 36:683–712.

Munn, C. A., and J. W. Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81:338–347.

Orejuela, J. E., R. J. Raitt, and H. Alvarez. 1980. Differential use by North American migrants of three types of Colombian forests. Pp. 253–264 in A. Keast and E. S. Morton (editors), Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC.

Page, G., and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

Powell, G. V. N. 1979. Structure and dynamics of interspecific flocks in a Neotropical mid-elevation forest. Auk 96:375–390.

Powell, G. V. N., J. H. Rappole, and S. A. Sader. 1992. Neotropical migrant landbird use of lowland Atlantic habitats in Costa Rica: a test of remote sensing for identification of habitat. Pp. 287–298

in J. M. Hagan and D. W. Johnson (editors), Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

Pulliam, H. R., and G. C. Millikan. 1982. Social organization in the nonreproductive season. Avian Biology 6:169–197.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

Rappole, J. H. 1988. Intra- and intersexual competition in migratory passerine birds during the non-breeding season. Proceedings of the International Ornithological Congress 19: 2308–2317.

Rappole, J. H., D. I. King, and W. C. Barrow Jr. 1999. Winter ecology of the endangered Golden-cheeked Warbler. Condor 101:762–770.

Rappole, J. H., D. I. King, and J. Diez. 2003. Winter- vs. breeding-habitat limitation for an endangered avian migrant. Ecological Applications 13:735–742.

Rappole, J. H., and E. S. Morton. 1985. Effects of habitat alteration on a tropical avian forest community. Ornithological Monographs 36:1013–1021.

Rappole, J. H., M. A. Ramos, and K. Winker. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. Auk 106:402–410.

Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pp. 353–393 in A. K. Keast and E. S. Morton (editors), Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC.

Remsen, J. V., and T. A. Parker. 1984. Arboreal dead-leaf-searching birds of the Neotropics. Condor 86:36–41.

Rosenberg, K. V. 1993. Diet selection in Amazonian antwrens: consequences of substrate specialization. Auk 110:361–375.

Rosenberg, K. V. 1997. Ecology of dead-leaf foraging specialists and their contribution to Amazonian bird diversity. Ornithological Monographs 48:673–700.

Sauer, J. R., J. E. Hines, and J. Fallon. [online]. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007, version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, MD. <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html> (1 April 2014).

Sherry, T. W., and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. Ecology 77:36–48.

Sherry, T. W., M. D. Johnson, and A. M. Strong. 2005. Does winter food limit populations of migratory birds? Pp. 414–425 in R. Greenberg and P. P. Marra (editors), Birds of two worlds. Smithsonian Institution Press, Washington, DC.

Sridhar, H., U. Srinivasan, R. A. Askins, J. C. Canales-Delgadillo, C. Chen, D. N. Ewert, G. A. Gale, E. Goodale, W. K. Gram, P. J. Hart, K. A. Hobson, R. L. Hutto, S. W. Kotagama, J. L. Knowlton, T. M Lee, C. A. Munn, S. Nimnuan, B. Z. Nizam, G. Péron, V. V. Robin, A. D. Rodewald, P. G. Rodewald, R. L. Thomson, P. Trivedi, S. L. Van Wilgenburg, and K. Shanker. 2012. Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. American Naturalist 180:777–790.

Stouffer, P. C., and R. O. Bierregaard. 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76:2429–2445.

Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. Conservation Biology 20:1212–1223.

Stratford, J. A., and P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. Conservation Biology 13:1416–1423.

Streby, H. M., J. P. Loegering, and D. E. Andersen. 2012. Spot-mapping underestimates song-territory size and use of mature forest by breeding Golden-winged Warblers in Minnesota, USA. Wildlife Society Bulletin 36:40–46.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Sutherland, W. 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56:801–809.

Townsend, J. M., C. C. Rimmer, and K. P. McFarland. 2010. Winter territoriality and spatial behavior of Bicknell's Thrush (*Catharus bicknelli*) at two ecologically distinct sites in the Dominican Republic. Auk 127:514–522.

Townsend, J. M., C. C. Rimmer, K. P. McFarland, and J. E. Goetz. 2012. Site-specific variation in food resources, sex ratios, and body condition of an overwintering migrant songbird. Auk 129:683–690.

Tramer, E. J., and T. R. Kemp. 1980. Foraging ecology of migrant and resident warblers and vireos in the highlands of Costa Rica. Pp. 285–296 in A. Keast and E. S. Morton (editors), Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC.

Tramer, E. J., and T. R. Kemp. 1982. Notes on migrants wintering at Monteverde, Costa Rica. Wilson Bulletin 94:350–354.

Willis, E. O. 1972. Do birds flock in Hawaii, a land without predators? California Birds 3:1–8.

Winker, K., J. H. Rappole, and M. A. Ramos. 1990. Population dynamics of the Wood Thrush in southern Veracruz, Mexico. Condor 92:444–460.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Wunderle, J. M. 1992. Sexual habitat selection in wintering Black-throated Blue Warblers in Puerto Rico. Pp. 299–307 in J. M. Hagan and D. W. Johnston (editors), Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

Zahavi, A. 1971. The social behaviour of the White Wagtail *Motacilla alba alba* wintering in Israel. Ibis 113:203–211.