COMPETITION FOR WINTER TERRITORIES IN A NEOTROPICAL MIGRANT: THE ROLE OF AGE, SEX AND COLOR

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ABSTRACT.—Hooded Warblers (*Wilsonia citrina*) defend long-term feeding territories during the nonbreeding season. Experimental removals of territory owners early in the fall in Mexico resulted in rapid replacement by nonterritorial individuals ("floaters"). The sex ratio of replacement birds was similar to that of territory owners in the same habitat, but virtually all replacements were hatching-year (HY) birds. Females were able to acquire and defend territories in the presence of male floaters. Loss of wintering habitat would likely increase the proportion of nonterritorial birds and, therefore, increase overwinter mortality rates, especially of HY birds. The extent of malelike coloration of females was not correlated with habitat, indicating that dark females were not more likely to obtain territories in forested habitat where males predominate. Furthermore, the aggressive response of male territory owners toward models did not depend on intruder color. These results suggest that malelike coloration in females does not function in competitive interactions with males. Intense competition for winter territories coupled with reduced survivorship of winter floaters could constrain breeding strategies if young produced late in the summer have little chance of obtaining winter territories. *Received 5 April 1993, accepted 30 September 1993.*

NEOTROPICAL MIGRANT songbird populations have declined in recent years (Askins et al. 1990). Habitat loss and fragmentation in the tropics is a major potential cause of this decline (Robbins et al. 1989). If habitat loss has a detrimental effect on wintering populations, then densities must be high relative to the carrying capacity of the habitat (Winker et al. 1990). Although many migrants are territorial on their wintering grounds (e.g. Greenberg 1986, Holmes et al. 1989), little is known about the intensity of competition for those territories (Morton et al. 1987, Winker et al. 1990) or the effects of such competition on population dynamics (Marra et al. 1993).

When resources become limiting, are females at a disadvantage in competing for territories with males? Do yearling birds have difficulty obtaining territories? Age or sex biases in competitive ability for winter territories could have important implications for overwinter survival and productivity on the breeding grounds (Marra et al. 1993). The existence of nonterritorial "floating" populations on the wintering grounds has been well documented only for the Wood Thrush (*Hylochichla mustelina*; Rappole et al. 1989, Winker et al. 1990) and American Redstart (*Setophaga ruticilla*; Marra et al. 1993), and has been reported anecdotally for the Black-throated Blue Warbler (*Dendroica caerulescens*; Holmes et al. 1989) and Hooded Warbler (*Wil-*

sonia citrina; Rappole and Warner 1980, Morton et al. 1987).

Experimental removal of territory owners is an important tool for studying floating populations (e.g. Krebs 1971), but has been performed on the wintering grounds for only a few species (Rappole and Warner 1980, Morton et al. 1987, Winker et al. 1990, Marra et al. 1993). I conducted removal experiments with wintering Hooded Warblers to determine: (1) the size of the nonterritorial floater population; and (2) the relative abilities of birds in particular age/sex classes to obtain territories. The winter ecology of the Hooded Warbler is among the best studied of any Neotropical migrant (Rappole and Warner 1980, Lynch et al. 1985, Morton et al. 1987, Morton 1990, Morton et al. 1993). There is habitat segregation by sex, such that most birds in the forest are males; however, both males and females are found in scrub habitat (Lynch et al. 1985). When territorial males are removed from forest habitat, females in adjacent scrub habitat do not move onto those territories even when such territories remain undefended, indicating that females are not being excluded from forest habitat (Morton et al. 1987). Experiments with hand-raised individuals and field data suggest that habitat segregation results from innate habitat preferences by each sex (Morton 1990, Morton et al. 1993).

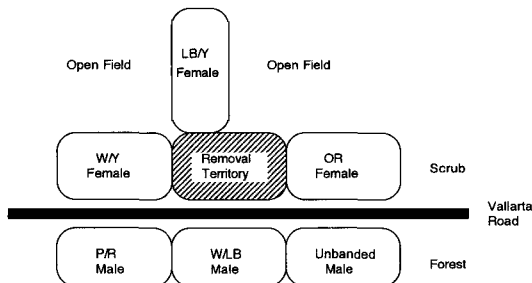During winter females must compete directly

Fig. 1. Illustration of removal experiment at one site in October 1991, showing color bands and sex of territory owners, location of removal territory, and habitat types.

with males for territories (Rappole 1988, Winker et al. 1990, Marra et al. 1993), unlike the breeding season where males and females share territories. Female Hooded Warblers vary greatly in the extent of malelike coloration on the head (Lynch et al. 1985). Lynch et al. (1985) suggested that malelike coloration in females could be important in enabling them to compete successfully with males on the wintering grounds. The malelike "badge" (Rohwer 1982) may signal status and fighting ability, which increases an individual's ability to acquire or defend a territory (Butcher and Rohwer 1989, Rohwer and Roskaft 1989, Stutchbury 1991). This hypothesis predicts that: (1) dark females are more likely to obtain territories in forested habitat among males than females that lack the badge; and (2) territorial males will be less aggressive toward light than dark females.

METHODS

This study was conducted 30 September to 10 November 1991 and 25 September to 15 October 1992 in Quintana Roo, Mexico, on Vallarta Road 4 to 6 km from the main highway near Puerto Morelos. Hooded Warblers begin to arrive in this area in mid-August and are abundant by mid- to late September (Morton et al. 1987, pers. obs.). In September 1988, Hurricane Gilbert struck this area causing widespread damage (Morton et al. 1993) and a subsequent fire. The main study site included previously burned forest and unburned scrub, and was adjacent to intact forest that had escaped the fire. Thus, all three habitat types were available for this study.

Hooded Warblers were captured using mist nets and playbacks of "chip" calls, and each was individually color banded. The degree of skull ossification (Pyle et al. 1987) was used to classify individuals as

hatching year (HY) versus after hatching year (AHY). Female plumage color was scored using a scale of 0 to 5 (Lynch et al. 1985) separately for extent of black coloration on the crown and throat, giving a total score out of 10. Territories were mapped by observing border disputes, sighting marked individuals, or observing individuals that responded to playbacks of conspecific chip calls (e.g. Morton et al. 1987), or a whistled imitation of a Ferruginous Pygmy Owl (*Glaucidium brazilianum*).

Removal experiments.—Most removal experiments (14 of 17) were conducted in scrub/burned habitat, where there was a mixture of males and females who shared territory boundaries. Thus, I could directly examine male-female competition in territory acquisition and defense. I conducted 14 removal experiments over the two years on nine different territories in scrub habitat. Of these nine original territory owners, eight were males. Three additional experiments were performed on two forested territories that were immediately adjacent to scrub habitat, both originally defended by males. Territories with male owners were preferentially chosen for removal experiments to determine whether females were capable of filling such vacancies. Overall, one removal was performed on 30 September, seven in early October, five in late October, and four in early November.

Prior to removing a territory owner, most immediate neighbors were individually color banded (Fig. 1). Removals were performed either in the morning (0600–0900 EST) or late afternoon (1600–1800). Removed birds were transported and released 60 to 80 km away. However, in three cases the owner was sacrificed to prepare mounts for model presentations (see below). Newly vacant territories were censused daily and when a replacement bird was detected, it was color banded as soon as possible. In six removal experiments, the replacement bird was in turn removed 4 to 28 days later to create another vacancy on the same territory.

Female coloration and territory.—To characterize the habitat of territories held by females along the continuum of scrub to forest, the number and diameter (at 1.5 m height) of trees ($\geq$ 10 cm) were determined on a 0.04-ha circular plot located near the center of 30 different territories (Lynch et al. 1985). Each territory was roughly 0.5 ha in size. For territories where the female was not color banded and the territory had not been mapped, the plot was centered where the female had first been sighted (Lynch et al. 1985). These latter females were assumed to be territory owners because they had responded aggressively to model presentations with playbacks of chip calls.

Model presentations.—To determine how plumage color of intruders affected aggression by male territory owners, stuffed mounts of Hooded Warblers were placed on the territory. Mounts had plastic eyes and were in a perched posture. The model intruders con-

TABLE 1. Sex ratio and age class (HY, hatching year; AHY, after hatching year) of territory owners (original owners on removal territories and other owners in scrub habitat) and replacement birds on removal territories in scrub and forest.

	Age class		Sex	
	HY	AHY	Male	Female
Owners (Scrub)				
Removed	3	6	8	1
Other	7	14	15	8
Replacements				
Scrub	13[a]	1	7[b]	7
Forest	2	0	1	1

[a] Three were neighbors.
[b] Two males and one female were neighbors.

TABLE 2. Year-to-year change in sex of territory owner at unmanipulated sites between years in forest and scrub habitats, and within-year change between removed birds and replacement birds on removal sites.

	Change in sex of owner		
Site	None	Male to female	Female to male
Forest	14	1	1
Scrub	13	1	3
All removals	7	7	2

sisted of a male, a dark female (plumage score 8), and a light female (plumage score 0). I prepared all mounts, and different models were used each year.

After a male territory owner was seen or heard, a randomly chosen model was placed 0.25 to 0.75 m high on natural vegetation in a relatively open area. A recording of the chip vocalization used in territorial defense (Lynch et al. 1985) was played throughout the trial (5 min). An observer continuously recorded the distance of the male to the model, the presence of any "wing droop" or "throat up" displays (Rappole and Warner 1980), and any direct attacks on the model.

All presentations were done on unbanded males off the main study site, in forest and scrub habitat. Models and playbacks were used to catch territory owners in the removal sites, so most of these birds would have had prior experience with the models. To avoid the possibility of habituation, each territory owner was tested only once. For analysis, only those presentations in which the owner came within 2 m of the model were used to ensure that the owner was responding to model color as well as the playback tape. Responses were categorized as none (no display or approach within 0.5 m), display only (no approach within 0.5 m), close approach (within 0.5 m), and direct hits on the model.

RESULTS

Removal experiments.—In all 14 experiments in scrub habitat a replacement bird occupied the territory of the removed bird. In four cases the replacement was detected within one to two days of the removal, in seven cases within three to four days, and in two cases within five to seven days. Replacement birds were often secretive during their first few days of occupancy, so some may have been present on the territory

before being detected. Only 3 of 14 replacement birds in scrub habitat were banded neighbors; the other replacements were either unbanded ($n = 10$) or had been banded as intruders on another territory ($n = 1$).

A replacement occured in two of three experiments in forested habitat. In the other experiment, no replacement occupied the territory during the following 10 days. Both replacements in the forest habitat were unbanded birds.

The sex ratio of replacement birds was equal in scrub habitat (Table 1), and did not differ significantly from the sex ratio of the original owners on these nine territories (Table 1; G-test with Yate's correction, $G = 1.42$, df $= 1$, $P > 0.2$). A comparison of replacements that claimed vacant territories with birds who obtained territories under normal conditions would reveal whether certain age/sex classes are more likely to be floaters. There was no significant difference in sex ratio between replacements and all territory owners (experimental and other territories) in scrub habitat ($G = 0.57$, df $= 1$, $P > 0.40$). There was a significant difference in age class of replacements and all territory owners in scrub habitat (Table 1; $G = 11.3$, df $= 1$, $P < 0.001$). Although two-thirds of territory owners were adults (AHY), virtually all replacement birds were HY. As has been documented previously (Lynch et al. 1985), the sex ratio in forest habitat was male biased (21 males to 11 females).

The sex of the replacement birds could not be predicted from the sex of the original owner of the territory (Table 1). In 9 of 16 experiments where a replacement occurred (forest and scrub combined), the sex of the replacement bird differed from that of the previous owner (Table 2). This was not simply a result of the removal itself; changes in owner sex between years also
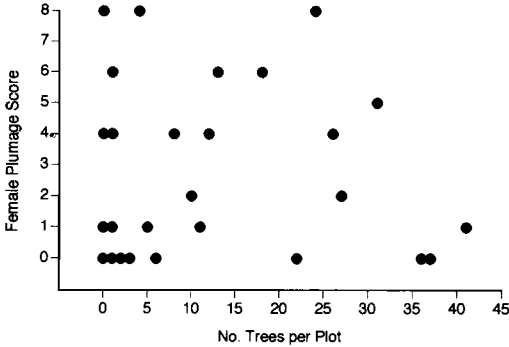
Fig. 2. Relationship between female plumage score (0 = nonmelanistic) and number of trees per sample plot for territorial females in 1991. Territories with more than 20 trees/plot were in forested habitat.

occurred on unmanipulated territories, although less frequently (Table 2). Most birds in this latter sample were not banded; therefore, we could not control for the effects of site tenacity of returning individuals.

Multiple removals on the same territory did not result in similar age/sex classes of replace-

ments. One territory that bordered forest habitat was used for repeated removals over both years (Fig. 1). This territory contained a mixture of open forest and scrub, and its boundaries were very discrete making it ideal for monitoring replacements. In 1991 three removals were conducted from 30 September through 2 November. The owners of this territory were, in order: HY female (original owner), HY male replacement, HY female replacement, AHY male neighbor (color banded W/LB). The AHY male defended both his original territory in the forest and the removal territory after the last removal. This male (W/LB) was still defending both territories late that winter (D. Niven pers. comm.) and again in September 1992. When this male (W/LB) was removed 1 October 1992, the original removal territory in scrub habitat was occupied the next day by an HY female, and his original territory in the forest was occupied two days later by a different HY female.

Female color and habitat.—Malelike females were not more likely to be found in forest habitat (Fig. 2). Of the eight females in well-forested territories (20 or more trees/plot), five were dull
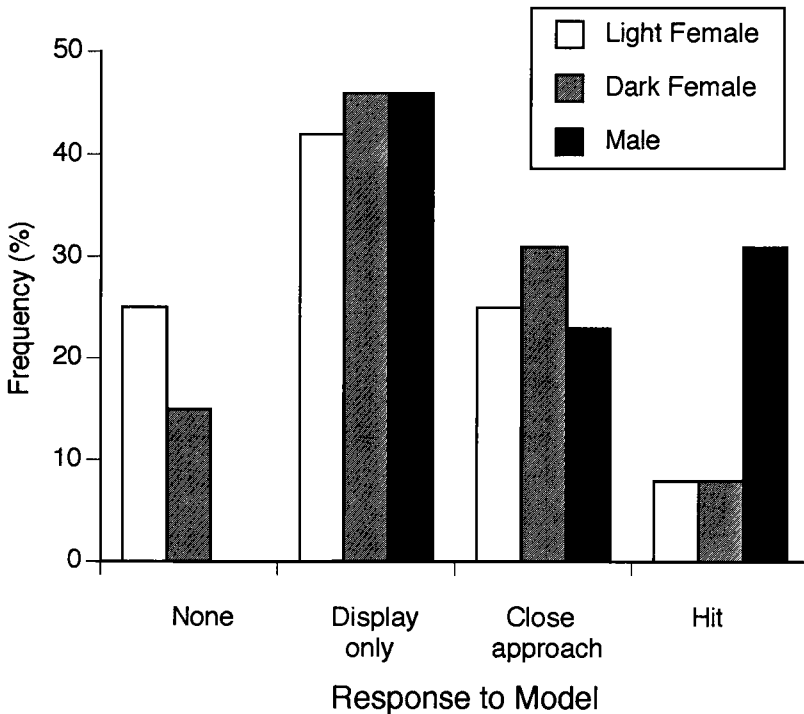

Fig. 3. Response of territorial males to presentations of light female (n = 12), dark female (n = 13), and male (n = 13) models placed on their territory with playback of chip call.

(plumage score 0–2). There was no significant correlation between female plumage score and number of trees within the plot (Fig. 2; $r = -0.10$, $n = 30$, $P > 0.50$) or total basal area of trees ($r = -0.09$, $n = 30$, $P > 0.50$).

Model presentations.—Male territory owners responded aggressively to models by displaying from a distance (17 of 38 trials), approaching within 0.5 m (10 of 38 trials) or attacking the model (6 of 38 trials). The intensity of male response did not differ significantly between light and dark female models (Fig. 3; $G = 0.40$, $df = 3$, $P > 0.90$). There was also no significant difference in aggressive response to male models versus all female models (G-test with William's correction, $G = 2.49$, $df = 3$, $P > 0.10$).

DISCUSSION

Most removal experiments (13 of 17) resulted in replacement by unbanded birds, rather than by banded neighbors ($n = 3$). Not all territory owners on the study site were banded, so it is possible that some unbanded replacement birds were more distant neighbors moving from lower-quality territories (e.g. Krebs 1971). The successional habitat in which most removals were performed was extensive and fairly uniform. Indirect evidence suggests these replacement birds were nonterritorial floaters (Brown 1969, Smith 1978). First, virtually all unbanded replacements were HY birds, in contrast to territory owners (Table 1). Second, unbanded birds were frequently caught intruding on territories where neighbors were banded, suggesting these individuals may have been nonterritorial. Third, a demographic model (Robertson and Rendell 1990) based on an annual adult return rate of 0.40 for breeding Hooded Warblers (unpubl. data) suggests that the winter population should contain at least 50% yearlings, which is more than the 30% represented in the territorial population.

There is likely a cost to being a nonterritorial bird during the nonbreeding season, rather than this representing an alternative and equally successful winter social organization (Winker et al. 1990). Nonterritorial individuals quickly claimed territories when given the opportunity (Rappole and Warner 1980). Nonterritorial Wood Thrushes suffer a higher mortality rate from predation than territorial birds (Rappole et al. 1989, Winker et al. 1990). It is not known how long Hooded Warblers remain nonterri-

torial over the winter, but Rappole and Warner (1980) reported rapid replacement on a territory where the owner died late in February.

Morton et al. (1987) removed four males from forested habitat adjacent to scrub, and found two unbanded replacement birds occupying parts of the experimentally vacated territories. Females did not occupy vacated forest habitat, despite the fact that in two cases parts of the territory remained undefended. In my study, removals in both scrub and forest resulted in unbanded replacements (Table 1). Loss of wintering habitat, in forest or successional habitat, likely results in an increase in the proportion of nonterritorial Hooded Warblers and, therefore, may also increase overwinter mortality rates (Winker et al. 1990), especially of HY birds.

Habitat selection.—Hooded Warblers exhibit habitat separation by sex, with forest habitats containing virtually all males (Lynch et al. 1985). Laboratory and field experiments have shown that each sex has innate habitat preferences, and uses verticality of the vegetation as a cue for habitat selection (Morton 1990, Morton et al. 1993). However, in my study, the sex of the original territory owner did not predict the sex of the replacement bird on the same territory (Table 2). Given the intensity of competition for territories, nonterritorial individuals apparently will claim any vacancy that arises, even if it does not match their innate preference. Nevertheless, one would expect the nonterritorial floater population to be more male biased in forest habitat than the floater population in this study.

Female-male competition.—Habitat segregation may evolve because it reduces intersexual competition (Morton 1990). My study demonstrates that females can successfully compete with males for territories, because females claimed territories despite the presence of male floaters. Female models did not receive a lower aggressive response from territorial males than male models. However, the relative costs to females of competing with males versus other females remains unknown. In a similar removal experiment with American Redstarts, females were more likely to be excluded from territories than males (Marra et al. 1993). American Redstarts exhibit partial habitat segregation by sex (Lopez and Greenberg 1990), and the removal experiments were conducted in preferred male habitat, suggesting that females were being actively excluded by males (Marra et al. 1993). In Hood-

ed Warblers, however, several removal experiments in the male-dominated forest did not result in females occupying those territories (Morton et al. 1987). Nevertheless, males and females do compete with each other for territories in more open successional habitat, and females can compete successfully with males for territories in these habitats.

The hypothesis that dark coloration in females is adaptive for competing with males during the nonbreeding season (Lynch et al. 1985) was not supported. Dark females were not more likely to obtain territories in forested habitat where males predominate, and male territory owners were not less aggressive toward light female model intruders.

The majority of replacement birds were HY, suggesting that HY birds often have difficulty acquiring winter territories. HY females have little or no black coloration on their head (Lynch et al. 1985). This inconspicuous color pattern does not appear to function in reducing aggression from territory owners (Fig. 3). However, an inconspicuous plumage could be adaptive for an open habitat where females are most often found (Morton 1976, 1990), either by reducing predation risk as a nonterritorial individual (Rappole et al. 1989, Winker et al. 1990) or avoiding detection by territory owners. Although previous studies of winter subadult coloration have focused on males (Rohwer and Butcher 1988), many species of warblers have a winter subadult plumage in females as well (Rappole 1983, Spellman et al. 1987).

Implications for breeding strategies.—I found that there is intense competition for wintering territories, and HY birds seem to be at a disadvantage in acquiring winter territories. Two important factors that influence an individual's ability to acquire a territory are arrival date and site dominance. When breeding territories are being established, there is strong selection for individuals to arrive relatively early in spring to claim a territory (Hill 1989, Morton and Derrickson 1990), and in many species late-arriving HY birds often become nonterritorial (e.g. Stutchbury and Robertson 1987, Hill 1989). By analogy, early arrival on the wintering grounds must also be an advantage in territory acquisition (Morton 1976, Winker and Rappole 1992). Site dominance on breeding territories allows individuals to reclaim the same territory in subsequent years, even if other individuals arrive there first (e.g. Nolan 1978). Territory site te-

nacity is high in wintering migrants of some species (Greenberg 1986, Holmes et al. 1989, Marra et al. 1993), so older individuals with site dominance from the previous year would have an advantage over yearlings.

Intense competition for winter territories probably results in an advantage to early arrival on the wintering grounds (Winker and Rappole 1992). Therefore, winter territoriality could be an important constraint on migratory songbirds by curtailing their breeding late in the summer (Rappole et al. 1979). Young produced late in the summer may have lower value if their survival prospects are low due to a shortage of winter territories. In addition, late season parental effort could delay an adult's departure for the wintering grounds by delaying the onset of the molt, and slowing the rate of molt due to the overlapping energy demands of molting and feeding fledglings (Morton and Morton 1990). In Hooded Warblers, parents that attempt second broods begin molting about two to three weeks later than individuals that do not breed late in the season (Evans, Ogden, and Stutchbury unpubl. data). Many females do not attempt to produce second broods, despite adequate time to renest. This reproductive restraint may be due in part to the hidden costs to parents and offspring of failing to acquire a good quality winter territory.

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