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CONSEQUENCES OF DOMINANCE-MEDIATED HABITAT SEGREGATION IN AMERICAN REDSTARTS DURING THE NONBREEDING SEASON

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ABSTRACT.—Several species of migratory songbirds exhibit a distinct form of habitat segregation while on their Neotropical wintering grounds in which males and females occupy different habitat types. In the American Redstart (*Setophaga ruticilla*), that sexual habitat segregation is a result of behavioral dominance of older males. In that study, we examined whether such dominance behavior and the resulting differential habitat segregation has consequences for the condition or survival of excluded individuals. We quantified the physical condition and survival of redstarts (both males and females) occupying two habitat types that differed in the proportion of males and females present in Jamaica. Both sexes of redstarts occupying female-biased habitat lost significantly more mass over-winter and had lower annual survival and longevity compared to individuals in male-biased habitat. These results suggest that nonbreeding habitats differed in suitability, with the least suitable habitat being occupied predominately by females. Because most female redstarts are forced to over-winter in these kinds of habitats, they may often be in poor physiological condition prior to departing on spring migration for the breeding grounds. This in turn may influence dynamics of the breeding period by determining their condition and perhaps reproductive success. Furthermore, because winter habitat segregation appears to lower female survivorship, it may also limit the number and availability of breeding females. These results implicate events that occur during the nonbreeding period as playing a critical role in the annual dynamics of this migratory species. *Received 30 September 1999, accepted 8 August 2000.*

IDENTIFYING THE FACTORS that limit abundance of organisms is essential to understanding their population dynamics. Unfortunately, this is difficult because of the complex life cycles of most organisms and problems in assessing relative importance of factors such as weather, food, habitat, and intra- and interspecific interactions. The complexities associated with determining limiting processes becomes especially apparent for long-distance migratory birds that range over large geographical areas.

Progress toward identifying factors that control population dynamics of migratory birds has been further hindered because most studies have focused on describing patterns (e.g. distribution and habitat associations: see papers in Keast and Morton 1980, Hagan and Johnston 1992, Martin and Finch 1995) rather than understanding population processes. This emphasis is especially true for research on migrant songbirds in their Neotropical wintering

grounds where work has only recently started to focus on the demographic processes affecting population dynamics (e.g. Holmes et al. 1989, Greenberg 1997, Wunderle 1995, Marra and Holberton 1998, Marra et al. 1998). Critical data on how habitat occupancy influences population demography, including physical condition and survival, in such species during the nonbreeding period are almost nonexistent. Such information is essential to assess the degree to which the winter period is limiting for Neotropical migrant species.

Patterns of habitat occupancy can greatly influence the condition and survival of birds. During the nonbreeding season, many species of migratory birds occupy and defend individual and exclusive territories in a wide array of both disturbed and natural habitat types, and are thus often considered to be habitat generalists (see Stiles 1980, Hutto 1992, Wunderle and Waide 1993, Sherry and Holmes 1995). Recently, however, more detailed investigations involving an increasing number of migratory bird species have revealed that although many species are widely distributed, the proportion of males and females present can vary depend-

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ing on the habitat. This pattern of habitat distribution in which some habitats have high proportions of males and others have high proportions of females is referred to as "sexual habitat segregation" (Lynch et al. 1985, Ornat and Greenberg 1990). Sexual habitat segregation is important because it implies a form of intraspecific habitat specialization that could lead to different demographic consequences for males and females, thus affecting population dynamics. To date, at least 14 species of migratory songbirds have been shown to exhibit sexual habitat segregation on their nonbreeding grounds (e.g. Nisbet and Medway 1972, Ornat and Greenberg 1990, Greenberg et al. 1997, P. P. Marra unpubl. data).

Two hypotheses have been proposed to explain proximate causal mechanisms that underlie sexual habitat segregation, and each predicts specific outcomes for the physical condition and survival of birds that occupy those habitat types. These are not necessarily mutually exclusive hypotheses, although they can operationally be treated as such. The first hypothesis proposes that males and females each specialize in a particular habitat type (Morton 1990), and that consequences of habitat occupancy will be within a sex and within each habitat type and are the result of intrasexual competition. The second hypothesis proposes that more dominant individuals (mostly males) exclude subordinate birds (mainly females) from preferred habitats (Gauthreaux 1978, Lynch et al. 1985, Marra et al. 1993, Marra 1998), and implies that males and females compete with one another for limiting resources. Evidence from removal experiments, from observations of habitat choice by young, naive birds, and from measurements of aggression in American Redstarts (*Setophaga ruticilla*) in Jamaica supports the second hypothesis, that is, that behavioral dominance structures patterns of sexual habitat segregation (Marra et al. 1993, 1998; Marra 1998, Marra 2000). Therefore, an additional predicted outcome of the behavioral-dominance model is that, because some individuals exclude others from the more suitable habitat, excluded individuals should in most years incur some demographic consequence. Specifically, we proposed that both males and females will maintain good physical and physiological condition and survive better in the male-biased habitat over the nonbreed-

ing period, compared to those individuals (i.e. mostly females) excluded by males via dominance behavior and being forced to occupy inferior habitats. To test these predictions, we examined population density, changes in overwinter bird density, over winter persistence, annual return rates, annual survival, longevity, and changes in body mass of American Redstarts occupying two habitat types that differed in their proportions of males and females. American Redstarts are ideal for such a study because they can be sexed and aged, they exhibit strong territoriality and they are easily captured, and are readily observable during the nonbreeding period. Furthermore, they exhibit sexual habitat segregation throughout most of their winter range (Sherry and Holmes 1997, Marra and Holberton 1998).

STUDY AREAS AND METHODS

Study area.—We conducted this research at the Font Hill Nature Preserve (18°02'N, 77°57'W, <5 m above sea level), about 13 km west of Black River, St. Elizabeth Parish, Jamaica. This southwestern coast is one of the driest regions of Jamaica (<1,000 mm of rain per year) and, as is typical of many tropical regions, experiences strong seasonality in levels of precipitation. At this site, rainfall level was high from August to November, when average monthly rainfall typically exceeded 100 mm, and then declined after November, with <25 mm of rain per month until May (Petroleum Corporation of Jamaica unpubl. data).

Two habitat types were considered in this study, mangrove forest and second-growth scrub. Study sites in mangrove forest were dominated by black mangrove (*Avicennia germinans*) but also contained some white mangrove (*Languncularia recemosa*) and red mangrove (*Rhizophora mangle*). Mangrove stands typically were inundated with 0.5–1.0 m of standing water in October and November (hereafter "autumn") during the rainy season, but then water levels became progressively lower toward February and March (hereafter "spring"). No understory or ground level vegetation was present except for the pneumatophores of the mangrove trees. Black mangroves, ranged in diameter at breast height (dbh) from 25 to 75 cm, were regularly dispersed at intervals of 10 to 15 m, and had dense and continuous canopies averaging about 12 m in height. These trees retained the majority of their leaves as the dry season approached, keeping this habitat moist and shady throughout the time that redstarts were present.

Study sites in second-growth scrub contained trees ranging from 2 to 5 cm in dbh and 2 to 8 m in height forming a dense understory and ground layer of vegetation. Although a nature preserve, cattle

roamed freely on these sites and trees were often cut for charcoal and fence-posts, creating a mosaic of thickets, vine tangles and grassy patches. Vegetation in the scrub was dominated by logwood trees (*Haematoxylon campechium*), a thorny species with a fluted trunk introduced into Jamaica from Central America in the nineteenth century (Adams 1972). Scrub sites also contained several less common tree species including *Bursera simaruba*, *Terminalia latifolia*, and *Crescentia alata*. Unlike mangroves, trees and other vegetation in the scrub sites dropped most of their leaves during the dry season in spring, and standing water was never present on these sites.

This research was conducted on three 5 ha study sites in mangrove habitat and two 5 ha study sites in scrub habitat. The additional site in mangrove was necessary to obtain larger sample sizes of female redstarts in that habitat type. Two of the mangrove sites were separated by 200 m and both of these were ≈ 1 km away from the third mangrove site. The sites in scrub were separated by 1 km. Study sites were gridded at 25 m intervals to facilitate locating redstarts and for mapping their territories.

Data collection.—Redstarts were captured in October and early November using mist nets accompanied by broadcasts of songs and chip notes and a redstart decoy (Holmes et al. 1989, Marra and Holberton 1998). In spring, because response rates to song playbacks decline (P. P. Marra unpubl. data), especially in birds that were captured the previous autumn, most redstarts had to be captured or recaptured with intensive mist-netting within each territory. At the time of capture, all individuals were banded with unique color band combinations, aged, sexed, measured (unflattened wing chord, tarsus length, bill length, width, and depth to ± 0.1 mm) and weighed to ± 0.1 g on an Ohaus balance. Redstarts were sexed and then aged as either hatch-year (< 1 year-old, hereafter HY) or after hatch-year (> 1 year old, hereafter AHY) using criteria described by Marra et al. (1993), Pyle (1987), and Sherry and Holmes (1997).

Number of redstarts of each age and sex was estimated for each habitat by intensively mapping activities of color-marked individuals on study sites over a 4–6 week period in each autumn and spring, starting in autumn of 1994 and continuing through spring of 1996. Territory mapping consisted of finding a redstart and recording its movements for an average duration of 10 min, but observation periods occasionally lasted up to 1 h. Within each season, each redstart was observed for a total of several hours to identify territorial boundaries.

In spring 1994 and 1995, we recaptured as many color-marked redstarts as possible to quantify changes in body mass of individuals over the winter period (recaptured sample). We also caught a sample of redstarts in spring that had not been captured previously (population sample). To assess physical condition (defined here as mass corrected for body size;

Johnson et al. 1985, Ringleman and Szymczak 1985, Dufour and Weatherhead 1998), we first calculated scores of a principal-component analysis (PCA) based on unflattened wing chord and tarsus length of all birds in spring, including those recaptured. The scores from the first PCA were used as an estimate of skeletal body size. Body mass was then regressed against those PCA scores and residuals from that regression were used as an estimate of physical condition.

Between 1992 and 1997 we quantified over-winter persistence of redstarts in each habitat by resighting all color banded birds in spring that had been banded the previous autumn. When a bird was not resighted on the first visit, we revisited that territory a minimum of 5 times, often using song playbacks to establish that an individual was not present. We also searched surrounding habitat within 150 m in case redstart territories had shifted. For estimates of over-summer survivorship, we determined rate at which color-banded redstarts returned from one spring (March) to the following autumn (October) in each habitat. Finally, we also calculated annual survivorship, on the basis of returns of color-marked individuals from one October to the next October, and estimated longevity, which we defined as number of years following initial capture that individual redstarts returned to sites in each habitat. Because redstarts had been banded on those sites since 1986 (Holmes et al. 1989), some individuals banded in years prior to 1992 were also included in survivorship and longevity analyses.

Statistical analyses.—For mass change in recaptured redstarts, effects of sex (male vs. female), habitat (mangrove vs. scrub), and season (autumn vs. spring), and a random effect (i.e. individual) to control for repeated sampling of individuals, were analyzed with a mixed-model ANOVA. For physical condition of redstarts captured only in spring, effect of age (HY vs. AHY), sex (male vs. female), and habitat (mangrove vs. scrub) was examined with a three-way ANOVA. All data met assumptions of normality and equal variances. Analyses of annual survivorship were conducted with Kaplan-Meier tests (SAS 1997). The Kaplan-Meier survivorship model is the most appropriate for data such as these, compared to the more often used survivorship modeling techniques (i.e. Jolly-Seber and SURGE), because of the low probability ($< 5\%$) of missing a color-banded bird within a time period (Pollack et al. 1989, Bunck et al. 1995, Pollack et al. 1995, J. Nichols pers. comm.). Statistical analyses were made using JMP (SAS 1997).

RESULTS

Population structure.—Redstart densities ranged from 20–30 individuals per 5 ha in most

TABLE 1. Population structure of American Redstarts occupying mangrove and scrub habitats in autumn (late-October) of the nonbreeding period in Jamaica, West Indies.

	1994	1995	1996	1994–1996
Density (individuals per 5 ha ± SE)				
Mangrove (<i>n</i> = 3 plots)	25.8 ± 3.8	29.3 ± 5.5	56.3 ± 12.4	37.2 ± 6.3
Scrub (<i>n</i> = 2 plots)	21.0 ± 7.0	27.0 ± 11.0	20.0 ± 7.0	22.7 ± 4.1
Sex composition (proportion male; mean ± SE (<i>n</i>))				
Mangrove	0.60 ± 0.02 (48)	0.60 ± 0.04 (54)	0.60 ± 0.01 (102)	0.61 ± 0.02 (204)
Scrub	0.39 ± 0.04 (16)	0.26 ± 0.05 (13)	0.08 ± 0.00 (13)	0.24 ± 0.06 (32)
Age composition (proportion AHY; mean ± SE (<i>n</i>))				
Male				
Mangrove	0.50 ± 0.02 (24)	0.80 ± 0.06 (43)	0.47 ± 0.03 (48)	0.59 ± 0.05 (114)
Scrub	0.32 ± 0.02 (5)	0.61 ± 0.01 (8)	0.50 ± 0.50 (2)	0.47 ± 0.14 (15)
Female				
Mangrove	0.45 ± 0.16 (9)	0.93 ± 0.06 (28)	0.65 ± 0.01 (26)	0.70 ± 0.08 (63)
Scrub	0.50 ± 0.17 (7)	0.58 ± 0.15 (24)	0.64 ± 0.14 (20)	0.57 ± 0.07 (51)

^a AHY = after-hatch year or >1 year old.

years in both habitats (Table 1). In 1994 and 1995, redstart abundance was higher on mangrove study sites, but differences between habitat types were not statistically significant ($t = 1.7$, $df = 13$, $P = 0.11$; Table 1). In 1996, number of redstarts more than doubled on mangrove sites while staying constant in scrub sites (Table 1). From autumn to spring, densities of redstarts declined slightly in mangrove (37.2 ± 6.3 SE to 32.9 ± 3.7) whereas they increased slightly in scrub (22.7 ± 4.1 to 25.1 ± 4.8); these differences were not statistically significant (habitat, $F = 3.8$, $P = 0.08$; season, $F = 0.02$, $P = 0.88$; habitat \times season, $F = 0.33$, $P = 0.58$, $n = 12$).

Sex composition within each habitat remained constant over the winter period (mangrove, 0.61 ± 0.02 males in autumn to 0.61 ± 0.03 in spring; scrub, 0.24 ± 0.06 males in autumn to 0.23 ± 0.06 in spring). Sex composition was consistently male-biased in mangrove and female-biased in scrub (Table 1). Over the three year study period, mangrove sites contained an average 60% male and 40% female redstarts, whereas scrub had an average of 24% male and 76% female redstarts. Both sex ratios were significantly different from 50:50 (mangrove, $\chi^2 = 7.97$, $df = 2$, $P = 0.02$; scrub, $\chi^2 = 22.9$, $df = 2$, $P < 0.000$). Age composition was more variable between habitats and years, but there were significantly more AHY males and AHY females in mangrove than in scrub (Table 1). Over the three year study period, 59% of males in mangrove forest ($\chi^2 = 9.74$, $df = 2$, $P = 0.01$) and 47% in scrub ($\chi^2 = 1.60$, $df = 2$, $P < 0.45$) were

AHY. The age composition of females was significantly biased toward more AHYs in mangrove (70% AHY; $\chi^2 = 13.2$, $df = 2$, $P < 0.01$) but did not differ significantly from 50:50 in scrub (57% AHY; $\chi^2 = 4.53$, $df = 2$, $P < 0.10$).

Changes in body mass.—Redstarts in scrub, but not in mangrove, lost body mass over the winter period, regardless of age or sex. In a three-way ANOVA on mass change of redstarts captured in autumn and then recaptured in spring, only sex ($F = 8.84$, $df = 1$ and 35, $P = 0.005$), and the habitat by season interaction ($F = 15.1$, $df = 1$ and 35, $P = 0.0004$) were significant. In these cases, males were heavier than females, and both males and females lost mass from autumn to spring in scrub but not in mangrove. Female redstarts in mangrove maintained body mass over winter (6.75 ± 0.11 g SE to 6.77 ± 0.10 g; $n = 13$), whereas those in scrub lost body mass (6.89 ± 0.07 g to 6.68 ± 0.09 g; $n = 16$). Male redstarts in mangrove increased slightly in body mass over the winter period (7.12 ± 0.11 g to 7.33 ± 0.16 g; $n = 4$), whereas males in scrub lost significant amounts of body mass (7.18 ± 0.12 g to 6.85 ± 0.13 g; $n = 6$).

Some individuals were captured only in spring. Because no estimate of body mass was available for them from autumn, we could not quantify changes in body mass. Instead, we examined physical condition of those redstarts at the end of the winter period by analyzing their body mass while controlling for their body size, and we compared this between the two habitats. In a three-way ANOVA of these data, only habitat was significant ($F = 6.29$, $df = 1$

TABLE 2. Over-winter persistence of color-banded American Redstarts from October to March in mangrove and scrub habitats in Jamaica, West Indies.

	Percent persisting (<i>n</i>)					Total ^a
	1992	1993	1994	1995	1996	
Females						
AHY ^b						
Mangrove ^c	70.6 (17)	58.8 (17)	60.0 (15)	100 (21)	85.0 (20)	76.7 (90)
Scrub	58.3 (12)	75.0 (4)	80.0 (10)	81.0 (16)	81.0 (16)	75.9 (58)
HY ^d						
Mangrove	66.7 (6)	57.1 (7)	37.5 (16)	76.9 (13)	83.3 (24)	66.6 (66)
Scrub	22.0 (9)	—	69.2 (13)	61.9 (21)	85.7 (14)	63.2 (57)
Males						
AHY						
Mangrove	69.0 (29)	73.3 (15)	57.9 (19)	86.2 (29)	71.4 (28)	72.5 (120)
Scrub	33.3 (3)	33.3 (6)	16.7 (6)	66.7 (3)	100 (1)	36.8 (19)
HY						
Mangrove	50.0 (8)	81.8 (11)	70.6 (17)	80.0 (15)	85.1 (47)	78.6 (98)
Scrub	37.5 (8)	50.0 (4)	38.5 (13)	36.4 (11)	57.1 (7)	41.9 (43)

^a Fisher's exact test comparing mangrove versus scrub column totals and the likelihood of persisting versus not persisting in AHY females ($\chi^2 = 0.01$, $df = 3$, $P = 0.53$); HY females ($\chi^2 = 0.17$, $df = 3$, $P = 0.41$); AHY males ($\chi^2 = 8.9$, $df = 3$, $P = 0.0003$); and HY males ($\chi^2 = 17.8$, $df = 3$, $P < 0.0001$).

^b Data combined from three mangrove and two scrub sites.

^c After-hatch-year or >1 year old.

^d Hatch-year or <1 year old.

and 101, $P = 0.01$). Thus, in spring just prior to northward departure, redstarts in scrub were lighter given their body size, regardless of sex or age, than were redstarts in mangrove.

Site persistence and return rates.—Overwinter persistence, or rate at which color-banded redstarts remained on territory from mid-October to mid-March, was quantified for each habitat. Females persisted at equal rates over the winter period in both habitats, whereas males exhibited significantly higher persistence in mangrove than in scrub (Table 2). Considering effect of age, AHY females had slightly higher overall persistence than HY females in both habitat types. For males, both AHY and HY age classes persisted at higher rates in mangrove compared to scrub; however, samples sizes for males were small in scrub, so these estimates may not be reliable.

Spring to autumn return rates of redstarts were consistently higher in mangrove compared to scrub, but the difference was only significantly higher for females (Table 3). Overall mean return rates for males and females were between 60 and 70% in mangrove and between 40 and 44% in scrub. Furthermore, these return rates were consistently higher in mangrove, regardless of age (Table 3), although return rates of males in scrub are based on small sample sizes and thus may not accurately characterize

their return rates in that habitat. Overall, females persisted equally well in both habitats over winter, whereas males exhibited higher persistence in mangrove compared to scrub. Furthermore, both males and females of both age classes returned at higher rates year-to-year in mangrove compared to scrub.

Survivorship and Longevity.—Annual survivorship (October to October) was significantly higher for redstarts in mangrove habitat compared to scrub habitat for all age and sex groups ($P < 0.02$; Fig. 1), except for HY females, which exhibited higher but only marginally significant ($P = 0.08$) survivorship in mangrove compared to scrub. Average longevity (number of years an individual returned to a site after banding) of redstarts in mangrove habitat was also higher across all sex and age categories (Table 4). On average, longevity of color-marked redstarts in mangrove was 1.5 ± 0.16 years compared with 0.51 ± 0.08 years for redstarts in scrub. Maximum longevity was observed in mangrove with one male banded as an AHY (i.e. at least 1.5 years of age) returning for eight consecutive winter seasons and a female banded as an AHY returning for six years. In contrast, the oldest redstart in the scrub habitat was a female banded as an AHY, which returned four consecutive seasons.

TABLE 3. Return rates of color-banded American Redstarts (*Setophaga ruticilla*) from March to October in mangrove and scrub habitats in Jamaica, West Indies.

	Percent returning (<i>n</i>)					Total ^a
	1993	1994	1995	1996	1997	
Females						
AHY ^b						
Mangrove ^c	54.5 (11)	91.7 (12)	72.7 (11)	69.2 (26)	27.8 (18)	61.5 (78)
Scrub	12.5 (8)	33.0 (9)	50.0 (12)	50.0 (18)	25.0 (16)	36.5 (63)
HY ^d						
Mangrove	66.7 (6)	57.1 (7)	37.5 (16)	76.9 (13)	83.3 (24)	66.6 (66)
Scrub	0.0 (0)	0.0 (0)	55.6 (18)	53.3 (15)	20.0 (15)	41.0 (98)
Males						
AHY						
Mangrove	59.1 (22)	93.3 (15)	60.0 (15)	71.1 (31)	69.6 (23)	69.8 (106)
Scrub	0 (1)	50.0 (2)	50.0 (2)	50.0 (2)	33.0 (3)	40.0 (10)
HY						
Mangrove	42.9 (7)	80.0 (10)	57.1 (14)	78.6 (14)	53.7 (41)	60.5 (86)
Scrub	25.0 (4)	100 (2)	62.5 (8)	40.0 (5)	16.7 (6)	44.0 (25)

^a Fisher's exact test comparing mangrove versus scrub column totals and the likelihood of returning versus not returning in AHY females ($\chi^2 = 8.83$, $df = 3$, $P = 0.003$); HY females ($\chi^2 = 6.0$, $df = 3$, $P = 0.01$); AHY males ($\chi^2 = 2.27$, $df = 3$, $P = 0.12$); and HY males ($\chi^2 = 2.12$, $df = 3$, $P = 0.11$).

^b Data are combined from three mangrove and two scrub sites.

^c After-hatch-year or >1 year old.

^d Hatch-year or <1 year old.

DISCUSSION

Patterns of habitat occupancy can have profound effects on physical condition and ultimately fitness of individuals. During the nonbreeding period in Jamaica, male and female American Redstarts often occupy different habitats due to the despotic behavior of older males (Marra et al. 1993, Marra 2000). Results of this study show that this sexual habitat segregation has negative consequences for the physical condition and survival of redstarts occupying female-biased (scrub) habitat. Redstarts occupying scrub habitat lost body mass over the winter period, had lower return rates from March to October, and had lower annual survival compared with individuals in mangrove habitat. This indicates that these nonbreeding habitats differ in suitability, with less suitable habitats being those occupied predominantly by females. Below, we discuss implications of these results for the life history and population dynamics of this long-distance migratory bird and possibly other species that exhibit sexual habitat segregation during the nonbreeding season.

We measured condition of American Redstarts that occupy two different habitats, using both direct (i.e. body mass) and indirect indices. One indirect measure, density of individuals, has been considered to be positively cor-

related to habitat suitability. In this study, however, we found no clear patterns among density and more direct measures of condition. In two years (1994 and 1995), redstart density was the same in the two habitats, and yet those individuals in scrub habitat lost mass (this study) and had elevated corticosterone (Marra and Holberton 1998). Only in one year (1996) were densities different between the two habitats, and unfortunately, changes in body mass were not quantified in that year. The result that density of individuals in a habitat may not be a reliable indication of physical condition or quality of a particular habitat has important implications, because density is one of the most widely used indices of habitat suitability in both breeding and nonbreeding seasons. Several studies of migrants in winter have shown a positive correlation between resource abundance and bird density (Greenberg 1992, Lefebvre et al. 1994) and between individual condition and density (Sherry and Holmes 1996), but others have failed to find such a relationship (Winker et al. 1990, Wunderle 1995). Therefore, density can sometimes provide misleading information regarding habitat suitability. This may be especially so if social dominance is involved in structuring patterns of habitat occupancy, as illustrated by this study. Despots may exclude a disproportionate num-

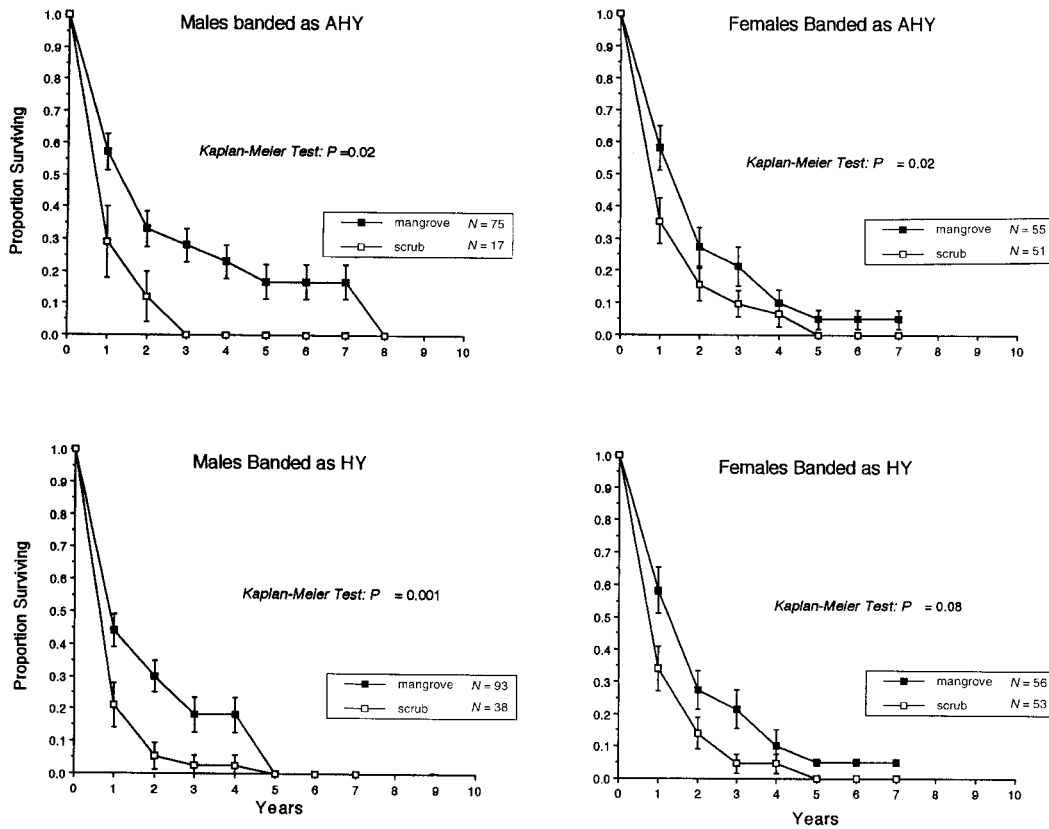


FIG. 1. Annual survivorship of male and female American Redstarts banded as after hatch-year (AHY) and hatch-year (HY) in scrub and mangrove habitats on the non-breeding grounds in Jamaica, West Indies. Means \pm 1 SE.

ber of individuals into suboptimal habitats which result in those habitats having equal or higher densities than in more suitable habitats (Rosenzweig 1985, Holt 1985). In support of that, our data show declines in density of redstarts over-winter in mangrove habitat and a slight increase in scrub habitat. Therefore, caution should be exercised when using density to infer habitat suitability for migrant birds (Wiens and Rotenberry 1981, Van Horne 1983, Vickery et al. 1992), especially during the non-breeding season (Winker et al. 1995).

Turnover rates of territorial individuals are predicted to be higher in habitats of lower suitability (e.g. Brown 1969, Pulliam 1988, McPeck and Holt 1992, Winker et al. 1995). Redstart densities, however, remained fairly stable over the winter period in both scrub and mangrove habitats, and females, but not males, persisted equally well in both habitats. The lower over-

winter persistence for males in scrub habitat probably results from the ability of males to move into habitats of higher suitability when vacancies occur, not necessarily higher over-winter mortality. Males are slightly larger and exhibit higher levels of aggression than females and are more likely to acquire territories in habitats of higher suitability, such as mangrove (Marra 1998, Marra 2000). Furthermore, several color-banded male redstarts with territories in scrub habitat were observed to shift to mangrove habitat, but the reverse pattern was never seen (P. P. Marra unpubl. data). It is interesting that females in scrub habitat, despite their deteriorating physical condition, exhibited high levels of over-winter persistence. This suggests that habitats may be saturated and limiting—at least for individuals of inferior competitive abilities that can not compete for territorial vacancies in better habitats.

TABLE 4. Longevity^a (October to October) of color-banded American Redstarts in mangrove^b and scrub habitats in Jamaica, West Indies (1988–1997).

	Mean longevity (years) \pm SD					
	<i>n</i>	Mangrove	Max.	<i>n</i>	Scrub	Max.
Females						
Banded as AHY ^c	56	1.14 \pm 0.18	6	57	0.60 \pm 0.15	4
Banded as HY ^d	53	0.88 \pm 0.18	4	56	0.43 \pm 0.09	3
All females combined	109	1.04 \pm 0.13		113	0.59 \pm 0.10	
Males						
Banded as AHY	75	2.08 \pm 0.36	8	17	0.41 \pm 0.17	2
Banded as HY	93	1.10 \pm 0.18	4	38	0.26 \pm 0.09	3
All males combined	168	1.79 \pm 0.26		55	0.31 \pm 0.08	
Sexes combined	276	1.50 \pm 0.16		162	0.51 \pm 0.08	

^a Longevity estimates were calculated using Kaplan-Meier analyses (JMP 1995).

^b Data were combined from three mangrove sites and two scrub sites.

^c After-hatch-year or >1 year old. All AHY redstarts are at least 1 year old at the time of banding. Therefore, values do not take into account age prior to capture.

^d Hatch-year or <1 year old.

Few studies have attempted to quantify changes in the physical condition of migrant birds occupying different habitat types over the nonbreeding period. Niven (1996), who studied Hooded Warblers (*Wilsonia citrina*) in Mexico in a highly disturbed and a moderately disturbed habitat, found no differences in physical condition in late winter compared to early winter. In his study, however, both habitats were equally male-biased ($>70\%$), an indication, given our results, of high habitat suitability. If so, we would not expect differences in physical condition to occur over the winter period. Sherry and Holmes (1996), working in Jamaica, demonstrated that redstarts in drier habitats had, on average, lighter body mass in spring relative to fall compared to redstarts in wetter habitats. Although those conclusions are based on comparisons of mean body mass of a population sample of redstarts in each season, not mass changes for the same individuals, they are in agreement with our results. Both studies, however, are based on the same species in Jamaica. More research is needed—with additional species across an array of habitats—to test further whether physical condition changes differentially over the winter season in different habitat types and if these changes correspond to patterns of sexual habitat segregation.

Changes in redstart body mass are most likely due to catabolism of muscle. Redstarts had no visible subcutaneous fat in the furcular region in either fall or spring (P. P. Marra unpubl. data), and furcular fat is known to correlate

positively with total body fat composition (Rogers 1987, Kremetz and Pendleton 1990). Furthermore, Marra and Holberton (1998) measured plasma corticosterone levels, a hormone associated with changes in energy demand (Harvey et al. 1984), in the same redstarts described in this paper. They found that redstarts occupying scrub habitat exhibited elevated levels of corticosterone in spring relative to fall, whereas corticosterone levels of redstarts in mangrove habitat did not change over the winter period, and redstarts losing mass were indeed those individuals with elevated corticosterone. Chronic elevated levels of plasma corticosterone are known to result in muscle catabolism (Holmes and Phillips 1976, Harvey et al. 1984). Given this latter result, and the fact that these redstarts had no visible subcutaneous fat, mass loss in those birds most likely represents catabolism of muscle mass.

Does mass loss and reduced physical condition of American Redstarts during the nonbreeding season influence life-history strategies and population dynamics? As described above, only males experienced lower over-winter site persistence, and this is probably because of movement of males to better habitats rather than to mortality. Quantification of spring departure times of these same redstarts in Jamaica revealed that redstarts in scrub habitat that lost mass, regardless of age or sex, departed on spring migration significantly later than redstarts in mangrove habitat and were delayed in their arrival on North American breeding grounds (Marra et al. 1998). Elevated

corticosterone and resultant loss in skeletal muscle may play a part in determining when birds are physiologically able to depart on spring migration for the breeding grounds. The implications are important for both New and Old World migrants because early arrival and physical condition upon arrival to the breeding grounds are directly correlated with fitness (Price et al. 1988, Møller 1994, Lozano et al. 1996, Hasselquist 1998).

In addition to influencing spring departure and subsequent breeding-ground arrival times, deteriorated physical condition at the end of winter was also correlated with lower apparent survival and longevity for redstarts occupying scrub habitat, regardless of age or sex. Although it is possible that lower annual survival of redstarts in scrub represents dispersal to better habitats in subsequent seasons, we have no evidence that birds shift habitats between seasons. Because the majority of redstarts that are forced to over-winter in the less suitable scrub habitat are females, they are affected disproportionately. Thus, winter may be a potentially limiting season for females and could influence the dynamics of the breeding period by reducing the number of breeding females. Differential mortality of females during the nonbreeding season, resulting from effects of dominance (Marra 1998, 2000), may thus also contribute to the male-biased sex ratio observed in breeding populations of redstarts (Sherry and Holmes 1997) and perhaps of other species of socially monogamous birds (Breitwisch 1989). A similar conclusion was reached by Benkman (1997) for White-winged Crossbills (*Loxia leucoptera*). He found that female crossbills suffered depressed feeding rates because of agonistic interactions by males, and hypothesized that this could lead to lower female survival, resulting in the male-biased sex ratio commonly observed in this species. Previously, most theories have attributed sex bias to a higher cost of reproduction in females relative to males (Trivers 1972; see Breitwisch 1989).

As stated above, female limitation during the breeding season may play an important role in driving annual population dynamics by reducing number of females available to males for breeding (Marra and Holmes 1997). It may also lead to stronger sexual selection and brighter male coloration (Andersson 1994, Hill et al.

1994, Kvarnemo and Ahnesjö 1996, Benkman 1997). In this way, events during the nonbreeding season and their effects on female mortality schedules and biased sex ratios may be partly responsible for the evolution of sexual dimorphism in migratory birds. This could be tested by comparing winter social systems and degree to which sex ratios are skewed in sexually monomorphic species versus sexually dimorphic species.

For migratory birds wintering in tropical regions, consequences of sexual habitat segregation may be similar across species and across regions because of comparable patterns of rainfall seasonality. Late winter dry seasons occur in equatorial regions and their effects on vegetation and associated insects, and ultimately on birds, are thus probably similar. In Jamaica, both mangrove and scrub habitats have lush vegetation at the end of the wet season in autumn (October) when migrants first arrive, but diverge dramatically over the winter period as the tropical dry season approaches in March and April (Parrish and Sherry 1994). In spring, water in the black mangrove habitats in Jamaica typically dries up but trees retain most of their leaves, whereas in the second-growth scrub habitat, conditions are drier and trees lose the majority of their leaves. This change in vegetation likely influences habitat suitability indirectly by decreasing available vegetative substrate for phytophagous insects and by influencing local microclimate for thermal refugia, thereby reducing amount of food available to insectivorous birds. Insect abundance declines with the onset of the tropical dry season (Janzen 1973, Wolda 1978, LeFebvre et al. 1994, Parrish and Sherry 1994). In fact, Price (1981), Faaborg et al. (1984), and Baillie and Peach (1992) have all found relationships between declining precipitation and declines in habitat condition and bird abundance in India, the Caribbean, and Africa, respectively. Thus, end of winter may represent a period of severe food limitation in many tropical locations (Brown 1969, Gauthreaux 1978) during a critical time when individuals must prepare for spring migration, in some species molt, and to arrive at breeding areas in optimal condition as early as possible.

The nonbreeding season plays a critical role in the annual cycle of American Redstarts. Availability of suitable wintering habitat can

determine physical condition, survival, and ultimately fitness of redstarts and in this way can affect population dynamics of these organisms. That is an important finding because several lines of evidence thus far support the idea that optimal winter habitats are saturated and possibly limiting (Terborgh 1980, Sherry and Holmes 1996, Marra et al. 1998). To understand the role that habitat availability during the non-breeding season plays in regulating population dynamics of migratory birds, it is necessary to consider events during the entire annual cycle (Dolman and Sutherland 1994, Goss-Custard et al. 1995, Sherry and Holmes 1995). We propose here a modification to the Dolman and Sutherland (1994) and Sherry and Holmes (1995) density-dependent models—an incorporation of not only habitat availability in winter and summer, but also the consequences of different habitat occupancy of males and females.

Suppose that reproductive success in a given year produces equal quantities of males and females and these individuals migrate to their wintering grounds where their numbers exceed the carrying capacity of the optimal habitats. Number of males, because of their ability to dominate and exclude females (Marra 1998, 2000), determines how many females can settle in highest quality habitats and maintain optimal physical condition until the end of winter. In this way, quantity and quality of winter habitat available and number of males interact to regulate female condition and survival. In years when male abundance is high, more females will be excluded from optimal habitat, female survival will be lower, and the male-biased sex ratio will be exacerbated on the breeding grounds. In such years, male-male competition on the breeding grounds will be high and reproductive success low, causing adult males to experience higher mortality. Overall, number of new males recruited into the population and old males persisting will be reduced. During the subsequent settlement period on the nonbreeding grounds, because of the lower number of males, more females will be permitted to settle in sites of high suitability, increasing female survival and reducing the male-biased sex ratio. In this way, events on the wintering grounds may act in a site-dependent manner (Rodenhouse et al. 1997) to influence population dynamics. Therefore habitat availability on both wintering and breeding grounds

can interact with abundance of males and females to regulate populations of these migratory birds. Understanding how events in different parts of annual cycles interact is probably the biggest challenge facing students of migration ecology, but it is also important for understanding the factors that control population dynamics of such species. Furthermore, our results illustrate the critical links that exist between tropical wintering grounds and temperate breeding areas and suggest that loss and maintenance of high-quality winter habitat could be a major factor affecting the long-term stability of migratory bird populations.

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