SEXUAL HABITAT SEGREGATION BY AMERICAN REDSTARTS WINTERING IN JAMAICA: IMPORTANCE OF RESOURCE SEASONALITY

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ABSTRACT.—We tested the hypothesis that wintering populations of American Redstarts (*Setophaga ruticilla*) segregate into different habitats by sex in response to ecological conditions associated with an extensive dry season, which typically develops after migrants arrive in northern Neotropical sites. Sex-specific distribution and overwinter persistence of redstarts were quantified at a Jamaican mangrove-scrub ecotone. We also contrasted vegetation structure and food availability in winter territories of the two sexes and in both habitats within and between seasons. Male and female redstarts were significantly segregated by habitat, with males holding territories in mangroves and females predominantly in contiguous scrub habitat. However, we found no significant sex-based difference in overwinter persistence on territories. The average mangrove territory had a higher canopy and more-open understory, higher relative humidity, and greater insect biomass within a season for several insect orders important in redstart diets. Canopy (leaf) cover and abundances of several insect taxa remained more constant over the dry season in mangrove than in scrub habitat. We argue that these between-habitat differences, especially seasonal stability of vegetation features and food abundances in mangrove habitats, affect winter habitat quality for nonbreeding redstarts. *Received 3 March 1993, accepted 31 May 1993.*

NEOTROPICAL-NEARCTIC MIGRANT songbird populations alternate geographically between a relatively short period of breeding in temperate or boreal climates, and a longer period of self-maintenance and survival in tropical habitats. Although early efforts to understand population dynamics of these birds focused on the breeding season, the importance of the nonbreeding season has come to be appreciated increasingly as our understanding of winter habitat use has increased. For example, evidence that nonbreeding habitats vary in quality comes from widespread examples of winter territorial behavior and site tenacity (Rappole and Warner 1980, Greenberg 1986, Holmes et al. 1989, Holmes and Sherry 1992), habitat-specific variation in overwinter site persistence (Greenberg 1992), sexual differences in winter habitat use (Lynch et al. 1985, Morton et al. 1987, Morton 1990, Lopez Ornat and Greenberg 1990, Wunderle 1992), and experimental evidence of nonbreeding habitat competition (Marra et al. 1993). Moreover, the importance of the amount and

quality of wintering habitat is suggested by population declines that are correlated with winter-habitat changes (Terborgh 1989, Robbins et al. 1989, Askins et al. 1990, Leisler 1990, Morton 1992). Yet, we know relatively little about how winter habitats differ, what resources are most important, or the mechanisms of winter habitat choice.

Most Neotropical-Nearctic migrants winter in the northern Neotropics (Terborgh 1989), where rainfall is usually strongly seasonal. Depending on latitude and elevation, a dry season develops in many parts of the Caribbean and Meso-America between December and April after wintering migrant populations have arrived. Seasonal rainfall patterns may influence resource abundance and foraging opportunities for birds (Schwartz 1980, Karr and Freemark 1983, Lefebvre et al. 1992, Poulin et al. 1992), and the degree of seasonal change may differ among habitats (Janzen and Schoener 1968, Janzen 1973, Walter 1973, Wolda 1978, Greenberg 1992). Thus, the stability of resource abundances into the dry season may itself become an important variable affecting winter habitat quality and habitat-selection patterns in Neotropical-Nearctic migrants.

In this study, we explored the possible eco-

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logical bases for variation in habitat quality for overwintering American Redstarts (*Setophaga ruticilla*) inhabiting a Jamaican mangrove-scrub ecotone. We hypothesized that the scrub habitat existing on excessively well-drained, sandy soils would exhibit greater change in structure and resources over the course of the dry season than would adjacent mangrove forest, which occurs on low-lying, waterlogged substrate. We asked whether there is sex-specific variation in habitat occupancy, and whether overwinter persistence on territories is habitat specific. We also measured habitat differences within both the fall and spring seasons as indicators of arrival and departure conditions for redstarts. Finally, we compared the degree of seasonal change in resource abundance (insect biomass) or resource-influencing habitat characteristics (vegetation, micrometeorological factors) in these two habitats over the course of the dry season.

METHODS

Study site.—Fieldwork was conducted at Luana Point, along the southwest coast of Jamaica, West Indies, approximately 13 km west of Black River, St. Elizabeth Parish. Two study sites (9 and 5 ha in size) 155 m apart were selected for their interdigitating mangrove swamp and scrub habitats. The vegetation of the mangrove swamp was dominated by black mangrove (*Avicennia germinans*), with some white mangrove (*Laguncularia racemosa*) and red mangrove (*Rhizophora mangle*) locally. Throughout the mangrove zone there was little understory, and tree bases were constantly submerged in standing water at least 0.5 m in depth during the period preceding the dry season, regardless of tidal cycles. The main swamp forest canopy grew to a height of 8 to 15 m. Adjacent nonmangrove habitat (hereafter referred to as scrub) was between 2 and 8 m tall and was characterized by thick shrub and vine tangles dominated by logwood (*Haematoxylon campechianum*) and red birch (*Bursera simaruba*), with several other tree and shrub species at lower density (for further description of general vegetation, see Holmes et al. 1989).

Both study sites were gridded and flagged at 25-m intervals so that movements of individual birds could be accurately mapped to establish territory boundaries. The mangrove boundary on each plot was mapped in detail by measuring the distance from each 25-m interval point bordering the swamp to the line of pneumatophores originating from the roots of black mangrove trees.

Data on habitat and resource variables associated with territories over winter were collected in autumn (19–29 October 1990) soon after redstarts first arrived on their wintering grounds in Jamaica. Those environmental variables that were expected to change during the winter dry season at our study site (percent canopy and ground cover, micrometeorological variables, and insect abundance) were remeasured during the following spring (23 March–2 April 1991).

Territories and site persistence.—We captured 16 male and 16 female redstarts in the two habitats using mist nets with playbacks of redstart songs and mounted decoys (Holmes et al. 1989, Sliwa and Sherry 1992). Captured individuals were aged by skull pneumatization and sexed according to standard plumage criteria (Pyle et al. 1987, Marra et al. 1993). Each individual was given a combination of two colored plastic bands and an aluminum U.S. Fish and Wildlife Service band to allow subsequent identification and assessment of overwinter persistence. The term "persistence" is used in this study to refer to the continued presence of banded individuals in the study area later in the nonbreeding season. Persistence is assumed to be a rough index of survivorship, but it also reflects local movements in and out of the study area. Although local movements out of the study site do not represent mortality, they are interpreted here to signify movement from less-suitable habitats.

Upon detecting a marked redstart in the field, movements and territorial behaviors were recorded on gridded maps of the study site. All observations of the bird were transferred to a composite Vidalon transparency, and territories were demarcated as the smallest convex polygons enclosing all observations and movements of each individual. To quantify environmental characteristics of a bird's territory, we defined the territory as the smallest circle enclosing the polygon connecting all recorded sightings of an individual during the first four days of observation. The center of a bird's activity area, defined as the geometric center of this circle, was flagged and labelled in the field. Each territory so delineated was also categorized as either mangrove or scrub (regardless of the occupant's sex) based on accurately scaled, gridded habitat maps of each plot. Any territory that straddled the habitat boundary was assigned to that habitat that constituted the majority of its area. Because of the dual classification (by sex and habitat) of territories, analyses were performed with territories using habitat classifications and classifications according to the sex of the occupant.

Many individual redstarts observed in fall persisted on the study site until spring, in which case their territories were remapped. In spring efforts were concentrated on determining the persistence of only those individuals marked in fall, using vocalization playbacks to resight and remap territories of remaining birds. Site persistence of individual redstarts was used as an index of habitat suitability. Data collected by Holmes et al. (1989, unpubl. data) at Luana Point from 1986 to 1990, based on identical methodology, were analyzed to increase sample sizes for sex-specific overwinter persistence of redstarts.

Vegetation and meteorological measurements.—For each territory, the following five habitat variables were measured within a circle of 11.3-m radius (0.04 ha) from the designated territory center, using methods slightly modified from James and Shugart (1970): (1) Canopy height (in m) to the top of the tallest tree was measured within the circular plot using a clinometer and 50-m tape. (2) Percent canopy cover was quantified as the percent of 20 vertical points (located across two perpendicular transects of each circle) obstructed by leaves. A specially designed ocular tube with a cross hair was used to determine the presence/absence of vegetation at each point by sighting vertically over the observer's head. This tube was constructed of PVC pipe approximately 6 cm in diameter and mounted on a heavy wire handle that permitted the tube to swing freely and, thus, hang vertically. (3) Percent ground cover was measured using the same protocol as that employed to evaluate canopy cover, but while sighting downward to determine the presence/absence of herbaceous vegetation. (4) Shrub density was recorded as the number of woody stems less than 7.5 cm dbh (diameter at breast height, approximately 1.5 m) intercepted by the outstretched arms, of roughly 1.8-m span, on both perpendiculars of the circle along the cardinal compass directions. Thus, an area of approximately 80 m² was sampled for shrub density, canopy cover, and ground cover. A single observer measured variables 2, 3, and 4 to minimize measurement variation. (5) Tree density and tree basal area were determined for all standing trees more than 7.5 cm dbh within the circle. Temperature and relative humidity were measured for all territories on one day per season with a sling psychrometer. These meteorological measurements were taken within 2 h of midday at three points per territory (center, northern- and southern-most points of the 11.3-m radius circle), which were then averaged by territory.

Insect abundance.—To quantify food availability for redstarts, a standard Malaise insect trap (2 m high, pyramidal construction, Bioquip; Cooper and Whitmore 1990) was erected within 2 m of the territory center, with the bottom edge of trap netting just above the ground. Malaise traps catch mainly flying insects (e.g. Diptera, Hymenoptera, Homoptera). These are the principal prey of wintering redstarts at the study site (T.W.S. unpubl. stomach analyses), which forage principally by aerial flycatching and foliage gleaning. Six to eight traps were operated daily over a six-day period to sample the insect abundances of the 32 territories. Traps were operated for 24 h on equal numbers of male and female territories over the sample period to balance daily subsamples as a control for daily weather variability. Lepidopteran adults were presorted from the collections in the field and stored in plasticine envelopes; other arthropods were stored in 70% ethanol. In the laboratory, insects were sorted to order (cf. Wolda 1990), except for Diptera (sepa-

rated into Nematocera [mosquitoes and midges] and non-Nematocera) and Hymenoptera (separated into two groups, Formicidae [ants] and other families). Insect samples were dried to constant mass (24 h at 85–90°C in a Fisher Isotemp 500 laboratory oven) and weighed to the nearest 0.0001 g using a Mettler electronic balance. For each territory, insect samples were analyzed both separately by taxon and pooled over all taxa.

Statistical analyses.—Data from the two study plots were combined for all analyses. Chi-squared tests were used to compare habitat use and overwinter persistence by the two sexes. All other variables were tested for normality of distribution, and transformed where necessary to meet assumptions of parametric statistics. Natural logarithmic transformations were used for canopy height, shrub density, tree density, tree basal area, and average basal area per tree. Variables measured as percentages (percent canopy cover, percent ground cover, and percent mangrove trees) were arcsine transformed. For within-season analyses of vegetation and micrometeorological data, *t*-tests were performed on normally distributed data, and Mann-Whitney *U*-tests were performed on those variables whose distributions were not normalized even after transformation (fall percent ground cover and percent mangrove trees). Seasonal comparisons of vegetation and micrometeorological variables were performed with two-way ANOVAs. Insect data were tested by ANOVA using a repeated-measures design, with sex, habitat, and season, as well as the season-sex and season-habitat interactions, entered into the model as independent variables. All individual results were considered significant at $P < 0.05$. A sequential Bonferroni correction for tablewide significance was used for the string of simultaneous component tests for insect seasonality (see Rice 1989).

RESULTS

Sexual habitat segregation and overwinter persistence.—The 32 birds (16 male, 16 female) marked in the fall on the two study plots were significantly segregated by sex between the two habitats (Fig. 1; $X^2 = 10.17, P < 0.01$). Twelve males (80%) and three females established territories in mangrove habitats, whereas only four males (23.5%), and 13 females occurred in the scrub habitat.

Of the 32 birds marked in the fall of 1990, 21 individuals (65.6%; 10 males and 11 females) were present on the study site in the spring of 1991. The sexes did not differ in overwinter persistence ($X^2 = 0.0476, P > 0.05$), nor was there a significant difference in persistence between habitat types (regardless of sex of territory owner) in the winter of 1990–1991 ($X^2 = $
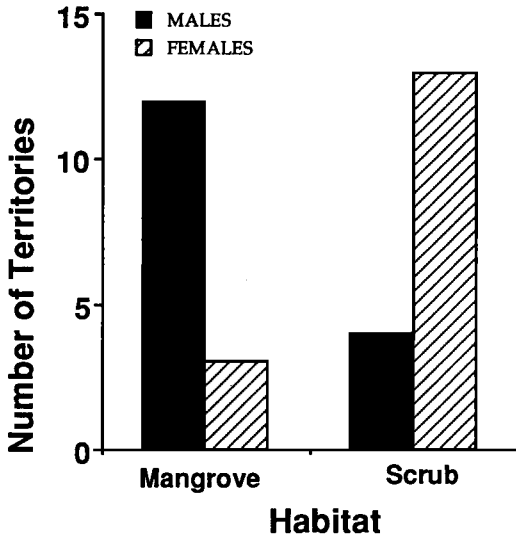
Fig. 1. Frequency of occurrence of male and female American Redstarts in mangrove and scrub habitats. Habitat segregation was significant ($X^2 = 10.17$, $P < 0.01$, $n = 32$).

TABLE 1. Overwinter persistence of 32 banded American Redstarts categorized by habitat of occupation and sex of bird from fall of 1990 to spring of 1991.

	Number of birds (%)	
	Fall	Spring
Habitat		
Mangrove	15 (46.9)	8 (38.1)
Scrub	17 (53.1)	13 (61.9)
Sex		
Male	16 (50.0)	10 (47.6)
Female	16 (50.0)	11 (52.4)

0.4311, $P > 0.05$, Table 1). Data from previous investigations (1986–1990) at the same study site were pooled with ours to increase the sample size; again, no difference was found in overwinter persistence of male versus female redstarts ($X^2 = 0.035, P > 0.5, n = 106$), nor of birds whose territories were established in mangrove versus scrub habitat ($X^2 = 0.028, P > 0.5, n = 73$).

Vegetation variables.—We compared redstart territories by sex and by habitat with respect to vegetation and physiognomic variables measured in the fall of 1990. Of these variables, only percent mangrove trees and canopy height differed significantly between male and female territories (Table 2), with males occurring in areas of taller canopy and more mangroves. When territories were analyzed by habitat, regardless of sex, mangrove territories had significantly higher canopies, lower shrub densities, greater tree diameters, less canopy and ground cover, and different tree species composition than did scrub territories (Table 2).

Of the vegetation variables considered here, only percent canopy cover and ground cover were remeasured in the spring. Although mangrove and scrub territories differed with respect to these variables in the fall, these differences had disappeared by spring (Table 2).

Canopy and ground cover changed signifi-

cantly in all territories over the winter dry season (Table 3). Moreover, percent canopy cover showed a nonsignificant tendency to decrease more in female than in male territories (Fig. 2). Percent canopy cover decreased significantly more from fall to spring in scrub territories than in mangrove territories (two-way ANOVA, $F = 9.55, P < 0.01$; Fig. 2). Percent ground cover did not differ in the degree of seasonal change with respect to the sex of the bird or habitat in which a territory occurred.

Micrometeorological variables.—In the fall temperature and humidity did not differ significantly between territories by sex or habitat, although the probability value for relative humidity being higher for territories of males than for those of females was close to being significant ($P = 0.057$). In the spring, mangrove territories were significantly more humid than scrub territories ($P < 0.05$). While these variables showed seasonal change when data from all territories were combined (Table 3), territories did not differ significantly by sex or by habitat in the seasonality of micrometeorological variables. Scrub territories tended to decrease in relative humidity over winter more than mangrove territories, although this difference was not significant ($P = 0.072$).

Insect biomass.—The biomass of insects collected by Malaise traps in the fall of 1990 showed both sex-specific and habitat-specific differences. Samples from female territories had greater biomass of nonnematoceran Diptera ($F = 9.95, P < 0.01$) than those from male territories. Although P-values were not significant, there was a tendency for samples from female territories to have a greater total biomass ($F = 3.54, P = 0.07$) and coleopteran biomass ($F = 3.28, P = 0.08$). Comparisons across habitats re-

TABLE 2. Vegetation variables ($\bar{x} \pm$ SD) for territories by season, habitat, and sex.

Habitat variable	Mangrove	Scrub	P	Male	Female	P
		Fall				
Canopy height (m)	14.7 ± 3.5	11.9 ± 2.3	*	14.6 ± 3.3	11.8 ± 2.5	*
Shrub density (stems/80 m²)	24.9 ± 18.0	75.9 ± 40.7	**	36.8 ± 28.7	67.3 ± 46.1	ns
Tree density (trees/0.04 ha)	26.3 ± 16.0	29.5 ± 7.8	ns	29.2 ± 14.3	26.8 ± 10.1	ns
Tree basal area (m²/ha)	438.4 ± 226.8	378.6 ± 103.9	ns	456.6 ± 214.3	356.8 ± 100.9	ns
Basal area/tree (m²/tree)	17.5 ± 3.4	12.9 ± 1.7	**	16.0 ± 3.2	14.1 ± 3.7	ns
Canopy cover (%)[a]	71.3 ± 19.6	83.5 ± 10.6	*	77.8 ± 15.1	77.8 ± 18.2	ns
Ground cover (%)[a]	5.7 ± 8.6	19.7 ± 21.5	*	6.9 ± 11.2	19.4 ± 21.4	ns
Mangrove (% of total)[a]	77.7 ± 34.3	6.8 ± 16.4	**	60.3 ± 46.1	19.9 ± 32.6	*
		Spring				
Canopy cover (%)[a]	59.7 ± 21.5	44.7 ± 20.3	ns	58.4 ± 22.3	45.0 ± 19.9	ns
Ground cover (%)[a]	1.3 ± 2.3	5.9 ± 7.5	ns	1.6 ± 3.0	5.9 ± 7.6	ns

ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$.
[a] Arcsine transformed.

vealed greater homopteran biomass in scrub territories ($F = 5.14, P < 0.05$; Fig. 3) and greater biomass of nematoceran Diptera ($F = 9.53, P < 0.01$; Fig. 3) in mangrove territories. Neither total insect biomass of all orders combined nor the biomasses of any other insect orders differed significantly during the fall between habitats.

During spring no significant differences existed between male and female territories in total insect biomass or in the biomasses of individual orders. However, mangrove territories had significantly greater biomass of nematoceran Diptera than did scrub territories ($F = 6.76$, $P < 0.05$; Fig. 3). There was a suggestion of a trend for mangrove territories to have greater homopteran biomass (Fig. 3), although this difference was not significant. In contrast, scrub territories had greater biomasses of nonnematoceran Diptera in spring than did mangrove territories ($F = 5.92, P < 0.05$; Fig. 3).

Insect abundance changed significantly over the winter dry season (Table 3, Fig. 3). The biomass of nonnematoceran Diptera decreased in female territories, whereas the biomass of this taxon increased in male territories over the same interval (ANOVA, $F = 8.54, P < 0.01$). Total insect biomass did not differ in the degree of change between territories of the two sexes. When the degree of seasonal change was compared by habitat, scrub territories showed increased nonnematoceran Diptera biomass, while mangrove territories showed decreases over the winter (ANOVA, $F = 12.72, P < 0.01$; Fig. 3F). In contrast, homopteran biomass increased significantly in mangrove territories and decreased in scrub territories from fall to spring (ANOVA, $F = 7.40, P = 0.011$; Fig. 3E). While

total biomass did decrease significantly over the dry season (ANOVA, $F = 4.33, P < 0.05$; Fig. 3), it did not differ according to habitat in the degree of change during that interval.

DISCUSSION

Despite their close proximity, the mangrove and adjacent scrub habitats differed significantly in several variables that are of ecological importance to wintering redstarts. Sexual segregation of redstarts between the habitats was marked, indicating that the habitats were perceived as being different by the birds themselves. Moreover, vegetation parameters differed significantly between the two habitats in ways that could provide cues at the time the birds are establishing their territories in fall. The resources (and corresponding vegetation and micrometeorological parameters) of importance to redstarts differed significantly between habitats both within and between seasons. We propose that these results have important implications for understanding sexual differences in habitat use and in the overwinter survivorship of these birds.

Habitat seasonality.—The two habitats we studied in Jamaica differed in structural and climatic characteristics both in fall and spring, as well as in resource persistence throughout the fall-spring dry season. Mangrove territories, occupied predominantly by male American Redstarts, showed less seasonal variation than scrub habitats in canopy cover and homopteran biomass. Habitat variables such as canopy cover, ground cover, temperature, and relative humidity are potentially important because they

TABLE 3. Seasonality of habitat characteristics from fall to spring (1990–1991) for 32 American Redstart territories (F-values from ANOVAs).

| Variable | Season | Interaction with | |
		Sex	Habitat
Canopy cover[a]	30.26***	2.44	9.55**
Ground cover[a]	8.29**	1.68	2.34
Average temperature	12.34**	0.19	0.00
Relative humidity	4.43*	3.44	3.36
Orthopteran biomass	0.06	0.21	0.58
Homoptera	0.86	0.20	7.97**
Coleoptera	0.00	2.02	0.20
Lepidoptera	2.86	1.65	0.03
Nematoceran Diptera	15.66***	0.09	2.70
Nonnematoceran Diptera	0.18	7.39**	11.07**
Formicid Hymenoptera	0.64	3.70	2.39
Nonformicid Hymenoptera	0.58	0.39	0.29
All taxa	4.33*	3.43	1.86

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. All others nonsignificant ($P > 0.05$).
[a] Arcsine transformed.

A. Distribution by sex

■ Male
▨ Female

B. Distribution by habitat

■ Mangrove
◪ Scrub

SEASON

Fig. 2. Seasonal changes in percent canopy cover from fall to spring compared by (A) sex of territorial occupant, and (B) habitat in which a territory occurred. Whiskers indicate standard deviations.
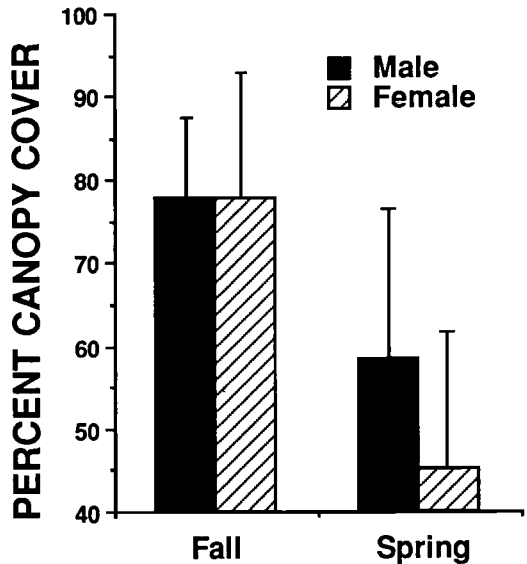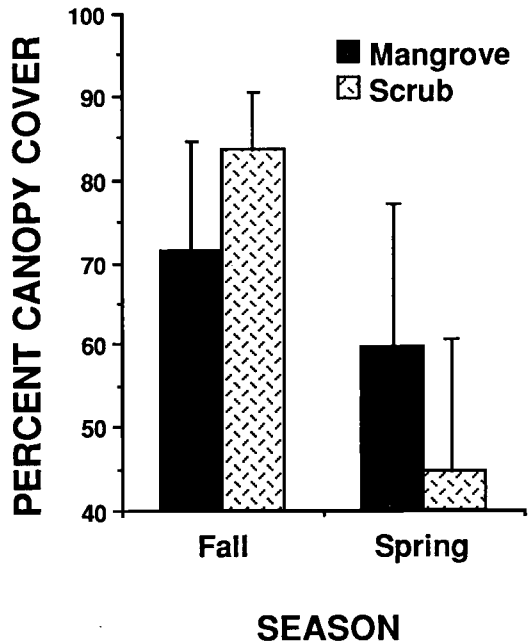
can influence the distribution, activity period, and abundance of insects (Wolda 1988). Biomass of some insect orders tended to increase in mangrove habitats over the winter more than in scrub habitats (Fig. 3), or at least showed greater constancy in mangroves, perhaps as a function of significantly greater persistence of leaf cover. Several vegetation, micrometeorological, and insect variables showed trends, which were not significant at the 0.05 probability level, toward being more constant (i.e. showing less decline) or increasing in territories of males or in mangroves. Statistical significance may not have been reached for these variables because of insufficient sample sizes, even though they may still be of biological significance. Nonetheless, mangroves appear to be more reliable in some resources for overwintering redstarts than scrub habitats over the nonbreeding period.

Redstart stomach analyses for dietary preferences (T.W.S. unpubl. data) suggest that Malaise traps are appropriate to quantify abundance of insect orders consumed by overwintering redstarts. The stomachs of seven redstarts collected at Luana Point, Jamaica, fed primarily on nematoceran Diptera (24.8% of total prey number), nonformicid Hymenoptera (24.2%), Coleoptera (15.4%), Homoptera (9.4%), and Hemiptera (primarily Tingidae, 9.4%). Of these insect taxa, nematoceran Diptera showed significantly greater biomass in spring and Homoptera showed significantly greater constancy

A. Total Insect Biomass

B. Lepidoptera

C. Orthoptera

D. Nematoceran Diptera

E. Homoptera

F. Nonnematoceran Diptera

G. Coleoptera

H. Nonformicid Hymenoptera

BIOMASS (g/24 h)

Fall   Spring

SEASON

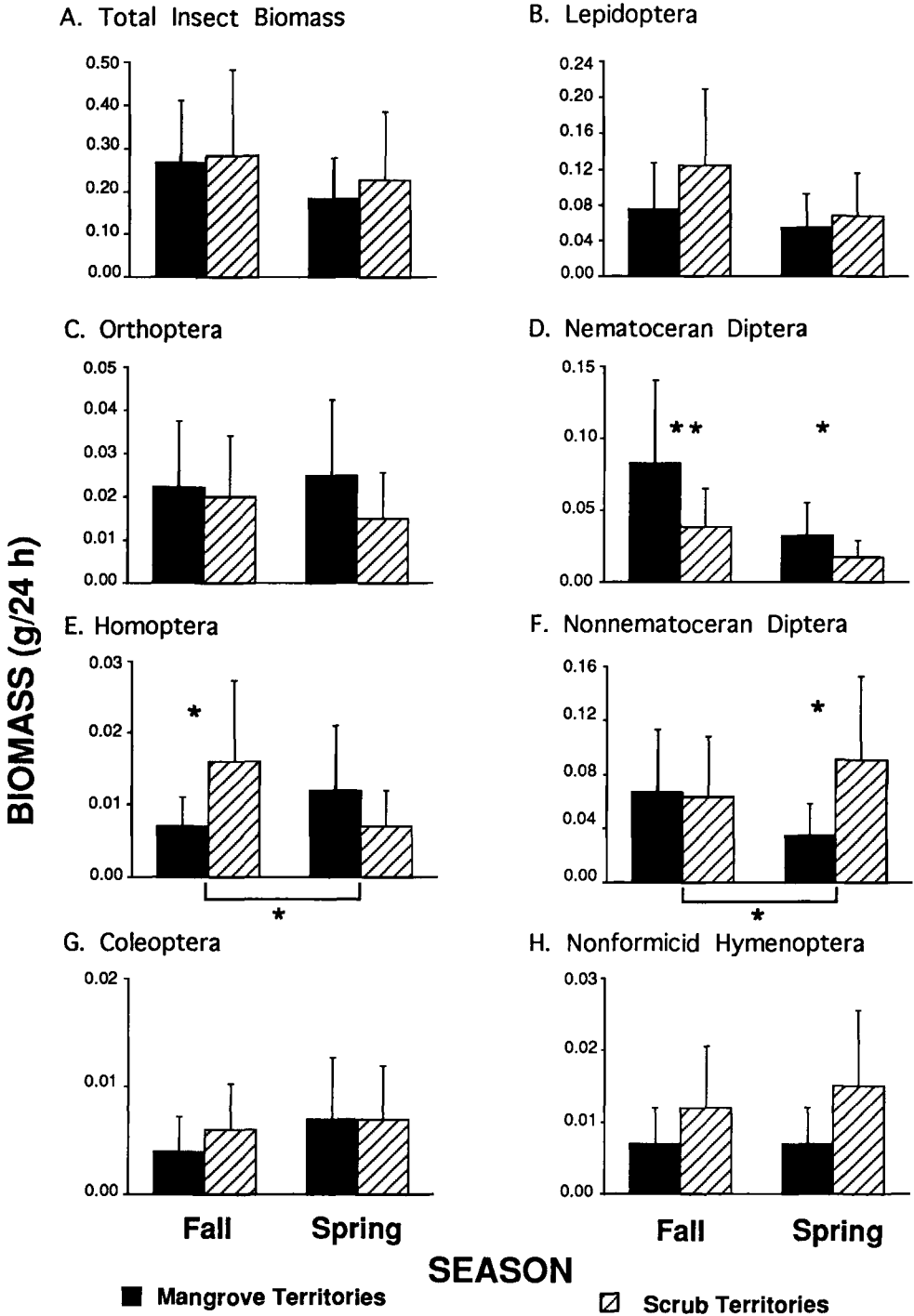■ Mangrove Territories   ☒ Scrub Territories

Fig. 3. Seasonal changes in biomass of insect taxa collected by Malaise traps on redstart territories during fall of 1990 and spring of 1991 compared by habitat. Asterisks indicate significance levels (*, $P < 0.05$; **, $P < 0.01$) within and/or between seasons. Whiskers indicate standard deviations.

(less seasonal variation) over the winter in mangrove habitat (Fig. 3). Furthermore, several lines of evidence suggest that we may have underestimated insect biomass in the spring mangrove habitat, in which case mangroves are even more constant from the birds' perspective than indicated by our data. First, mangrove habitat was significantly taller than scrub habitat (Table 2), and Malaise traps set on the ground were relatively far removed from the majority of mangrove tree vegetation, where most insects would be expected to occur. Ground-level traps, therefore, might bias insect captures in favor of the shorter scrub territories of females; however, captures were not heavily skewed in this direction. Second, because mangrove vegetation retained more leaves over the winter than did scrub vegetation (Fig. 2), mangroves probably contained many more insects that depend on vegetation for cover or food than did scrub habitat at the end of the dry season.

A third factor that probably caused us to underestimate typical insect abundance late in the dry season in mangroves results from the unusual weather conditions during the 1990–1991 wintering season. This particular season at Luana Point was extremely dry in comparison to any other winter between 1986–1987 and 1991–1992, when studies have been conducted at the site (T.W.S. unpubl. data). The mangrove swamp dried completely by March of 1992, except for a few small residual pools, such that almost all exposed ground was baked, cracked substrate that had been submerged (>1 m water depth in many places) in the fall of 1990. In other years the water level receded in the mangroves less than 0.5-m depth between October and March. Thus, mangrove habitat in this unusual spring of 1991 produced relatively few of the insects such as nematoceran Diptera that require water in their life cycles compared to typical spring seasons. These insects were, nonetheless, significantly more abundant in Malaise trap samples from mangrove territories in both the fall and the spring. Even when mangrove swamps retain water at the end of a typical winter dry season, the adjacent scrub, which rests on extremely porous soils, is dry; its vegetation is essentially leafless. Relative estimates of insect biomasses in mangroves during our study probably severely underestimated the usual spring abundance of food resources in this habitat. In support of this interpretation, overwinter persistence of redstarts in 1990–1991 (ap-

proximately 65%) was lower than the 80 to 90% persistence observed in other winters (R. T. Holmes and T.W.S. unpubl. data).

Our results suggest that habitat suitability may vary seasonally for migrant passerines. Whereas factors such as availability of safe nest sites may be important determinants of habitat quality on breeding grounds (Morse 1985, Martin 1992), food availability is probably the main component of habitat suitability for avian habitat selection in winter (Hutto 1985, Greenberg 1986, Rappole 1988, Leisler 1990). However, food availability and, consequently, habitat suitability are severely impacted in much of the northern Neotropics by the winter dry season (Orejuela et al. 1980, Schwartz 1980, Karr and Freemark 1983), as has also been suggested for Palearctic migrant passerines in highly seasonal areas of Africa (Dingle and Khamala 1972, Lack 1986) and Asia (Price 1981). As we have shown, lack of water during a dry season can dramatically affect vegetation density and cover (Morton 1980, Whitmore 1990); primary productivity of many tropical tree species can decrease up to 40% as a result of even slight canopy thinning over the dry season (Walter 1973). Differences between adjacent habitats in their ability to retain water due to edaphic factors (e.g. soil type and soil depth) may cause different degrees of facultative leaf loss. As a result, contiguous habitats can differ dramatically in microclimate and seasonal production of arthropods (Janzen 1973, Walter 1973, Wolda 1978), which in turn influence bird populations (Willis 1980, Karr and Freemark 1983, Winker et al. 1990). The pattern of greater insect abundances or less decline in insect abundances in forest habitats than in scrub was also reported by Greenberg (1992) for wintering migrant sites on the Yucatan Peninsula of Mexico. Certain habitats that are relatively well buffered against seasonal declines in food are thus potentially limiting resources for overwintering migrants (Lynch et al. 1985, Morton 1990).

If seasonality influences winter habitat quality, then seasonality should affect habitat-specific carrying capacity, and possibly broader-scale spatial and temporal abundances of Neotropical-Nearctic migrants. Temporal (seasonal) fluctuations in habitat suitability should be considered in future studies of the population dynamics of overwintering migrants and in assessing habitat quality for management purposes. For example, the population size of

breeding male Kirtland's Warblers (*Dendroica kirtlandii*) in the temperate zone is correlated significantly with rainfall on the species' wintering grounds in the Bahamas (H. Mayfield unpubl. presentation). Our study suggests that this correlation may be due to the influence of moisture availability on late dry-season food abundance in Bahamian habitats. Knowledge of resource seasonality would be useful in quantifying habitat suitability and its effects on population dynamics of wintering migrant species such as Kirtland's Warbler.

Sexual habitat segregation.—The pattern of habitat segregation documented here for the American Redstart is similar to that found in other species of sexually dimorphic migratory warblers. Redstart males tended to use tall, forested mangrove habitat, whereas females were most prevalent in habitats with lower canopy, greater shrub densities, and smaller trees. This is the same pattern observed in the Hooded Warbler (*Wilsonia citrina*; Lynch et al. 1985) in the Yucatan Peninsula of Mexico, the Black-throated Blue Warbler (*Dendroica caerulescens*; Wunderle 1992) in Puerto Rico, and several other warbler species in Mexico (Lopez Ornat and Greenberg 1990). Holmes et al. (1989) did not find sexual habitat segregation in previous studies of American Redstarts at our Luana Point study site, but our work involved more plots within which to detect sexual segregation. The local segregation of redstarts in our study, on a scale of territories in interdigitating habitats, is corroborated by larger-geographic scale patterns in redstarts across Jamaica (Sliwa 1991), where males are the most numerous sex in taller, forested habitats throughout the country. This local intraspecific segregation was not complete; male redstarts comprised 75% of individuals in forested habitat. This percentage corresponded closely with 74 to 80% male redstarts found in forested habitats on the Yucatan Peninsula by Lopez Ornat and Greenberg (1990). The similar results of these two distantly separated sites in the degree of sexual habitat segregation suggests the pattern may be widespread in wintering redstarts, at least where the species occurs at relatively high density.

Differences in forest structure, such as those we have documented for male and female redstart territories in winter, could provide cues by which the sexes innately recognize appropriate habitat, as suggested by experiments with naive Hooded Warblers (Morton 1990). Indi-

viduals of one sex could also constrain what habitats are available to other, socially subordinate individuals (Gauthreaux 1978), an hypothesis that assumes that some habitats are more suitable than others. Our results suggest that mangrove habitats may be more constant than adjacent scrub habitat with respect to vegetation characteristics and possibly insect-food resources. The greater dependability (and presumably suitability) of one habitat over another is consistent with the assumption of the social-dominance hypothesis. A removal experiment, including replicates at our Luana Point study site, indicated that females are excluded by males from mangrove habitats (Marra et al. 1993). This conflicts with the findings for Hooded Warblers of Morton et al. (1987), which were based on relatively small sample sizes. Studies of temperate resident birds also have shown experimentally that males constrain the microhabitat use and foraging behavior of females through dominance hierarchies (Peters and Grubb 1983, Desrochers 1989). Thus, social dominance is a plausible mechanism for the sexual habitat segregation we observed, but we cannot exclude innate habitat recognition or other mechanisms.

If mangrove habitat were of higher quality than adjacent scrub habitats, we might expect to observe greater overwinter persistence by males than by females, or at least greater persistence of birds occupying mangrove habitat than those in scrub. We did not find any such evidence. We offer two possible explanations for why we were not able to demonstrate differential persistence between habitats or between the sexes. First, older males and females may persist equally well over the winter. This is likely, because both sexes are highly site tenacious between years in Jamaican habitats (Holmes and Sherry 1992), and persistence through one winter suggests discovery in that year of a suitable wintering site in which to survive subsequent winters (Schwartz 1980). Accordingly, hatch-year birds, particularly females if they are socially subordinate (Marra et al. 1993), might then be expected to show less persistence than older birds on winter sites. Our sample sizes were too small to test this statistically, but yearling females seem to persist less well overwinter in Jamaica than older males, older females, and yearling males (R. T. Holmes, T.W.S., and P. P. Marra unpubl. data). A second possibility is that the sexes persist equally well

in different winter habitats, but males prefer (and defend) habitats that are relatively constant throughout the winter because such habitats allow premigratory fattening and earlier northward migration in spring. Early male arrival on breeding areas is presumably adaptive because of competition among males for females and selection for optimal territories on the breeding grounds (Ketterson and Nolan 1983, Francis and Cooke 1986). Although not significant, the number of birds remaining in scrub habitat in spring was greater than that of mangrove habitat. The adverse dry season of 1990–1991 produced effects which would have been much more unusual for mangrove territory holders than for scrub-territory holders, for which the observed dry season effects are typical (R. T. Holmes and T.W.S. unpubl. data). If mangrove resource constancy is important for males to depart early for the breeding grounds, greater emigration and therefore lower persistence of mangrove birds would be expected in this year of extremely dry conditions. Further research is necessary, however, to investigate these explanations.

The evidence we have presented suggests that ecological differences may exist between habitats occupied differentially by the two sexes in a winter resident population of American Redstarts. Our results also suggest the importance of seasonality to habitat suitability for nonbreeding migrant landbirds as a group in the northern Neotropics. Replication of study sites was not logistically feasible in our study, but studies at another Jamaican site (Portland Ridge) suggest that we can generalize our results in Jamaica beyond the two particular habitats investigated. Redstart sexes also segregate by habitat at Portland Ridge. Males occur in tall stature forests in the valleys characterized by relatively greater soil depth and less dry-season leaf fall than in the low-stature vegetation of rocky limestone slopes and hilltops, where females are proportionately more abundant (Sliwa 1991). In all species for which winter sexual habitat segregation has been reported (see references above), males tend to be in taller stature habitats, where insect resources may be less seasonal than in scrub habitats because of the buffering effect that forests provide on microclimate.

We conclude that degree of seasonal resource constancy may differ in habitats occupied by the two sexes of overwintering Neotropical-Nearctic migratory passerines. During the tropical dry season, the constancy of resources important to wintering migrants appears to vary inversely with degree of available moisture, which for migrant species wintering in forested habitats may vary with slope, soil depth, and canopy height. We hope that evidence of between-habitat differences in resource variables within and between seasons will encourage further research into proximate mechanisms for male-female habitat segregation in long-distance migrants, and into the evolution of winter habitat exploitation patterns by migrant songbirds. Even for nonterritorial populations or species of wintering tropical birds, better understanding of seasonality and predictability of resource distributions will be important to increasing our understanding of the life-history strategies of these animals (Ramos 1988, Levey and Stiles 1992).

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