The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season

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Several species of territorial migratory birds exhibit sexual habitat segregation on their wintering grounds, with some habitats containing mostly males and others mostly females. The objective of this study was to determine if in the American redstart (*Setophaga ruticilla*) in Jamaica habitat segregation is due to social mechanisms or due to sex-specific habitat specialization. I used habitat-specific patterns of arrival by young males and females, observations of territorial displacements, removal experiments, and simulations of territorial intrusions to differentiate between these two mechanisms. Redstarts were studied in two habitat types, a male-biased mangrove forest and a female-biased scrub habitat. In autumn, male and female hatch-year redstarts initially settled in equal numbers in each habitat, and segregation of the sexes occurred gradually and mostly later in the arrival period. This shift corresponded with an increase in density of older birds and an increase in territorial displacements. Removal experiments showed that vacancies in male-biased habitat were filled more rapidly and with greater frequency than those in female-biased habitat and that vacated male territories in mangrove were replaced more often by females than by males. Simulations of territorial intrusions and analyses of body size indicated that levels of aggression and body size of both males and females were greater in mangrove habitat, suggesting that these factors may be important in determining the outcomes of dominance interactions. I conclude that patterns of sexual habitat segregation in redstarts are structured by the dominance behavior of older and more dominant individuals, and these are mostly males. *Key words:* American redstarts, behavioral dominance, habitat specialization, migratory birds, nonbreeding season, removal and playback experiments, *Setophaga ruticilla,* sexual habitat segregation. *[Behav Ecol 11:299–308 (2000)]*

I n migratory birds, many species exhibit a habitat distribution pattern in which males and females are spatially segregated during the stationary portion of the nonbreeding period. This is characterized by males and females occurring in different proportions, either at different latitudes (e.g., Ketterson and Nolan, 1976, 1983; van Eerden and Munserman, 1995) or at the same latitude but in different habitat types. This latter pattern is known as sexual habitat segregation and appears to be a widespread phenomenon during the nonbreeding period for migratory passerines in both the New (e.g., Lynch, 1992; Lynch et al., 1985; Ornat and Greenberg, 1990; Sliwa, 1991; Wunderle, 1992; Wunderle and Waide, 1993) and Old World (Nisbet and Medway, 1972).

Two mechanisms have been proposed to underlie sexual habitat segregation. First, the habitat specialization hypothesis proposes that males and females are each habitat specialists, with males choosing to establish territories in one type of habitat (hereafter "male-biased habitat") and females in another (hereafter "female-biased habitat") (Lynch et al., 1985; Morton, 1990; Morton et al., 1987). It assumes, based on the abundance of each sex, that habitat suitability is highest for females in female-biased habitat and for males in male-biased habitat. Second, interference behavior of dominant individuals (e.g., males) may lead to the exclusion of subordinate individuals (e.g., females) from some habitats (Gauthreaux, 1978; Lynch et al., 1985). Such social dominance can be considered a result of intraspecific competition for limiting resources and would result in the most suitable habitats becoming male-bi-

ased and less suitable habitats becoming female-biased. Below, I describe several tests designed to separate habitat specialization from behavioral dominance mechanisms responsible for structuring patterns of sexual habitat segregation in a long-distance migrant passerine, the American redstart (*Setophaga ruticilla*).

The first test examines the settlement patterns of migrant birds on their wintering quarters. The habitat specialization hypothesis predicts that naive male and female hatch-year (HY) birds, arriving in winter habitats for the first time, should settle preferentially into the appropriate male- or female-biased habitat when they first arrive in autumn. In contrast, the behavioral dominance hypothesis predicts territory settlement patterns of HY redstarts over the first few weeks to be either random with respect to habitat and sex, especially if habitats are of equal suitability in autumn, or skewed toward the male-biased habitat if this habitat is of higher suitability relative to female-biased habitat. Under either scenario, subordinate HY males and females will begin to settle with greater frequency in female-biased habitat, most likely due to the increase of aggressive encounters and resulting territory displacements by older returning redstarts (after-hatch year redstarts; AHY). Thus, the first objective of this study was to quantify the settlement patterns and the frequency of territorial displacements of HY and AHY males and females into known male and female-biased habitats in autumn.

In a second test, I removed individuals from female- and male-biased habitats and examined the frequency and rate of replacement as well as the sex and age of the replacement birds. If sexual habitat segregation is driven by habitat specialization, the frequency and rate of replacement should be equal between the two habitats, whereas behavioral dominance predicts faster replacement in male-biased compared to female-biased habitats because male-biased habitat is assumed to be of higher suitability. The habitat specialization

hypothesis predicts that when males or females are removed from their territories in either habitat type, they should be replaced by the same gender, assuming the presence of floaters or of neighboring individuals interested in moving. Alternatively, the behavioral dominance hypothesis predicts the removal of individuals from male-biased habitat may result in a shift in the sex or possibly age (older to younger) of the new territory owner, at least in the absence of older males and presence of excluded subordinates.

On their wintering quarters, both sexes of several species of Neotropical migrant birds have been shown to defend territories vigorously and exhibit stereotypical aggressive behaviors (e.g., Greenberg, 1986; Greenberg and Ortiz Salgado, 1994; Greenberg et al., 1994, 1996; Holmes et al., 1989; Rappole and Warner, 1980). Thus, a third test designed to separate habitat specialization from behavioral dominance hypotheses involved quantifying this aggressive behavior of territorial birds. The habitat specialization hypothesis predicts that each sex will exhibit higher levels of aggression in the habitat type with which it is most commonly associated. The behavioral dominance hypothesis predicts that males and females obtaining territories in male-biased habitat do so either because they are more aggressive, have larger body size (see below), or possibly both. Increased aggressiveness by individuals in male-biased habitat would suggest an asymmetry in habitat suitability, a finding inconsistent with the habitat specialization hypothesis. To test these predictions I performed playback experiments in the territories of individuals in each habitat type in autumn and quantified the aggressiveness of their response.

Large body size has been shown to allow some individuals greater access to limited resources (Fretwell, 1969; Smith and Metcalfe, 1997). Thus, an additional prediction consistent with the behavioral dominance hypothesis is that individuals with territories in male-biased habitat, regardless of sex, should be larger than individuals in female-biased habitat. Thus, I also measured wing chords and tarsus lengths of individuals occupying both habitat types to determine if body size was a possible mechanism allowing some individuals to win territorial disputes and exclude smaller, subordinate birds from male-biased habitats.

The study species was the American redstart (*Setophaga ruticilla*), a Nearctic-Neotropical migrant well suited for testing the hypotheses and predictions outlined above. Redstarts breed in North America and spend the nonbreeding period in the Caribbean, Central America, and northern South America (Sherry and Holmes, 1997). They exhibit sexual habitat segregation throughout most of their winter range (Marra and Holberton, 1998; Sherry and Holmes, 1997), and individuals can be sexed and aged reliably (Holmes et al., 1989; Marra et al., 1993; Pyle et al., 1987; Sherry and Holmes, 1997).

METHODS

Research was conducted at the Font Hill Nature Preserve, 13 km west of Black River, St. Elizabeth Parish, in southwestern Jamaica. Redstarts were studied in two habitat types with approximately equal densities but different sex ratios. In mangrove forest, redstart density over 2 years (1994 and 1995) averaged 20.1 ± 0.9 SE/5 ha, of which 65% were male and 35% were female. Second-growth scrub habitat had 20.6 ± 1.4 SE redstarts/5 ha, of which approximately 30% were male and 70% were female.

The mangrove habitat was predominately black mangrove (*Avicennia germinans*) with small amounts of white (*Laguncularia racemosa*) and red (*Rhizophora mangle*) mangrove along the periphery. The mangrove stands had continuous canopies averaging 12 m in height, had almost no ground or shrub level vegetation, and were flooded with up to 1 m of water. Second-growth scrub habitat was predominated by logwood (*Haematoxylon campechianum*), a 2–8 m tall, thorny tree, with larger, scattered trees (e.g., *Bursera simarubra, Terminalia latifolia,* and *Crescentia alata*) and many vines and tangles.

I studied redstarts on three 5-ha study sites in mangrove and two 5-ha sites in second-growth scrub adjacent to these mangrove sites. All sites were gridded at 25-m intervals, which allowed me to locate and map redstart territories. The third mangrove site was necessary to obtain larger sample sizes of females in that habitat type. Removal experiments in mangrove and second-growth scrub were conducted on smaller study plots in nearby areas at Font Hill (see below).

American redstarts were captured using a song playback technique (Holmes et al., 1989), measured (tarsus, wing chord, body mass), aged, sexed, and given a unique set of color-bands. I aged all redstarts as either HY or AHY using skull ossification and then sexed them using several plumage characters. Criteria for aging and sexing have been described in detail elsewhere (Marra et al., 1993; Pyle et al., 1987; Sherry and Holmes, 1997), and were confirmed by observation and recaptures of color-banded individuals of known sex over several years (Marra PP et al., unpublished data).

Arrival and settlement patterns

In 1994 and 1995, my assistants and I censused redstarts for 8 weeks from early September to late October. Censuses were conducted in each site twice per week (2–3 days apart), and alternated between observers. Censuses began at 0600 h on alternating sides of the plot, lasted 2–4 h, and consisted of an observer walking at a slow pace on each of five 250-m transects that were 50 m apart. Redstarts were detected by either sight or sound, located, identified as banded or unbanded, and classified as female, HY male, or AHY male, or, if sex could not be ascertained with confidence, as a female-plumaged individual. If an unmarked redstart was seen in that same area again on the next census, it was captured within the next few days and color-banded, aged, sexed, and measured. We recorded all territorial displacements, which were defined as a territorial color-banded bird seen on two consecutive census visits that subsequently shifted at least one full territory away (ca. >50 m) or disappeared and was replaced by a neighboring or new redstart.

Removal experiments

Individual American redstarts were removed from one male-biased (mangrove) and one female-biased (second-growth scrub) site in 1994 and 1996. Because extensive removal experiments had already been conducted in mangrove at this same site (Marra et al., 1993), the major effort of these experiments was to conduct removals in female-biased habitat. I also made smaller scale removals, however, in mangrove to control for annual differences in population density and floater abundance.

Before removal, I mapped territories of all individuals on one 3-ha plot in female-biased habitat and one 1.5-ha plot in male-biased habitat. Overall, six observers spent a total of 25 preremoval h mapping the territories of 17 redstarts on the female-biased sites and a total of 12 h mapping the territories of 16 redstarts on male-biased sites (less time was necessary for territory mapping in the mangrove habitat because its open vegetation made following birds easier than in the thicker second-growth scrub). Mapping of redstarts continued until no further changes in the size and shape of the territories could be detected (Marra et al., 1993). After mapping was complete, 12 redstarts in scrub and 6 in mangrove were cap-

tured and permanently removed from their territories on 15 October 1994 and 9 November 1996. We visited each site and checked for the presence of redstarts 1 day, 1 week, and then 2 weeks after removal. Song playbacks were used to facilitate finding birds and to confirm densities. In each year, 8 h after removal were spent mapping redstarts in the female-biased removal plot and 5 h in the male-biased plot.

Simulations of territorial intrusions

I quantified behavioral responses of redstarts using a vocalization playback in both habitat types in the autumn of 1996. Each playback experiment consisted of placing a taxidermic mount of an AHY male redstart approximately 0.5 m above the ground in the center of a focal bird's territory. An amplified speaker was concealed at the base of the model with a speaker cable leading to a remote tape recorder at a hidden location approximately 15 m away. One person operated the recorder, while two other observers were stationed approximately 15 m on the opposite side of the decoy and approximately 20 m apart. Each experiment consisted of a 10-min broadcast of American redstart vocalizations at a constant volume. Three different tapes were used, each containing a mix of AHY male song and AHY male chips in equal proportions and from different individuals (Kroodsma, 1986). Although chips are the most common vocalization made by redstarts during the winter, the use of the song–chip combination in equal proportions produced a stronger and more consistent response from the redstarts (Holmes et al., 1989; Marra PP, unpublished data).

Each of the two observers independently scored three parameters on the focal bird as soon as it appeared in the vicinity (about 15–20 m) of the decoy: (1) the total number of dives (defined as a flight over the model accompanied by a sharp drop in flight directed toward the decoy), (2) the total number of separate physical attacks on the decoy (defined as a hit on the decoy), and (3) an overall response score (1 = no response; 2 = mild response with occasional chips and remains in vicinity but always more than 10 m away; 3 = strong response, obviously agitated with close approaches within 2 m of the model; 4 = very strong response, highly agitated and attacks model). Intermediate scores (1.5, 2.5, and 3.5) were also used.

None of the focal redstarts used in these experiments had been previously exposed to a playback that season, although some had responded to a playback in previous years when they were first banded. Birds banded within a season exhibit a reduced response to song playback in that same season, but when exposed to playbacks a year later their responses were at preexposure strength (Marra PP, unpublished data). Experiments on the same day were always conducted on individuals more than 200 m apart to avoid exposing other potential experimental birds to the sound of the playback or sight of the decoy.

Data analysis

I used chi-square analysis to test if (1) the proportion of territorial displacements differed between habitats, (2) males did more displacing than females in mangrove, (3) AHYs did more displacing than HYs in mangrove, (4) the sex ratio of birds removed within each habitat differed from the replacements, and (5) the proportion of each sex present between habitats changed after removal. The effects of habitat (mangrove versus scrub) and sex (male versus female) on the number of dives, attacks, and response score exhibited by redstarts during playbacks experiments were examined by standard two-way analysis of variance. Because sample sizes were too

small for males in female-biased habitat to include age (HY versus AHY) in the model, a separate analysis was conducted on females to test for the effects of habitat and age. All playback data were natural-log transformed to meet assumptions of equal variance and normality.

To examine body size relationships, I first calculated the scores of a principal component analysis based on unflattened wing chord and tarsus length. A natural-log transformation was performed on the scores from the first principal component to meet assumptions of normality and equal variances, and these transformed data were used as an estimate of skeletal body size. I analyzed these data using a three-way ANOVA including sex (male verus female), age (AHY versus HY), and habitat (mangrove versus scrub) and then analyzed the data separately for males and females. All statistical analyses were made using JMP (SAS Institute, 1997).

RESULTS

Behavior during the arrival period

I predicted that if sexual habitat segregation was caused by sex-specific habitat specialization, naive HY male and female redstarts, upon arrival in their wintering grounds, would settle differentially into male- (mangrove) and female-biased (scrub) habitats, respectively. In general, I found that male and female HY redstarts initially arrived and settled approximately equally in both habitat types. In 1994, the numbers of HY males were the same in both habitat types through the first 4 weeks and then increased more rapidly in mangrove habitat (Figure 1). The numbers of HY males leveled off between 3.5 and 4 individuals/5 ha in second-growth scrub and approximately 6.5/5 ha in mangrove habitat at the end of the censusing period. The rate of settlement did not differ between habitats in 1995, with mean numbers by week 8 of 3.5 individuals/5 ha in scrub and 3.7/5 ha in mangrove. In 1995, the numbers of HY male redstarts were lower at the end of October than those in the previous year (mean for week 8 of 5.4 ± 1.4 in 1994 versus 3.1 ± 1.5 individuals/5 ha in 1995; $t = 2.2$, df $= 6$, $p = .07$; Figure 1).

In 1994, HY females settled into both habitats at similar rates through week 6 (Figure 1). During week 7 and 8, however, numbers of HY females increased in scrub, while numbers remained stable in mangrove. Mean number of HY females in mangrove remained constant over the final 2 weeks of October at 4.5 HY females/5 ha, while numbers increased in scrub to 6.0 HY females/5 ha by the end of October. In 1995, HY females exhibited settlement patterns similar to those in 1994, increasing to 5.0 individuals/5 ha in scrub and only 2.0 individuals/5 ha in mangrove.

Because American redstarts exhibit strong site fidelity to their winter territories of the previous year, testing predictions regarding habitat choice cannot be done with older (AHY) birds (Holmes et al., 1989; Holmes and Sherry, 1992; Marra and Holmes, in press). Nevertheless, I quantified AHY arrival patterns to assess changes in numbers of all redstarts. The patterns of arrival and settlement of AHY redstarts in 1994 were similar to those of HY individuals (Figure 2). The settlement patterns of AHY males by habitat diverged, with mean numbers increasing to 8.0 individuals/5 ha in mangrove and never exceeding 2.0 individuals/5 ha in scrub. By week 8 the mean number of AHY males was 14.7 individuals/5 ha in mangrove and had yet to asymptote, compared to 2.5 ± 0.5 individuals/5 ha in scrub habitat. For AHY females, there were no differences among habitats in patterns of settlement in either year. In 1994, AHY females never exceeded 4 individuals/5 ha by the end of October (week 8) in either habitat. In 1995, AHY females exhibited similar rates of increase to
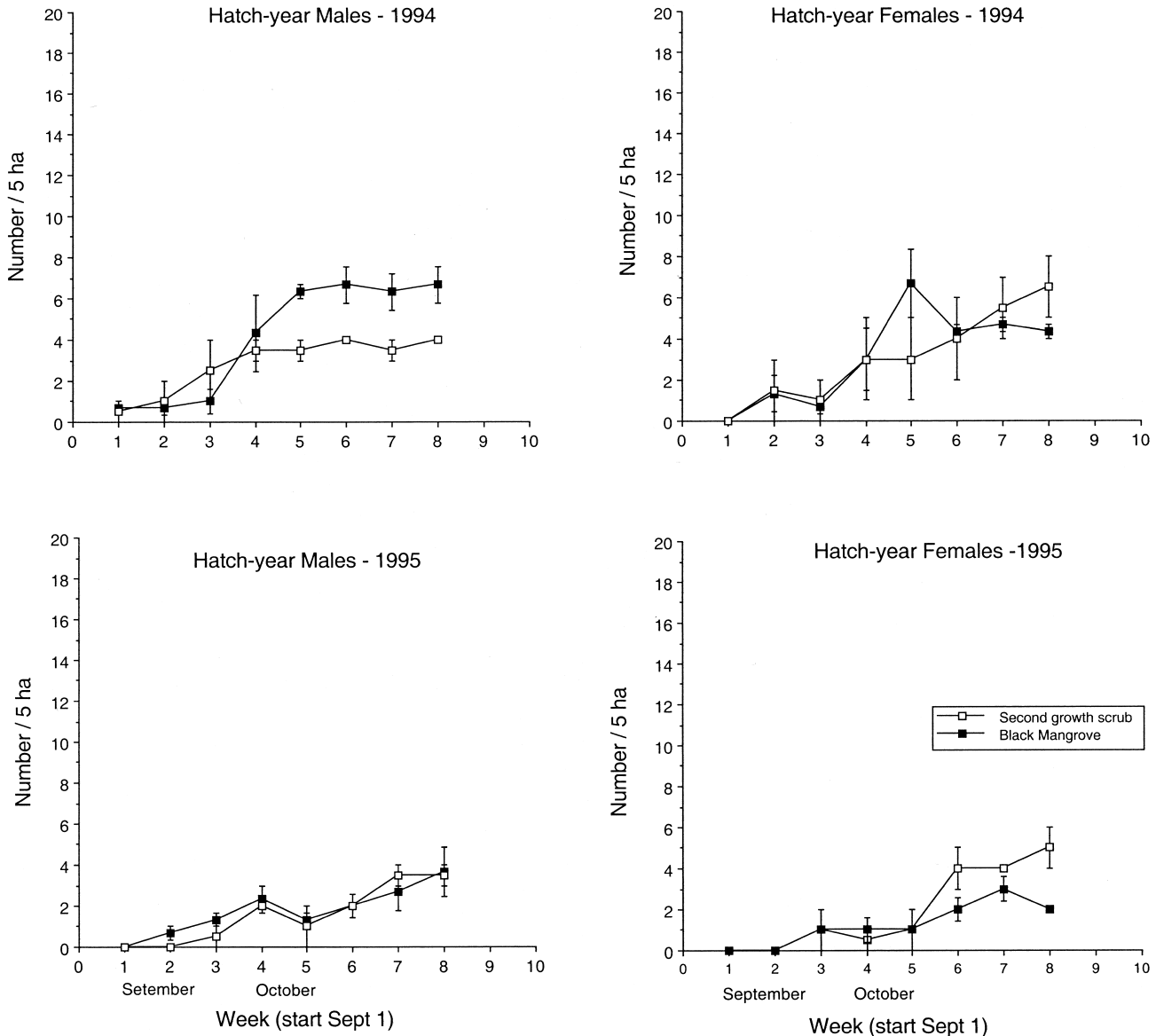
Figure 1
Arrival and settlement patterns of hatch-year (HY; <1 year old) male and female American redstarts onto mangrove (male-biased) and second-growth scrub (female-biased) habitats in 1994 and 1995 on the nonbreeding grounds in Jamaica. Values in each week represent the mean (± 1 SE) number of American redstarts on all plots combined by habitat.

AHY males, however, in contrast to males, there were no habitat-specific patterns in settlement, although by week 8 females had not shown signs of asymptoting.

Significantly more territorial displacements occurred on the mangrove sites (40/3 plots) compared to scrub sites (4/2 plots) in both 1994 and 1995 ($\chi^2 = 8.0$, df = 1, $p = .007$), and these were mainly males displacing females ($\chi^2 = 14.4$, df = 1, $p = .000$) or AHYs (predominantly males) displacing HYs (males and females; $\chi^2 = 19.6$, df = 1, $p = .000$; Table 1). Over both years, 87% of territorial displacements took place in mangrove, compared to only 13% in scrub, and the majority (80%) of these displacements were by males or by AHY individuals (85%). Displacements were by both returning color-banded AHY redstarts (65%) and by new individuals (35%) establishing site dominance for the first time.

Removal experiments

Territory replacement was more rapid and complete in male-biased than in female-biased habitats. One day after the re-

movals in mangrove in 1994 and 1996, 4 of 6 (67%) of the vacated territories had new redstarts present, compared to only 1 of 12 (8%) of the vacated territories in scrub (Figure 3). Furthermore, on the first day after the removals, new redstarts in mangrove were engaging in aggressive interactions with neighbors, whereas the one redstart in scrub was a single foraging bird seen briefly. One week after removals, 100% of the vacated territories in mangrove had been filled, compared to only 58% in scrub. Two weeks after removal the percentage of replaced redstart territories leveled off to 50% in scrub, while the sites in mangrove remained occupied.

In scrub, the sex ratio went from a 3:1 ratio of females to males removed to 5:1 females to males after replacement, but this change was not significant ($\chi^2 = 2.66$, df = 1, $p = .1$; Table 2). In these same years, I removed a total of four males and two females from mangrove. Combining these data with those of removal experiments conducted in mangrove in 1989 (Marra et al., 1993) shows that 13 vacated territories in man-
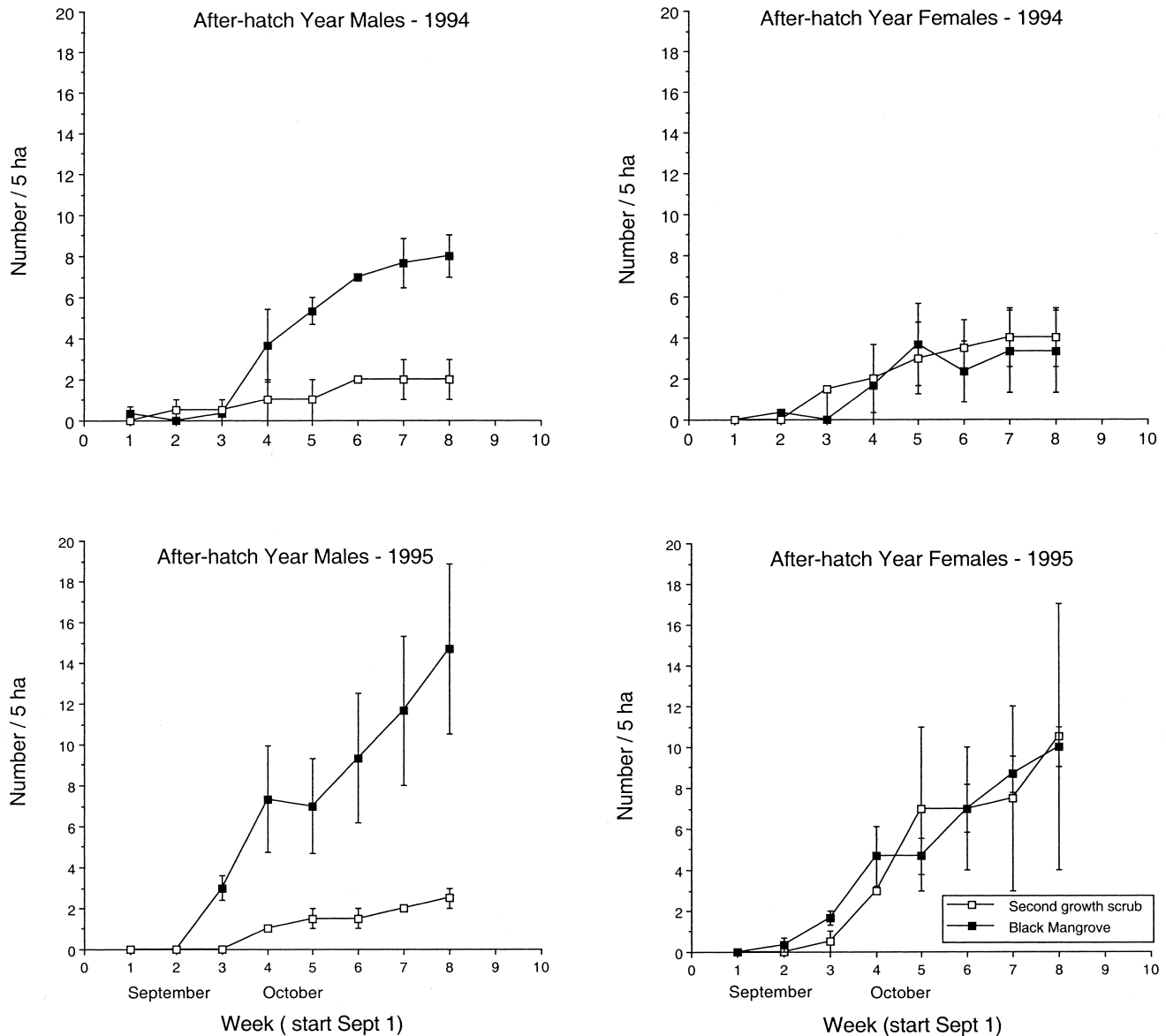
Figure 2
Arrival and settlement patterns of after hatch-year (AHY; >1 year old) male and female American redstarts in mangrove (male-biased) and second growth scrub (female-biased) habitat in 1994 and 1995 on the nonbreeding grounds in Jamaica. Values in each week represent the mean (± 1 SE) number of American redstarts on all plots combined by habitat.

grove were filled within 2 weeks by 7 males and 7 females, representing a 108% replacement rate. The sex ratio in this habitat shifted from a 1:3.3 female to male ratio before removal to a 1:1 ratio in the replacement birds ($\chi^2 = 3.6$, df = 1, $p = .06$). In comparing between habitats, the proportion of males present declined equally in mangrove (77% to 50%) and scrub (25% to 17%) as a result of the removal ($\chi^2 = 0.14$, df = 1, $p = .71$). In contrast, the proportion of females increased in both habitats after removal (23% to 50% in mangrove; 75% to 86% in scrub), but significantly more in mangrove compared to scrub ($\chi^2 = 58.12$, df = 1, $p = .000$).

In mangrove, none of the replacement birds were observed before removal, even though the experiments were done after the main arrival period. It did not appear that any of the replacement in mangrove was due to shifting neighbors. Color-banded neighbors remained on territory and exhibited intense aggressive interactions with new replacement redstarts. This contrasts with scrub habitat, where approximately 50%

of the replacement birds observed were color-banded individuals shifting from neighboring territories.

Simulations of territorial intrusions

American redstarts in mangrove habitat responded more aggressively to tape playbacks than conspecifics in female-biased, scrub habitat (Table 3). Both male and female redstarts in mangrove dived significantly more often toward a stuffed AHY male decoy during the 10-min tape playback than did redstarts in scrub (habitat: $F = 7.7$, $p = .009$; sex: $F = 0.83$, $p = 0.37$; habitat × sex: $F = 0.02$, $p = .89$). Only males attacked the decoy, and this occurred in both habitats (habitat: $F = 1.0$, $p = .32$; sex: $F = 4.4$, $p = .04$; habitat × sex: $F = 1.0$, $p = .32$). Response scores were significantly higher in mangrove (habitat: $F = 8.3$, $p = .007$), although males in scrub also responded aggressively, resulting in a marginally significant sex effect and habitat × sex interaction (sex: $F = 3.9$, $p = .06$, habitat

Table 1

Frequency of territorial displacements by American redstarts by habitat, sex, and age during settlement in autumn of the nonbreeding period in Jamaica

	% Displaced
Habitat	
Black mangrove	87%
Second-growth scrub	13%
Sex	
Female displaced by male	40% (16/40)
Male displaced by male	40% (16/40)
Male displaced by female	10% (4/40)
Female displaced by female	10% (4/40)
Age	
HY displaced by AHY	50% (20/40)
AHY displaced by AHY	35% (14/40)
AHY displaced by HY	5% (2/40)
HY displaced by HY	10% (4/40)

Habitat: mangrove was male-biased habitat, and scrub was female-biased habitat. The number of displacements in each habitat were adjusted to individuals per 5 ha: 40/3 plots = 13.3/5ha and 4/2 plots = 2.0/5ha. Age: AHY = after-hatch year or > 1 year old, HY = hatch year or < 1 year old.

$\times$ sex $F = 3.3$, $p = .08$; Table 3). Because of small sample sizes of males in scrub, age effects could not be assessed in the full model. A separate analysis conducted for just females showed that the response scores in females were higher in mangrove habitat (habitat: $F = 19.56$, $p = .001$), regardless of age ($F = 1.73$, $p = .21$; habitat $\times$ age: $F = 4.1$, $p = .07$).

Body size

Male American redstarts were significantly larger than females. Within a sex, no differences were found in male body size across habitats, but females in mangrove were larger than females in scrub, regardless of age (Figure 4). In a three-way ANOVA including sex, age, and habitat, males were significantly larger than females, and there were no significant interactions (age: $F = 0.86$, $p = .35$; sex: $F = 66.12$, $p = .0001$; habitat: $F = 2.39$, $p = .12$; age $\times$ habitat $F = 0.33$, $p = .56$; sex $\times$ habitat: $F = 2.55$, $p = .11$; age $\times$ sex $\times$ habitat: $F = 0.12$, $p = .73$). When sexes were considered separately, I found that females in mangrove were larger than those in scrub habitats, regardless of age (age: $F = 0.02$, $p = .88$; habitat: $F = 5.47$, $p = .02$; age $\times$ habitat $F = 0.48$, $p = .49$), and there were no differences in male body size either between
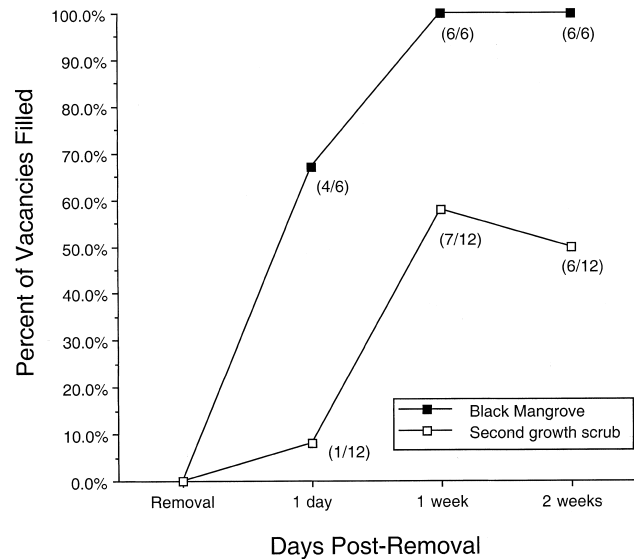

Figure 3
Replacement rate of American redstarts on experimentally vacated territories in mangrove (male-biased) and second-growth scrub (female-biased) habitat 1 day, 1 week, and 2 weeks after removal of territorial individuals in Jamaica. Results of removal experiments in 1994 and 1996 were combined for each habitat.

age or habitat classes (age: $F = 2.03$, $p = .16$; habitat: $F = 0.001$, $p = .97$; age $\times$ habitat $F = 0.02$, $p = .88$).

DISCUSSION

My results support the hypothesis that dominance behavior of older males excludes females and younger males from preferred mangrove habitat and is the primary mechanism responsible for creating patterns of sexual habitat segregation in American redstarts during the nonbreeding period. Habitat specialization by males and females did not appear to play a role in driving patterns of habitat occupancy in this species.

Arrival and settlement patterns of both hatch-year males and females in September and early October was random with respect to habitat type, a finding inconsistent with the habitat specialization hypothesis. Furthermore, the fact that HY redstarts did not settle disproportionately in mangroves suggests either that habitats were of equal suitability at the time of settlement or that HY birds could not detect differences in suitability. In early to mid-October, however, as older, more dominant redstarts arrived, HY males continued to settle with

Table 2

Number of American redstarts removed from and replaced in mangrove (male-biased) and scrub (female-biased) habitats during the nonbreeding period in Jamaica

	Black mangrove		Second-growth scrub	
	Removed	Replaced	Removed	Replaced
Males				
AHY	7 (4)	4 (3)	1	0
HY	3 (2)	3 (1)	2	1
Females	3 (1)	7 (4)	9	5
Total	13	14	12	6

Removals were conducted in October–November, 1994 and 1996. Data from identical experiment in mangrove conducted in 1989 (Marra et al., 1993) are also included (numbers in parentheses). AHY, after-hatch year (> 1 year-old) males; HY, hatch-year (< 1 year-old) males.

Table 3

Responses (mean ± SE) of male and female American redstarts to 10-min song-chip playback experiments conducted in October (1996) on territories in mangrove (male-biased) and scrub (female-biased) habitat during the nonbreeding period in Jamaica

Habitat	*n*	No. of dives	No. of attacks	Score
Black mangrove				
Male	17	5.8 ± 1.3	0.12 ± 0.1	2.9 ± 0.2
Female	5	4.2 ± 1.7	0	2.8 ± 0.2
Second-growth scrub				
Male	3	1.3 ± 0.9	0.3 ± 0.3	2.5 ± 0.9
Female	14	0.2 ± 0.1	0	1.3 ± 0.2

greater frequency in mangrove, but HY females began to increase in abundance in scrub. The latter of these shifts of females was due to a disproportionate increase in displacements among redstarts in mangrove habitat. Overall, 87% of the displacements observed were in mangrove forest, and these were predominately males displacing females and older birds displacing younger ones, common patterns with dominance hierarchies in birds (e.g., Balph, 1977; Wilson, 1975). Furthermore, both returning color-banded redstarts and individuals arriving for the first time were responsible for displacements, suggesting that both prior site dominance and intrinsic dominance determine the outcomes of behavioral interactions.

Dominance hierarchies form because some critical resource is limiting, and individuals of varying abilities compete for access to that resource (see Gauthreaux, 1978). In the case of American redstarts in Jamaica, food is probably the limiting resource (Lovette and Holmes, 1995; Parrish and Sherry, 1994), and individuals compete over access to territories that will provide sufficient and consistent food levels for the duration of the nonbreeding period. Therefore, if behavioral dominance structures patterns of habitat occupancy, the most intense competition for territories should take place in habitats that are the most suitable. Removal experiments are an effective and informative way to assess the importance of dominance behavior and resource competition in driving spacing patterns. Differential replacement by males and females in male- and female-vacated territories provides strong evidence for differences in habitat suitability and for the role of behavioral dominance. Morton et al. (1987) removed four male hooded warblers (*Wilsonia citrina*) and found that two were replaced by new males and none by females, leading them to suggest that sexual habitat segregation in winter might be due to innate preferences (i.e, habitat specialization) by males and females. This idea was further supported by laboratory studies with hand-reared birds (Morton, 1990) and additional field data (Morton et al., 1993). More recent removal experiments with this species, however, in female-type habitat found that the sex of the replacement bird could not be predicted by the sex of the removed territory owner (Stutchbury, 1994).

When I removed redstarts from male- and female-biased habitat types, replacement occurred in both habitats, mostly by females and younger males, suggesting that territorial exclusion was keeping individuals out of both sites. However, significantly more territories were reoccupied in mangrove compared to scrub, and those territories were reoccupied more rapidly, suggesting that competition for sites there was more intense. In addition, vacated male territories in mangrove were occupied disproportionately by females rather than by males, indicating that mostly females had been ex-
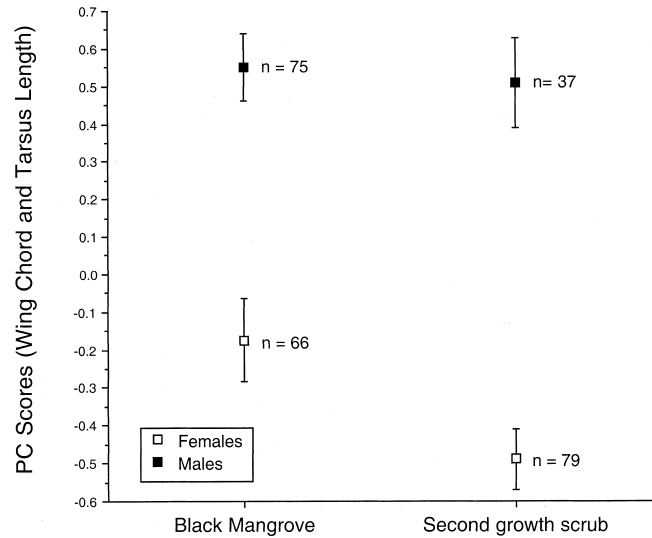
Figure 4
Body sizes (mean ± 1 SE) of male and female American redstarts occupying mangrove (male-biased) and second-growth scrub (female-biased) habitat in Jamaica. Body size calculations are the first principal component scores from an analysis including wing chord and tarsus length. Data are from individuals captured in the autumn (October and November) of 1994 and 1995.

cluded from male-biased habitat and that these territories were not sex specific. The more rapid and complete settlement by excluded individuals in one habitat relative to another supports the behavioral dominance hypothesis.

Simulations of territorial intruders with a stuffed decoy accompanied by a vocalization playback demonstrated that male and female redstarts in mangrove responded more aggressively than females but only slightly more than males in female-biased scrub habitats. Higher levels of aggression by redstarts in mangrove may be due to several factors. First, aggressiveness of individuals in mangrove may represent a quality intrinsic to those redstarts, possibly regulated by circulating levels of plasma testosterone (e.g., Ketterson and Nolan, 1992; Wingfield et al., 1987). Second, differences in measured levels of aggression may represent a frequency-dependent response. In other words, redstarts in mangrove may have exhibited higher levels of aggression to a vocalization playback because they have been involved in interactions more frequently. A third possibility is that mangrove habitat is of higher suitability, and individuals exhibit higher levels of resource defense because they have more to lose (e.g., Brown, 1964; Elwood et al., 1998). Finally, higher levels of aggression may be due to prior residence advantage of older, returning birds (Beletsky and Orians, 1989; Holberton et al., 1990; Krebs, 1982). Although my experiments do not allow for differentiation of these four causes of higher aggression, they do demonstrate that redstarts in mangrove exhibited higher levels of aggression than individuals in scrub, a finding consistent with the behavioral dominance hypothesis but not with the habitat specialization model. Therefore, differences in aggression, regardless of their ultimate causation, may in part be responsible for determining the outcomes of behavioral interactions and ultimately habitat occupancy patterns.

The ability of males to dominate and exclude females and some younger males is also associated with differences in body size. Overall, males were significantly larger than females, and 40% of all displacements were by males displacing females rather than males being displaced by females (10%). Despite this fact, some females were able to persist and establish ter-

ritories in mangrove habitats. These females were not only more aggressive as indicated by results of playback experiments (see above), but they were also significantly larger than those in scrub habitat. This suggests that body size, at least for females, could be partially responsible for allowing them to persist in mangrove habitat. To test for the effect of female body size in winning antagonistic encounters, neutral-ground experiments between females of small and large body size from both habitats will be required.

In summary, results of removal experiments, combined with data on autumn settlement patterns, territory displacements, and aggressive behavior, support the hypothesis that behavioral dominance is responsible for structuring winter habitat segregation in American redstarts. Patterns of sexual habitat segregation, at least in Jamaica, appear to be formed by adult males settling into high suitability habitats and excluding subordinates, which are predominately females and some HY males. Factors other than sex and age may affect the ability of some individuals to acquire territories in male-biased habitat. In winter, both sexes of redstarts exhibit overt agonistic behaviors involving vocalizations, aerial displays, posturing, and physical contact (Ficken, 1962; Holmes et al., 1989; Sherry and Holmes, 1997), and this behavior eventually results in displacement or at least territory boundary adjustments (Marra, 1998). Differences among individuals in these aggressive behaviors may be partially responsible for the outcomes of dominance interactions and may explain why some females can acquire territories in male-biased habitat.

A predicted outcome of behavioral dominance is that birds forced into less suitable habitat will have lower survival or decline in physical condition. Marra and Holberton (1998) measured circulating levels of corticosterone, a hormone associated with behavioral and physiological changes in energy demand (Harvey et al., 1984; Wingfield, 1994) in redstarts occupying these Jamaican mangrove and scrub habitats in autumn just after territory establishment and then again in these same individuals in spring. Their results demonstrated that in autumn, regardless of sex and age, redstarts had similar baseline corticosterone concentrations across both habitat types. However, 6 months later, in March at the end of the tropical dry season, redstarts in the female-biased, scrub habitat had significantly higher basal corticosterone concentrations, whereas redstarts with territories in mangrove had corticosterone concentrations similar to those in autumn. High levels of corticosterone suggest that these birds were in relatively poor energetic condition. Corticosterone is thought to increase foraging effort in an attempt to increase or maintain energy reserves (Astheimer et al., 1992; Gray et al., 1990; Wingfield, 1988; Wingfield and Silverin, 1986). Redstarts with territories in scrub also lost significantly more body mass compared to birds in mangrove, had lower annual survival rates (Marra and Holmes, in press), and departed later on spring migration (Marra et al., 1998), regardless of sex or age. Taken together, these results demonstrate that population consequences can arise from sexual habitat segregation.

Gauthreaux (1978, 1982) proposed that behavioral dominance and its consequences, such as the ones I have described here, are important factors regulating patterns of dispersal and migration within species. He argued that differential migration in the fall, as birds settle onto their wintering quarters, results from dominance interactions and can explain patterns such as latitudinal (Ketterson and Nolan, 1976, 1983, 1985; Myers, 1981) and altitudinal (Diamond and Smith, 1973) segregation of age and sex classes. He reasoned that subordinate individuals are forced to occupy more southern areas farther from breeding areas and as a result arrive back to breeding areas later than dominant individuals wintering closer to the breeding grounds. Empirical evidence, however, has thus far

failed to provide clear support for this hypothesis (Ketterson and Nolan, 1983, 1985; Rogers et al., 1989; but see Lundberg et al., 1981). In the case of American redstarts, intraspecific competition and resulting segregation among habitats occurs within a site at the same latitude and elevation and can affect the timing of spring migration (Marra et al., 1998). In this way, the data presented here for redstarts, a species exhibiting habitat segregation, support Gauthreaux's theory (1978, 1982) that behavioral dominance and resulting despotic distribution on the nonbreeding grounds may play a part in influencing dispersal and migration.

Behavioral dominance has been shown to be the underlying mechanism driving habitat occupancy patterns during the breeding season in many bird species (see Gauthreaux, 1978). Furthermore, its role in structuring winter social systems in birds forming flocks has been well documented (e.g., Enstrom, 1992; Holberton et al., 1990; Ketterson, 1979; Lahti et al., 1997, 1998; Nakamura et al., 1996; Piper and Wiley, 1989; Rohwer, 1977; Slotow and Paxinos, 1997; Smith and Metcalfe, 1997), and several studies have also shown that, within flocks, behavioral dominance results in lower overwinter survival for subordinates (Desrochers et al., 1988; Fretwell, 1969; Kikkawa, 1980; Smith et al., 1980). Little information, however, exists regarding the role that intraspecific dominance behavior plays in regulating habitat use during the nonbreeding season for territorial long-distance migrant passerines (Greenberg, 1986). My findings appear to be the first to identify and evaluate the potential effects of dominance behavior among sex and age classes in any territorial migrant passerine in winter. More research on additional species is needed to better understand the pervasiveness of behavioral dominance and its associated influences on individual condition and ultimately population dynamics. Habitat segregation is found throughout most of the winter range of American redstarts, and behavioral dominance may be the underlying mechanism structuring this habitat segregation throughout that distribution. Identification of the fundamental mechanisms involved in habitat choice, such as was done here, can lead to a better understanding of the factors that drive the population dynamics of these birds (Bernstein et al., 1991; Sherry and Holmes, 1996).

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