

WINTER SITE FIDELITY OF NEARCTIC MIGRANTS IN SHADE COFFEE PLANTATIONS OF DIFFERENT SIZES IN THE DOMINICAN REPUBLIC

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ABSTRACT.—We studied three Nearctic migrant species (American Redstart [*Setophaga ruticilla*], AMRE; Black-and-white Warbler [*Mniotilta varia*], BAWW; Black-throated Blue Warbler [*Dendroica caerulescens*], BTBW) wintering in 14 isolated shade coffee plantations (0.1 to 8.7 ha) in the Dominican Republic to determine if site fidelity was comparable to that in tropical forests and if it decreased with plantation size. Site fidelity was measured as the percentage of wandering birds captured in mist nets, as overwinter site persistence of uniquely marked birds observed on the same sites (November to March), and as annual return of marked individuals to previously occupied sites (January to January). The percentages of wanderers in net captures were mostly lower than values reported for natural forests (AMRE 21%, BAWW 12%, BTBW 41%) and did not vary with plantation size. Overwinter site persistence (AMRE 65%, BAWW 65%, BTBW 76%) and annual return (AMRE 34%, BAWW 40%, BTBW 31%) in the plantations fell within the range of values reported for natural forests. Overwinter site persistence decreased with plantation size only in AMRE, although BAWW showed lower persistence in small plantations from early to midwinter. Annual return decreased with plantation size only in AMRE. Despite diminished site fidelity in small plantations, these birds showed some fidelity to small plantations, many of which were smaller than the mean size of winter home ranges. Received 8 January 1999, accepted 26 October 1999.

SHADE COFFEE plantations can attract a variety of birds (Wunderle and Latta 1996; Greenberg et al. 1997a, b), and they have the potential to serve as refugia for bird species in deforested regions of the tropics (Perfecto et al. 1996). Some shade coffee plantations provide a diversity of food resources (Wunderle and Latta 1998), but the availability of food may be highly seasonal, causing fluctuations in avian abundance (Greenberg et al. 1997b). However, except for the latter study, little is known regarding the persistence or site fidelity of birds in coffee plantations, despite the usefulness of such information for evaluating the conservation value of plantations.

Site fidelity of birds in coffee plantations can be compared with that in undisturbed forests as an indication of the adequacy of resources in plantations. Site fidelity is advantageous because it enables site dominance for resources, familiarity with fluctuations in resources, and increased ability to elude predators (Gauth-

reaux 1982, Shields 1984, Dobson and Jones 1986). Site fidelity occurs in numerous species on the breeding grounds (Gauthreaux 1982). Although fewer species have been studied on the wintering grounds, many Nearctic migrants return to the same winter location from year to year (Faaborg and Arendt 1984, Kricher and Davis 1986, Warkentin and Hernández 1996) and often reside on the site for the duration of the winter (Rappole and Warner 1980, Holmes et al. 1989). Migrants with high site fidelity on the wintering grounds may be the most vulnerable to declines associated with tropical deforestation because they may be less able to adapt to habitat perturbations (Warkentin and Hernández 1996).

Few studies have examined the effects of habitat fragmentation or patch size on wintering Nearctic migrants despite numerous studies demonstrating area sensitivity on the temperate breeding grounds (Lynch and Whigham 1984, Robbins et al. 1989). Some Nearctic migrants avoid small forest patches on the breeding grounds because small patches have increased nest predation and parasitism (see Martin and Finch 1995) or reduced food abundance (Burke and Nol 1998). Although it is un-

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known if predation or parasitism risk or food abundance varies with patch size on the wintering grounds, some evidence for area sensitivity exists for wintering migrants. For example, Askins et al. (1992) found that the average number of migrant species and individuals per survey point were significantly higher in extensive forest on the island of St. John than in small forest patches on nearby St. Thomas in the Virgin Islands. Robbins et al. (1987) found that two species of wintering migrants were restricted to large forest fragments, although the annual return rates for all migrant species were similar between large and small fragments in the Caribbean and Central America. Elsewhere, wintering migrants have been found to be common in some very small habitat patches (Greenberg 1992, Wunderle 1999), although site fidelity was not determined in these studies.

Shade coffee plantations occur in patches of different sizes, particularly in the Dominican Republic, where they often provide the only broadleaf tree cover at middle elevations. There, plantations are relatively uniform in age, composition, and structure and are mostly isolated by open farmland from other plantations or forest patches. We took advantage of these traits to study site fidelity in three forest-dwelling Nearctic migrants: American Redstarts (*Setophaga ruticilla*), Black-and-white Warblers (*Mniotilta varia*), and Black-throated Blue Warblers (*Dendroica caerulescens*). Our objectives were to determine whether winter site fidelity of migrants in shade coffee plantations differed from levels in native tropical forests and whether site fidelity decreased with plantation size. We expected winter site fidelity in shade coffee plantations to be equivalent to levels found in some tropical forests, given the abundance and diversity of migrants found in these plantations (Wunderle and Waide 1993, Wunderle and Latta 1996), as well as the abundance and consistency of food resources there (Wunderle and Latta 1996, 1998). Furthermore, we expected winter site fidelity to decrease with plantation size, given the possible area sensitivity of some migrants on the wintering grounds (Askins et al. 1992). Tests of these predictions enabled us to evaluate the importance of shade coffee as a habitat for wintering Nearctic migrants and the role of patch size for winter survival of migrants in tropical regions

beset with increasing deforestation and fragmentation.

STUDY SITE AND METHODS

Study site.—We sampled 14 shade coffee plantations near Manabao (16°06'N, 70°48'W) and Jarabacoa (19°09'N, 70°39'W), La Vega Province, at elevations of 540 to 850 m in the Cordillera Central, Dominican Republic. Plantations were located in the subtropical moist forest zone and received about 1,200 mm of rainfall annually (Hartshorn et al. 1981). Coffee is cultivated in areas that originally were native pine (*Pinus occidentalis*) forest. Pine forests, many of which have been selectively logged, remain as scattered patches on the steeper slopes, with variable amounts of broadleaf understory that has been degraded by fire, cutting, or grazing. Broadleaf trees are restricted primarily to shade coffee plantations, fruit and ornamental trees along fence rows and around homes, and in arroyos lined with the exotic *Syzygium jambos*. Broadleaf forest or woodland is absent whereas pastures and cultivated fields are the predominant cover types.

Plantations were selected on the basis of similarity of vegetation composition, structure, and management but differed in size. Quantitative descriptions of the plantations are provided in Wunderle and Latta (1996, 1998) and indicate that maximum canopy height averaged $15.6 \pm \text{SD of } 3.8$ m. The plantations are relatively uniform in structure and composition, with one predominate canopy species, *Inga vera* (Mimosoideae), although individual mango (*Mangifera indica*), avocado (*Persea americana*), various citrus species (*Citrus* spp.), and banana or plantains (*Musa* spp.) were scattered through some plantations. In a few plantations, an occasional pine (*Pinus* spp.) or palm (*Roystonea* spp.) extended into the overstory.

Habitat measurements.—We measured the outer perimeter of all plantations using a hip chain and a compass to obtain bearings and used a digitizer to estimate plantation area. We measured the error of closure to assess accuracy (all <5%) of field maps. Because aerial photographs were unavailable, we estimated plantation isolation along transects outside the plantations and along the plantation perimeter. We ran 100-m transects outside the plantations in the four cardinal directions from each plantation. Along each transect at 25-m intervals starting from the edge of the plantation, we determined canopy cover with a spherical densiometer and classified the habitat type at each point (16 points per plantation). Two spherical densiometer readings were taken at each point, one facing forward on the transect and the other facing in the opposite direction with the average computed for the point. The spherical densiometer measured the degree of open canopy associated with a site (Nuttall 1997). Habitats adjoining the pe-

rimeter of the plantation were classified and each habitat type's percentage contribution to the total perimeter was estimated. Habitats were classified as open pasture, cultivation of ground crops (height <1 m), shade coffee plantation, wooded arroyo, pine forest, road, stream, and building.

Plantation vegetation was measured in both circular plots and along transects. We used 16-m plots (0.02 ha) to obtain measures of basal area of *Inga*, *Musa* spp., and other tree species and to obtain measures of mean canopy height. In the small plantations, one plot was established in the center of the plantation, but in the four largest plantations three to seven plots were used, each 100 m apart and at least 25 m from the plantation edge. Stems of all standing trees and saplings were measured 1.3 m above the base and identified to species. Tree height of the 10 largest trees in the plot was determined using an optical range finder.

Foliage-height profiles of plantations were determined at randomly selected distances along parallel north-south transects spaced at 10-m intervals and at least 10 m from the plantation edge. A 3-m pole (2.0 cm in diameter) marked at 0.5-m intervals was placed vertically at each sample point. The number of sample points varied with plantation size (range 22 to 727). We recorded the presence or absence of foliage touching the pole within each height class as well as the identity of the foliage. For height intervals above 3 m, we sighted along the pole and recorded the presence or absence of foliage in each of the following height intervals: 3 to 4 m, 4 to 6 m, 6 to 8 m, 8 to 10 m, 10 to 12 m, 12 to 15 m, 15 to 20 m, and 20 to 25 m. For each height interval, percent cover was calculated by dividing the number of points in which foliage was present in that interval by the total number of sample points and multiplying by 100. The mean number of layers or height intervals in which *Inga* or coffee was detected was calculated for each plantation.

Data collection.—Field work was conducted over three consecutive winters and included visits in early winter (21 October to 6 November 1992; 25 October to 17 November 1993; 24 October to 16 November 1994), midwinter (11 January to 3 February 1993; 10 January to 2 February 1994; 9 January to 1 February 1995), and late winter (8 March to 5 April 1993; 14 March to 6 April 1994; 13 March to 5 April 1995). We also gathered data on annual return of banded birds during midwinter visits, as well as during an additional midwinter visit (8 to 31 January 1996) to calculate percentage annual return over three winters. Annual return was based on the percentage of observed birds that returned to previously occupied sites in midwinter (January to January).

During each field visit, we captured birds in mist nets that were placed throughout the plantations to obtain even coverage of captures. Consequently, the number of nets per site was variable depending on

plantation size (3 to 23 nets). Nets were set during early afternoon and opened until sunset, and on the following day, they were opened at sunrise and operated until midday (1100 or 1300). This effort resulted in the capture of 70 to 100% of the resident warblers per visit to a small plantation (<2 ha). It was not possible to sample the entire area of larger plantations, so netting was restricted to a smaller study site within the larger plantation. In two large plantations (L, N), half the study site was sampled with nets for an evening and morning netting session; afterward, nets were moved to the second half for an equivalent netting session. The locations of all nets and captures were recorded on field maps of each plantation. During the first winter (1992–93), playback of tape recordings of migrant songs and chips was used to attract birds to nets, but this was abandoned in subsequent years after it was evident that saturating a study site with nets provided a similar sample of captures (60 to 100% of warblers in large plantations). Birds captured by playback were not used in the analysis of wandering birds.

Standard measurements of morphology and mass were obtained for all captured birds, and sex and age were determined based on plumage characteristics (Pyle et al. 1987). Individuals less than one year old were classified as HY (hatching-year) birds prior to 31 December or as SY (second-year) birds as of 1 January. Older birds were designated as ASY (after second year). All captured warblers were banded with three plastic color bands and an aluminum U.S. Fish and Wildlife Service band before release at the capture site. We use abbreviations of warbler names throughout the text (AMRE, American Redstart; BAWW, Black-and-white Warbler; BTBW, Black-throated Blue Warbler).

We conducted intensive searches of the plantations (or study sites of large plantations) during mist netting and again three to five days after netting to locate color-banded birds during each period (early, mid-, and late winter). Searches were conducted from sunrise to 1200, during which time observers systematically traversed the plantation study sites and recorded locations and movements of all banded and unbanded birds on field maps. As observations of different individuals accumulated, observers concentrated efforts on locating missing birds. These included birds previously known from a site, birds recently captured but missing from the vicinity of the capture site, and areas of the plantation that seemed to lack birds. Perimeters were carefully searched to a distance of approximately 25 m from the edge of the plantation or study site. The effort allocated to a plantation search was related to the size of the plantation. For example, small plantations (<0.5 ha) often could be effectively sampled in a single morning by one observer, but if a marked bird was missed, a second and sometimes a third morning were required to establish the status of the individual(s) during

each winter period. In larger plantations, it was necessary to have observers (maximum of 5) search the site for as many as five or six mornings to confirm the status of marked individuals and delineate their home ranges during each winter period.

Definitions and analyses.—We determined winter home-range areas only for marked individuals that were present the entire winter, as verified during each of the three winter periods. Home-range size was based on the minimum convex polygon (Mohr 1947) calculated by drawing straight lines between the outermost points where the bird was observed over the winter, thereby producing a polygon that enclosed all locations where the bird was observed in the course of a winter. All estimated home ranges were at the asymptotic value based on number of sighting locations for each individual. Areas of these polygons were determined with a digitizer.

We use the terms "sedentary" and "wanderer" to describe spatial behavior (see Rappole et al. 1989, Winker et al. 1990). Wandering birds were defined as color-banded individuals that disappeared after initial capture and were never seen or captured again in the plantation of capture. In contrast, sedentary individuals were observed at least once after capture in the plantation of initial capture. Measures of site fidelity of sedentary individuals included both overwinter site persistence (birds present on home range in early to late winter) and annual return (present on home range in January of year x to January of year $x + 1$). Thus, site fidelity in a plantation was quantified by determining the percentage of wanderers captured in a plantation as well as the overwinter site persistence and annual return of sedentary birds to a plantation.

The percentage of wanderers in a plantation was determined only by mist-net samples that were pooled across the three periods for each winter. After each netting period, total numbers of wanderers (birds captured once and never again detected in the plantation of capture) and sedentary birds (excluding recaptures in same netting period) were tallied. The percentage of wanderers for each winter was calculated by dividing the total number of wanderer captures by the total net captures. Because sedentary individuals often were captured in more than one sampling period in a winter, an individual sedentary bird could contribute to a maximum of three captures in a winter.

Percentage site persistence and percentage annual return were summarized primarily by pooling within or among winter periods, which sometimes included using values from the same birds more than once. For instance, pooled site-persistence values included the percentage of birds remaining through each winter pooled for the three winter periods of the study. Pooled annual return rates were based on values obtained between winters 1 and 2, 2 and 3, and 3 and 4, such that some individuals were includ-

ed more than once. Pooling of all measures provided larger sample sizes for testing statistical significance, which violated assumptions of statistical independence because some individuals were included twice. However, it is unlikely that these assumptions were violated seriously, given that annual return rates were relatively low (30 to 40%), and analyses conducted using independent measures (values from known individuals used only once) gave results consistent with findings from analyses based on pooled values.

To assess the physical condition of birds, we calculated an index of body condition that controlled for structural size and related it to body mass (Marra et al. 1998). To correct body mass for structural size, we calculated the scores of a principal components analysis based on the length of the bill, wing chord, and tarsus, and then regressed body mass against the scores. The residuals of this regression constitute the index of body condition that estimates mass corrected for structural size. Birds with a positive value were considered to be heavy for their structural size, and those with a negative value were considered to be in poor condition in relation to their structural size. To maintain statistical independence, measurements of individuals were used only once by randomly selecting one winter period of capture.

Statistical tests.—We used a row \times column G-test of independence (Sokal and Rohlf 1981) to assess equality of sex ratios between large and small plantations, proportion of wandering birds among years, site persistence among years, and site persistence between large and small plantations within the first portion of the winter and within the later portion of the winter. To provide an indication of the power of the tests, we calculated sample size required to obtain significance ($P < 0.05$) using observed differences from this study. In addition, we calculated statistical power for the tests of independence (Zar 1984:398).

We used three-way tables in log-linear models to test for presence of three-factor interactions (Sokal and Rohlf 1981). For example, we used log-linear models to test for interactions among wandering behavior (wanderer vs. sedentary), sex, and plantation size (small vs. large); overwinter site persistence (persist vs. disappear), sex, and plantation size; and annual return (return vs. disappear), sex, and plantation size. Log-linear models were then used to test for conditional independence and for two-factor interactions.

The relation between percentage overwinter site persistence or percentage annual return and plantation area did not conform to homoscedasticity assumptions for linear regression, even with various transformations (Sokal and Rohlf 1981). Therefore, analyses were based on a gradient in proportions in which samples were ordered quantitatively (Fleiss 1981) and involved the use of chi-square statistics to

TABLE 1. Characteristics of shade coffee plantations in the Dominican Republic. Uninhabitable habitat included open pasture, croplands, roads, and buildings. Surrounding points and canopy cover were sampled every 25 m along 100-m transects in each of four cardinal directions from each plantation. Percent canopy cover was determined by spherical densiometer. Area of plantations in ha; basal area in m² per ha, canopy height in m. See text for description of vegetation traits.

Site	Area	Perimeter uninhabitable ^a	Mean canopy cover (%)	<i>Inga</i> basal area	Other tree basal area	<i>Musa</i> spp. basal area	Mean canopy height (±SD)	Mean no. <i>Inga</i> layers	Mean no. coffee layers
A	0.09	100 (115)	28.7	11.2	1.0	7.5	22.0 ± 1.6	1.2	1.1
B	0.11	100 (132)	7.9	11.7	0.0	0.0	16.0 ± 1.0	1.9	1.2
C	0.13	100 (162)	24.6	11.3	0.0	0.0	13.2 ± 1.3	1.3	1.1
D	0.26	100 (198)	15.0	6.7	0.6	0.0	14.6 ± 1.5	1.0	1.1
E	0.28	94 (204)	26.2	13.1	3.3	0.0	17.6 ± 1.1	1.8	0.9
F	0.31	100 (272)	6.7	11.9	1.4	0.8	13.6 ± 1.1	1.5	1.6
G	0.44	100 (266)	13.4	7.7	0.8	3.9	21.0 ± 1.6	1.3	0.8
H	0.52	100 (338)	8.8	6.2	0.0	6.1	20.1 ± 1.6	1.0	1.0
I	0.52	96 (276)	28.7	13.2	0.0	3.9	19.0 ± 1.6	1.4	1.1
J	0.59	100 (367)	2.9	11.5	0.3	0.8	15.0 ± 1.2	2.0	0.9
K	2.45	83 (961)	48.4	9.4	4.3	0.4	17.4 ± 3.3	1.1	0.9
L	4.56	98 (960)	45.3	6.6	0.0	0.0	13.3 ± 2.1	1.8	1.5
M	7.65	96 (2,107)	27.2	10.9	0.3	0.0	14.2 ± 3.9	1.2	0.8
N	8.65	72 (1,817)	38.1	9.3	2.4	2.8	15.3 ± 4.5	1.1	1.4

^a Percent of perimeter of plantation uninhabitable, with length of perimeter (m) in parentheses.

test the significance of slope and linearity as devised by Cochran (1954) and Armitage (1955). We used nonparametric Spearman rank correlations (Sokal and Rohlf 1981) to assess associations between variables that did not meet normality assumptions. We adjusted significance levels using Bonferroni sequential adjustment (Rice 1989) for the correlation of log plantation area with plantation isolation and vegetation variables. We used *t*-tests to compare home-range size of males and females and a two-way ANOVA with replication to compare the index of body condition among winter periods and between plantation sizes. In all analyses, a probability of type I error of 0.05 or less was considered significant.

RESULTS

Plantation characteristics.—The 14 coffee plantations sampled ranged in size from 0.09 to 8.65 ha (Table 1). Transects (100 m long) run in the four cardinal directions from each plantation with four sample points per transect indicated that 75% of the 224 points in the area surrounding the plantations were nonforest (67% pasture and 8% cultivation). Tree canopies covered 20% of the points (13% arroyo, 5% coffee plantations, 2% pine) in the surrounding area, and the remaining 5% of the points contained a heterogeneous mix of roads, buildings, rivers, etc. We defined open pasture, croplands, roads, and buildings as uninhabitable habitat and found a

nonsignificant negative correlation between log plantation area and the percentage of its immediate perimeter that was bordered by an uninhabitable habitat type ($r_s = -0.64$, $P = 0.47$). Also, we found no significant correlation between log plantation area and the mean percentage canopy cover at points surrounding the plantations ($r_s = 0.39$, $P > 0.99$). Thus, although the presence of trees and open farmland surrounding plantations (out to 100 m) did not vary with plantation size, the smaller plantations tended to be distinct woodlands bordering open areas, whereas the larger plantations had some portions that bordered other wooded habitat.

Our selection of plantations based on similarity of plant species composition and structure, but differing in size, reduced variation in vegetation among plantations and reduced the correlations between vegetation traits and plantation size (Table 1, Fig. 1). Light to moderate levels of pruning of the canopy overstory were observed in most plantations but did not differ consistently with plantation size as evidenced by the overlap in foliage cover in the *Inga vera* foliage height categories (Fig. 1). All plantation overstories were overwhelmingly represented by *Inga vera* (Fig. 1), and although other tree species were present in some plantations (range of basal area 0 to 4.3 m² per ha),

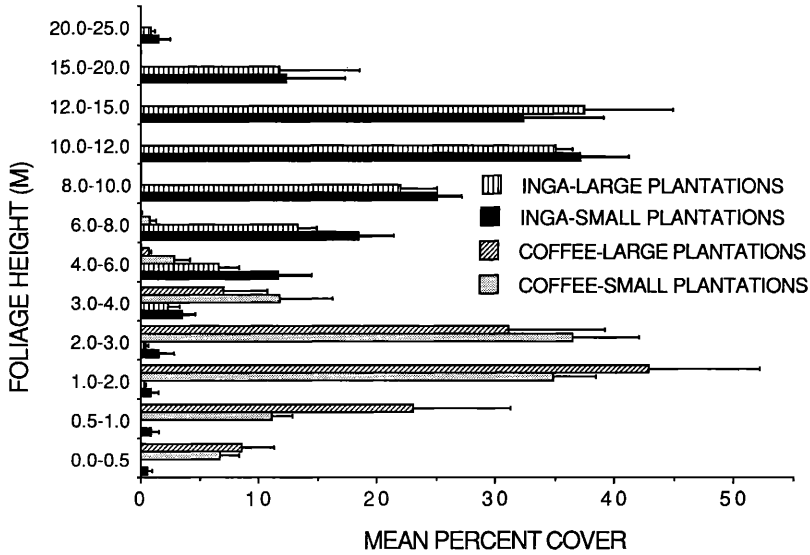


FIG. 1. Foliage height profiles for 10 small (0.09 to 0.59 ha) and 4 large (2.5 to 8.7 ha) shade coffee plantations in the Dominican Republic. Mean (\pm SE) percent cover represents the percentage of vegetation touches in a given height. Foliage height was measured at 973 points (range 22 to 175) in small and 2,402 points (range 325 to 727) in large plantations along parallel transects spaced at 10-m intervals from each other and from plantation edges.

the maximum percentage cover in a height class was only 14.0% (4 to 6 m in plantation D) for other tree species. *Musa* spp. contributed to variation among plantations (range of basal area 0 to 7.5 m² per ha) in the understory but constituted a maximum percentage cover of only 7.5 % (2 to 3 m in plantation N). Vegetation traits varied among plantations (Table 1), but we found no significant correlations between plantation area with any trait (SD canopy height, $r_s = 0.67$, $P = 0.32$; basal area of *Inga*, $r_s = -0.33$, $P > 0.99$; mean canopy height, $r_s = -0.21$, $P > 0.99$; mean *Inga* layers, $r_s = -0.17$, $P > 0.99$; basal area of other trees, $r_s = 0.11$, $P > 0.99$; mean coffee layers, $r_s = -0.11$, $P > 0.99$, *Musa* spp. basal area, $r_s = 0.03$, $P > 0.99$).

Home-range size.—Mean size of home ranges of migrants that resided in the largest plantations (K, L, M, N) for the duration of a winter did not differ significantly between the sexes (AMRE, $t = 1.43$, $df = 36$, $P = 0.61$; BAWW, $t = 1.28$, $df = 12$, $P = 0.22$; BTBW, $t = 0.67$, $df = 51$, $P = 0.51$). Home-range sizes of AMREs and BTBW were similar (AMRE, $\bar{x} = 0.44 \pm SE$ of 0.05 ha, $n = 38$; BTBW, $\bar{x} = 0.38 \pm 0.03$ ha, $n = 54$) but were smaller than those of BAWWs ($\bar{x} = 1.0 \pm 0.10$ ha, $n = 14$). Given the variation in home-range size in the four largest plantations,

we defined the remaining 10 plantations (range 0.09 to 0.59 ha) as “small” for categorical analyses.

Sex ratios.—Wunderle and Latta (1996) documented that male AMREs and BTBW were predominant in mist-net captures from these plantations. We found similar and statistically significant skews in sex ratios of sedentary individuals of these two species in each of the three winter periods (AMRE, range 71.7 to 79.2% males; BTBW, range 69.7 to 77.0% males; $P < 0.001$). However, we detected only a slight, nonsignificant skew toward males in sedentary BAWWs in the three winter periods (range 62.5 to 73.4% males; $0.11 < P < 0.51$). Despite male bias in sedentary individuals of these three species, we found no indication that sex ratios varied with plantation size. For example, the percentage of males among sedentary individuals in small versus large plantations in early winter was similar in AMREs (82.1% of 28 birds vs. 77.6% of 58 birds for small vs. large plantations, respectively; $G = 0.10$, $df = 1$, $P = 0.75$), BTBW (72.0% of 50 birds vs. 74.3% of 74 birds; $G = 0.08$, $df = 1$, $P = 0.77$), and BAWWs (61.1% of 18 birds vs. 54.4% of 22 individuals; $G = 0.18$, $df = 1$, $P = 0.67$).

Wandering birds.—We found no differences

TABLE 2. Percentage of wandering American Redstarts, Black-and-white Warblers, and Black-throated Blue Warblers in mist net captures in 10 small (0.09 to 0.59 ha) and 4 large (2.5 to 8.7 ha) shade coffee plantations in the Dominican Republic. "Wandering" birds were never observed in the plantation of original capture (vs. sedentary birds, which were observed after capture). Data are based on captures in early, mid-, and late winter pooled for the winters 1992–93, 1993–94, and 1994–95.

	Males			Females			Total
	ASY	HY/SY	All	ASY	HY/SY	All	
American Redstart							
Small plantations	17.6 (17)	8.1 (37)	11.1 (54)	36.4 (11)	33.3 (12)	34.8 (23)	18.2 (77)
Large plantations	11.1 (36)	17.6 (34)	14.3 (70)	44.4 (18)	36.4 (11)	41.4 (29)	22.2 (99)
Total	13.2 (53)	12.7 (71)	12.9 (124)	41.4 (29)	34.8 (23)	38.5 (52)	20.5 (176)
Black-and-white Warbler							
Small plantations	5.9 (17)	25.0 (8)	12.0 (25)	10.0 (10)	0.0 (6)	6.3 (16)	9.8 (41)
Large plantations	18.2 (11)	25.0 (12)	21.7 (23)	6.7 (15)	0.0 (2)	5.9 (17)	15.0 (40)
Total	10.7 (28)	25.0 (20)	16.7 (48)	8.0 (25)	0.0 (8)	6.1 (33)	12.4 (81)
Black-throated Blue Warbler							
Small plantations	25.0 (40)	48.2 (54)	38.3 (94)	43.5 (23)	42.9 (21)	43.2 (44)	39.9 (138)
Large plantations	25.3 (87)	47.3 (93)	36.7 (180)	51.6 (33)	50.0 (48)	50.6 (81)	40.9 (261)
Total	25.2 (127)	47.6 (147)	37.2 (274)	48.2 (56)	47.8 (69)	48.0 (125)	40.6 (399)

among winters in the percentage of wandering individuals in plantations (AMRE, $G = 1.49$, $df = 2$, $P = 0.48$; BAWW, $G = 2.02$, $df = 2$, $P = 0.37$; BTBW, $G = 1.11$, $df = 2$, $P = 0.58$). Therefore, analysis of percentage wanders in mist-net captures was based on the combined winters. No significant three-way interactions (log-linear analysis, $df = 1$, $P > 0.42$) were found between wanderers, sex, and plantation size in any of the species (Table 2). However, tests for conditional independence indicated a significant interaction in AMREs between the incidence of wanderers and sex given plantation size, in which females displayed a higher incidence of wandering than males ($G = 13.75$, $df = 2$, $P = 0.001$). BTBWs showed a similar but nonsignificant trend (conditional analysis, $G = 4.76$, $df = 2$, $P = 0.09$; independent analysis, wanderers \times sex, $G = 4.79$, $df = 3$, $P = 0.19$). BAWWs showed the opposite but nonsignificant trend (conditional analysis, $G = 2.51$, $df = 2$, $P = 0.29$; independent analysis, wanderers \times sex, $G = 0.93$, $df = 3$, $P = 0.93$). Thus, the incidence of wandering was related to sex in only one species, the AMRE.

We found no indication that the percentage of wanderers in mist-net captures was higher in small than in large plantations (Table 2). For example, the incidence of wanderers did not differ with plantation size in AMREs (test of complete interaction, $G = 0.001$, $df = 1$, $P = 0.99$; conditional analysis, wander \times plantation size given sex, $G = 0.08$, $df = 2$, $P = 0.96$), BAWWs

(test of complete interaction, $G = 0.22$, $df = 1$, $P = 0.64$; test of independence, $G = 2.61$, $df = 3$, $P = 0.46$), or BTBWs (test of complete interaction, $G = 0.65$, $df = 1$, $P = 0.42$; test of independence, $G = 4.79$, $df = 3$, $P = 0.19$).

The percentage of wandering individuals captured in mist nets (values pooled across winters) showed no significant change with log of plantation area (Fig. 2) for any migrant (AMRE, $\chi^2 = 0.09$, $df = 1$, $P = 0.94$; BAWW, $\chi^2 = 0.006$, $df = 1$, $P = 0.96$; BTBW, $\chi^2 = 0.27$, $df = 1$, $P = 0.68$). Thus, the proportion of wanderers relative to sedentary individuals did not vary with plantation size, indicating that wandering individuals were not concentrating in smaller plantations.

Overwinter site persistence.—Values of overwinter site persistence pooled across all plantations were relatively high for each species (Tables 3 to 5). For example, of all sedentary individuals present in early winter, 80.2% of AMREs, 82.5% of BAWWs, and 85.5% of BTBWs were still present in the plantations in midwinter; by late winter, values were 65.1%, 65.0%, and 75.8% for the three species, respectively. However, male BTBWs exhibited greater site persistence than females from early to late winter, as evidenced by a significant interaction between site persistence and sex, given plantation size ($G = 9.53$, $df = 2$, $P = 0.009$). Higher levels of male persistence were not significant in the other species (AMRE, conditional analysis given plantation size, $G = 2.44$, $df = 2$, $P = 0.30$;

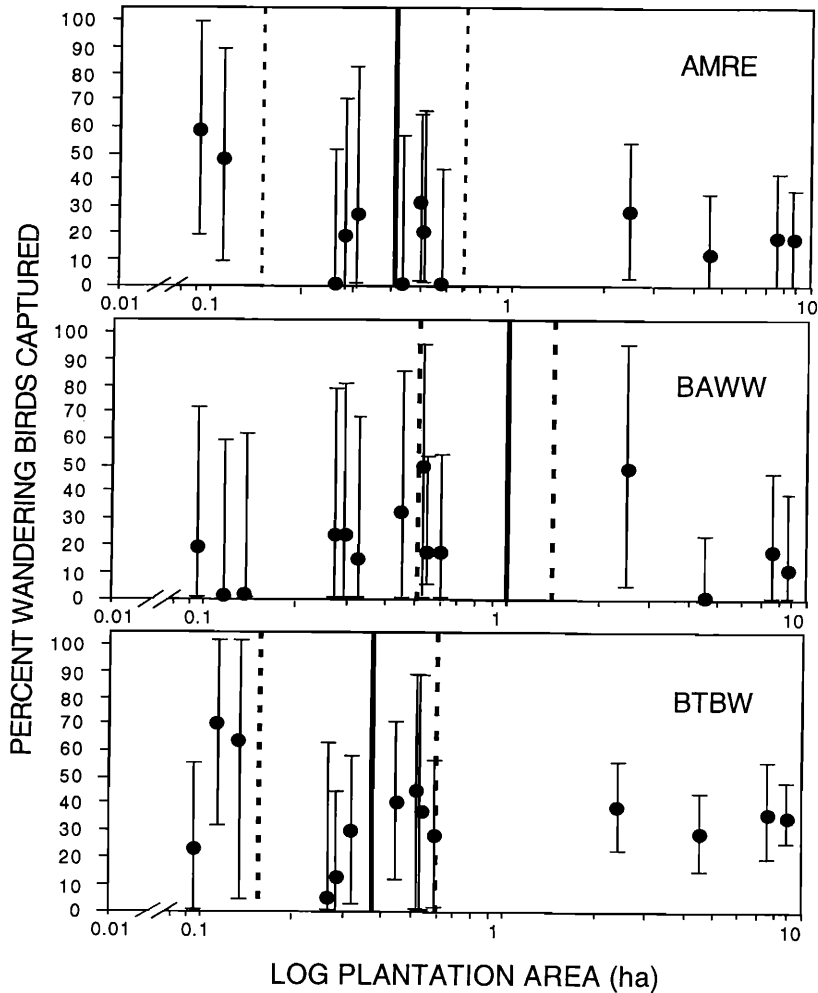


FIG. 2. Percent of "wandering" captures of American Redstarts (AMRE), Black-and-white Warblers (BAWW), and Black-throated Blue Warblers (BTBW) in 14 shade coffee plantations of different sizes in the Dominican Republic. Wandering birds were never observed in the plantation of original capture, and sedentary birds were observed after initial capture. The percentage of wandering birds is based on captures in early, mid-, and late winter for 1992–93, 1993–94, and 1994–95. Error bars are 95% confidence intervals. Thick vertical lines are mean winter home ranges, and dashed vertical lines are 1 SD as measured in the four largest plantations from early to late winter. The number of captures used to calculate percentages of wandering birds in plantations A to N, respectively, are 5, 2, 0, 5, 5, 7, 4, 14, 9, 8, 17, 23, 21, and 32 for AMRE; 5, 2, 2, 4, 4, 6, 3, 11, 6, 11, 6, 12, 16, and 16 for BAWW; and 13, 11, 6, 7, 14, 19, 15, 24, 7, 20, 47, 62, 44, 99 for BTBW (see Table 1 for letter designations of plantations).

independent analysis, sex \times persistence, $G = 2.12$, $df = 3$, $P = 0.55$; BAWW, conditional analysis given plantation size, $G = 0.44$, $df = 2$, $P = 0.80$, independent analysis, sex \times persistence, $G = 1.29$, $df = 3$, $P = 0.73$).

Overwinter site persistence for all individuals (both sexes and age classes) of a species, pooled for the three winters (Tables 3 to 5), did not differ significantly between large and small

plantations in AMREs (test of complete interaction, $G = 0.02$, $df = 1$, $P = 0.89$; test of independence, persistence \times plantation size, $G = 2.62$, $df = 3$, $P = 0.45$), BAWWs (test of complete interaction, $G = 0.31$, $df = 1$, $P = 0.58$; test of independence, $G = 0.48$, $df = 3$, $P = 0.92$), or BTBW (test of complete interaction, $G = 0.26$, $df = 1$, $P = 0.61$; test of independence, $G = 9.62$, $df = 3$, $P = 0.22$). However, the trend was for

TABLE 3. Overwinter site persistence of American Redstarts in 10 small (0.09 to 0.59 ha) and 4 large (2.5 to 8.7 ha) shade coffee plantations in the Dominican Republic based on resightings of individuals color banded in early or midwinter and subsequently observed in the same winter. Shown are the percentage of color-banded individuals remaining on the home range in which they were initially sighted (number in parentheses). Data include winters of 1992–93, 1993–94, and 1994–95.

	Males			Females			Total
	ASY	HY/SY	All	ASY	HY/SY	All	
Percent present in midwinter							
Small plantations	83.3 (12)	63.6 (11)	73.9 (23)	66.6 (3)	50.0 (2)	60.0 (5)	71.4 (28)
Large plantations	89.7 (29)	87.5 (16)	88.8 (45)	88.9 (9)	25.0 (4)	69.2 (13)	84.5 (58)
Total	75.6 (41)	77.7 (27)	83.8 (68)	83.3 (12)	33.3 (6)	66.6 (18)	80.2 (86)
Percent present in late winter							
Small plantations	91.6 (12)	72.7 (11)	82.6 (23)	100.0 (5)	100.0 (4)	100.0 (9)	87.5 (32)
Large plantations	86.1 (36)	100.0 (17)	90.6 (53)	77.8 (9)	100.0 (2)	81.8 (11)	89.1 (64)
Total	87.5 (48)	89.3 (28)	88.2 (76)	85.7 (14)	100.0 (6)	90.0 (20)	88.5 (96)
Percent present entire winter							
Small plantations	75.0 (12)	54.5 (11)	65.2 (23)	33.3 (93)	50.0 (2)	40.0 (5)	60.7 (28)
Large plantations	75.9 (29)	81.2 (16)	77.8 (45)	77.8 (9)	25.0 (4)	61.5 (13)	74.1 (58)
Total	75.6 (41)	70.4 (27)	73.5 (68)	50.0 (12)	33.3 (6)	55.5 (18)	65.1 (86)

lower rates of persistence in small than large plantations in all species. Given the relatively small sample sizes, a test of independence had little power to establish a statistical difference in persistence between the plantation sizes (AMRE, 0.34; BAWW, 0.25; BTBW, 0.18). Establishing statistical significance with the observed differences in persistence between small and large plantations required a prohibitively large increase in sample size of early winter birds (larger by 3 in AMRE, 3 in BAWW, and 7 in BTBW). Restricting analyses of site persis-

tence to individuals included only for one winter to eliminate problems of independence had little to no effect on detection of differences between small and large plantations (AMRE, 58.3% of 24 individuals in small vs. 71.7% of 46 individuals in large; row \times column test of independence, $G = 1.27$, $df = 1$, $P = 0.26$; BAWW, 60.0% of 15 individuals in small vs. 76.2% of 21 individuals in large; $G = 1.07$, $df = 1$, $P = 0.30$; BTBW, 72.9% of 37 individuals in small vs. 77.8% of 54 individuals in large; $G = 0.28$, $df = 1$, $P = 0.60$).

TABLE 4. Overwinter site persistence of Black-and-white Warblers in 10 small (0.09 to 0.59 ha) and 4 large (2.5 to 8.7 ha) shade coffee plantations in the Dominican Republic based on resightings of individuals color banded in early or midwinter and subsequently observed in the same winter. Shown are the percentage of color-banded individuals remaining on the home range in which they were initially sighted (number in parentheses). Data include winters of 1992–93, 1993–94, and 1994–95.

	Males			Females			Total
	ASY	HY/SY	All	ASY	HY/SY	All	
Percent present in midwinter							
Small plantations	83.3 (6)	60.0 (5)	72.7 (11)	50.0 (4)	66.7 (3)	57.1 (7)	66.7 (18)
Large plantations	83.3 (6)	100.0 (6)	91.7 (12)	100.0 (9)	100.0 (1)	100.0 (10)	95.5 (22)
Total	83.3 (12)	81.8 (11)	82.6 (23)	84.6 (13)	75.0 (4)	82.3 (17)	82.5 (40)
Percent present in late winter							
Small plantations	58.3 (12)	87.5 (8)	70.0 (20)	100.0 (3)	100.0 (2)	100.0 (5)	76.0 (25)
Large plantations	100.0 (6)	88.8 (9)	93.3 (15)	75.0 (12)	100.0 (2)	78.6 (14)	86.2 (29)
Total	72.2 (18)	88.2 (17)	80.0 (35)	80.0 (15)	100.0 (4)	84.2 (19)	81.5 (54)
Percent present entire winter							
Small plantations	83.3 (6)	60.0 (5)	72.7 (11)	50.0 (4)	33.3 (3)	42.8 (7)	61.1 (18)
Large plantations	66.7 (6)	83.3 (6)	75.0 (12)	77.8 (9)	100.0 (1)	80.0 (10)	77.3 (22)
Total	75.0 (12)	72.7 (11)	73.9 (23)	53.8 (13)	50.0 (4)	52.9 (17)	65.0 (40)

TABLE 5. Overwinter site persistence of Black-throated Blue Warblers in 10 small (0.09 to 0.59 ha) and 4 large (2.5 to 8.7 ha) shade coffee plantations in the Dominican Republic based on resightings of individuals color banded in early or midwinter and subsequently observed in the same winter. Shown are the percentage of color-banded individuals remaining on the home range in which they were initially sighted (number in parentheses). Data include winters of 1992–93, 1993–94, and 1994–95.

	Males			Females			Total
	ASY	HY/SY	All	ASY	HY/SY	All	
Percent present in midwinter							
Small plantations	83.3 (24)	83.3 (12)	83.3 (36)	77.7 (9)	60.0 (5)	71.4 (14)	80.0 (50)
Large plantations	87.1 (31)	95.8 (24)	90.9 (55)	75.0 (12)	100.0 (7)	84.2 (19)	89.2 (74)
Total	85.5 (55)	91.7 (36)	87.9 (91)	76.2 (21)	83.3 (12)	78.8 (33)	85.5 (124)
Percent present in late winter							
Small plantations	88.5 (26)	93.3 (15)	90.2 (41)	100.0 (9)	50.0 (10)	73.6 (19)	85.0 (60)
Large plantations	92.5 (40)	91.2 (34)	91.9 (74)	77.8 (18)	68.2 (13)	74.2 (31)	86.7 (105)
Total	90.9 (66)	91.8 (49)	91.3 (115)	85.2 (27)	60.9 (23)	74.0 (50)	86.1 (165)
Percent present entire winter							
Small plantations	79.2 (24)	83.3 (12)	80.6 (36)	66.7 (9)	40.0 (5)	57.1 (14)	74.0 (50)
Large plantations	87.1 (31)	87.5 (24)	87.3 (55)	58.3 (12)	57.1 (7)	57.8 (19)	79.7 (74)
Total	83.6 (55)	86.1 (36)	84.6 (91)	52.4 (21)	50.0 (12)	57.6 (33)	75.8 (124)

In BAWWs, site persistence was significantly ($G = 6.05$, $df = 1$, $P = 0.01$) higher in large (95.5%) than small (66.7%) plantations during the first half of the winter (early to midwinter; Table 4). By the second half of the winter, differences in site persistence of BAWWs between large and small plantations were not significant ($G = 0.93$, $df = 1$, $P = 0.54$). Site persistence did not differ significantly between small and large plantations during the first (early to midwinter) or last half of the winter (mid- to late winter) in AMREs or BTBW (Tables 3 and 5).

Percent overwinter site persistence of all marked individuals (values pooled for all winters) showed a significant increase ($\chi^2 = 4.02$, $df = 1$, $P < 0.05$) with log of plantation area only in AMREs (Fig. 3). However, this relationship ($y = 58.2 + 15.6 \log [\text{area}]$) departed significantly from linearity ($\chi^2 = 19.73$, $df = 9$, $P < 0.03$). Consistent with the potential sensitivity to small plantation size was the finding that the AMRE was the only species in which individuals failed to settle during early winter in the three smallest plantations (plantations A, B, and C; all < 0.15 ha). In contrast, BAWWs and BTBW settled in early winter in the smallest plantations, including several that were smaller than the size of the average winter home range measured in the largest plantations (Fig. 3). Percent site persistence in BAWWs ($\chi^2 = 2.31$, $df = 1$, $P = 0.22$) and BTBW ($\chi^2 = 1.57$, $df = 1$, $P = 0.37$) did not change with log of plan-

tation size, as evidenced by slopes that were not significantly different from zero.

Annual return rates.—Annual return, measured as the percentage of marked birds in midwinter that returned to the site in the following midwinter, includes overwinter site persistence. Thus, it is reasonable to expect a positive correlation between overwinter site persistence in a plantation and annual return rate to the same plantation. BTBW fit this expectation ($r_s = 0.63$, $P = 0.02$), but the other species did not (AMRE, $r_s = 0.34$, $P = 0.14$; BAWW, $r_s = 0.30$, $P = 0.40$).

Rates of annual return (pooled for the three winters) to plantations were similar for each of the species: AMRE, 34.3%; BAWW, 40.4%; BTBW, 31.3% (Table 6). A slightly higher percentage of females than males returned in all species, but differences were not significant (AMRE, conditional analysis given plantation size, $G = 2.75$, $df = 2$, $P = 0.25$, test of independence, sex \times annual return, $G = 3.46$, $df = 3$, $P = 0.33$; BAWW, conditional analysis, $G = 0.06$, $df = 2$, $P = 0.97$, test of independence, $G = 1.34$, $df = 3$, $P = 0.72$; BTBW, conditional analysis, $G = 1.16$, $df = 2$, $P = 0.56$, test of independence, $G = 1.43$, $df = 3$, $P = 0.70$). Thus, approximately one-third of the marked individuals of the three species returned in the following winter, and differences between sexes were not significant.

Annual return rates for all individuals pooled for the three winters (Table 6) did not

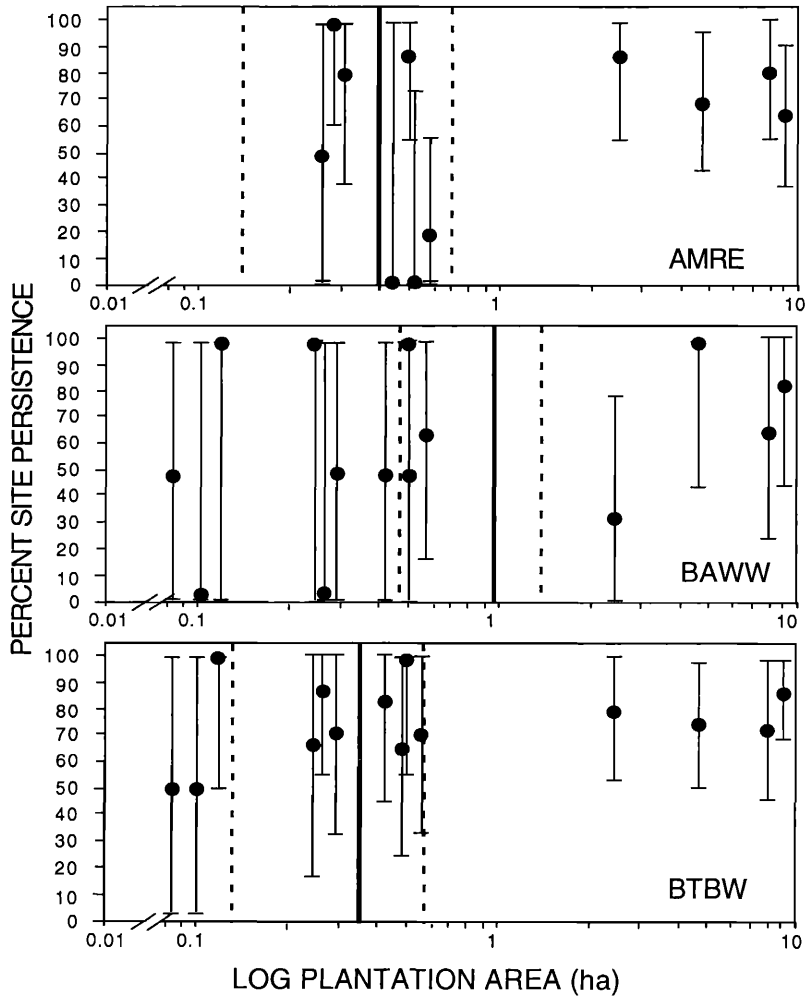


FIG. 3. Overwinter site persistence of American Redstarts (AMRE), Black-and-white Warblers (BAWW), and Black-throated Blue Warblers (BTBW) in 14 shade coffee plantations of different sizes in the Dominican Republic. Site persistence is the percentage of marked birds on home ranges in early winter that were re-sighted on the same site in late winter. Error bars are 95% confidence intervals. Data are from the winters of 1992–93, 1993–94, and 1994–95. Thick vertical lines are mean winter home ranges, and dashed vertical lines are 1 SD as measured in the four largest plantations from early to late winter. The number of birds used to calculate percentages for plantations A to N, respectively, are 0, 0, 0, 2, 4, 5, 1, 8, 3, 5, 8, 17, 16, and 17 for AMRE; 2, 1, 1, 2, 1, 2, 2, 2, 2, 3, 3, 7, 6, and 6 for BAWW; and 4, 4, 2, 3, 8, 7, 6, 6, 3, 7, 15, 20, 15, and 24 for BTBW (see Table 1 for letter designations of plantations).

differ significantly between large and small plantations in AMREs (test for complete interaction, $G = 2.51$, $df = 1$, $P = 0.11$; test of independence, annual return \times plantation size, $G = 3.05$, $df = 3$, $P = 0.38$), BAWWs (test for complete interaction, $G = 0.02$, $df = 1$, $P = 0.90$; test of independence, $G = 0.32$, $df = 3$, $P = 0.96$), or BTBW (test for complete interaction, $G = 0.22$, $df = 1$, $P = 0.64$; test of independence, $G = 2.07$,

$df = 3$, $P = 0.56$). However, the trend was for lower rates of return in small than large plantations. Given the relatively small sample sizes, a test of independence had little power to establish a statistical difference in annual return between size categories of plantations (AMRE, 0.18; BAWW, 0.18; BTBW, 0.11). Establishing statistical significance with the observed differences in annual return rates between small

TABLE 6. Percentage of color-banded American Redstarts, Black-and-white Warblers, and Black-throated Blue Warblers returning in midwinter (January 1993 to 1996) to home ranges occupied in previous January (number in parentheses) in 10 small (0.09 to 0.59 ha) and 4 large (2.5 to 8.7 ha) shade coffee plantations in the Dominican Republic.

	Males			Females			Total
	ASY	HY/SY	All	ASY	HY/SY	All	
American Redstart							
Small plantations	30.8 (13)	36.4 (11)	33.3 (24)	33.3 (3)	0.0 (4)	14.3 (7)	29.0 (31)
Large plantations	28.6 (35)	43.8 (16)	33.3 (51)	55.5 (9)	50.0 (2)	54.5 (11)	37.1 (62)
Total	29.2 (48)	40.7 (27)	33.3 (75)	50.0 (12)	16.7 (6)	38.9 (18)	34.3 (93)
Black-and-white Warbler							
Small plantations	36.4 (11)	20.0 (5)	31.3 (16)	25.0 (4)	66.6 (3)	42.8 (7)	34.8 (23)
Large plantations	28.5 (7)	55.6 (9)	43.8 (16)	41.7 (12)	100.0 (1)	46.2 (13)	44.8 (29)
Total	33.3 (18)	42.9 (14)	37.5 (32)	37.5 (16)	75.0 (4)	45.0 (20)	40.4 (52)
Black-throated Blue Warbler							
Small plantations	33.3 (27)	33.3 (15)	33.3 (42)	50.0 (6)	22.2 (9)	33.3 (14)	33.3 (57)
Large plantations	34.2 (41)	18.2 (33)	27.0 (74)	35.0 (20)	40.0 (15)	37.1 (35)	30.3 (109)
Total	33.8 (68)	22.9 (48)	29.3 (116)	38.5 (26)	33.3 (24)	36.7 (49)	31.3 (166)

and large plantations required a prohibitively large increase in sample size of midwinter birds (larger by 6 in AMRE, 6 in BAWW, and 24 in BTBW).

Migrants showed a decreasing trend in return rates with time after initial capture and moderate rates of return after the first year of capture (AMRE, 36.2%, $n = 69$; BAWW, 32.6%, $n = 46$; BTBW, 39.7%, $n = 131$), lower rates in the second year after capture (AMRE, 14.8%, $n = 54$; BAWW, 21.7%, $n = 23$; BTBW, 12.5%, $n = 96$), and no or low returns in the third year after capture (AMRE, 0%, $n = 32$; BAWW, 10.0%, $n = 10$; BTBW, 0%, $n = 43$). Although not statistically significant ($P_s > 0.15$), AMREs and BAWWs returned more frequently to large (42.9% of 42 AMREs and 56.5% of 23 BAWWs) than to small (25.9% of 27 AMREs and 42.1% of 19 BAWWs) plantations in the year of initial capture and in the year after initial capture (16.6% of 36 AMREs and 30.0% of 10 BAWWs in large plantations vs. 11.1% of 18 AMREs and 15.4% of 13 BAWWs in small plantations). BTBW showed the opposite trend after the year of initial capture (38.4% of 86 birds in large vs. 42.2% of 45 birds in small plantations) and in the next year (9.8% of 61 birds in large vs. 17.1% of 35 birds in small plantations), but differences were not significant ($P_s > 0.31$).

Percent annual return of all marked individuals (values pooled for all winters) increased significantly ($\chi^2 = 6.77$, $df = 1$, $P < 0.01$) with log of plantation area only in AMREs (Fig. 4). This relationship ($y = 27.0 + 16.3 \log[\text{area}]$) did

not depart significantly from linearity ($\chi^2 = 13.9$, $df = 10$, $P = 0.35$). Percent annual return in BAWWs and BTBW did not change significantly with log of plantation size (slopes not different from zero; BAWW, $\chi^2 = 0.03$, $df = 1$, $P = 0.86$; BTBW, $\chi^2 = 0.51$, $df = 1$, $P = 0.46$).

Body condition.—We found no significant variation in the index of body condition (Table 7) among the three winter periods (two-way ANOVA, $df = 1$ and 2; AMRE female, $F = 0.95$, $P = 0.39$; AMRE male, $F = 1.19$, $P = 0.31$; BAWW female, $F = 1.53$, $P = 0.23$; BAWW male, $F = 1.55$, $P = 0.22$; BTBW female, $F = 0.58$, $P = 0.56$; BTBW male, $F = 0.37$, $P = 0.69$). Nor did any species show significant variation in the index of body condition between small and large plantations (AMRE female, $F = 0.002$, $P = 0.96$; AMRE male, $F = 1.026$, $P = 0.31$; BAWW female, $F = 1.11$, $P = 0.30$; BAWW male, $F = 0.39$, $P = 0.54$; BTBW female, $F = 2.20$, $P = 0.14$; BTBW male, $F = 0.01$, $P = 0.92$). Thus, we found no evidence that body condition varied among the three winter periods or between small and large plantations.

DISCUSSION

Shade coffee as winter habitat.—Our results support previous findings (Wunderle and Latta 1996; Greenberg et al. 1997a, b) that some shade coffee plantations provide habitat comparable to natural forests, at least for certain species. For example, overwinter site persistence in plantations (AMRE, 65.1%; BAWW,

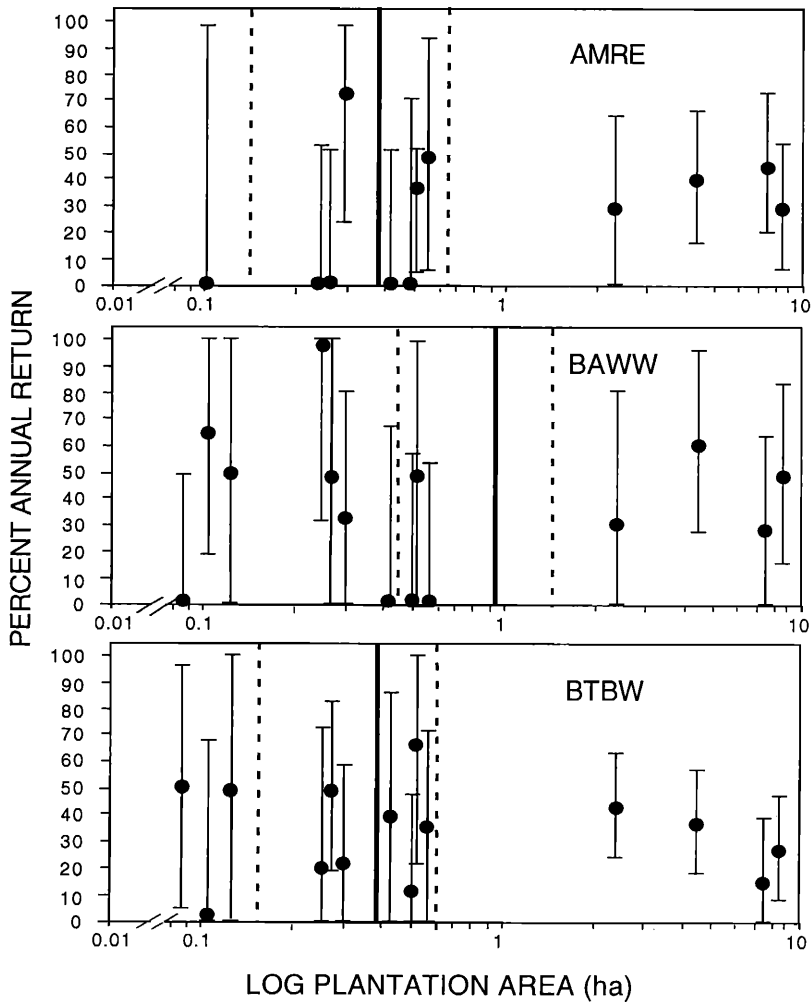


FIG. 4. Annual return of American Redstarts (AMRE), Black-and-white Warblers (BAWW), and Black-throated Blue Warblers (BTBW) in 14 shade coffee plantations of different sizes in the Dominican Republic. Annual return is the percentage of marked birds on home ranges in midwinter that were resighted on the same site in the following midwinter. Error bars are 95% confidence intervals. Data include January 1993 to 1996. Thick vertical lines are mean winter home ranges, and dashed vertical lines are 1 SD as measured in the four largest plantations from early to late winter. The number of birds used to calculate percentages for plantations A to N, respectively, are 0, 1, 0, 2, 4, 4, 3, 8, 3, 6, 10, 17, 15, and 20 for AMRE; 2, 3, 2, 2, 2, 3, 1, 3, 2, 3, 3, 8, 10, and 8 for BAWW; and 4, 2, 2, 5, 8, 9, 5, 8, 3, 11, 21, 27, 20, and 41 for BTBW (see Table 1 for letter designations of plantations).

65.0%; BTBW, 75.8%) fell within the range observed in natural forests elsewhere in the Caribbean (AMRE, 52.0 to 79.8% [Holmes et al. 1989, Sherry and Holmes 1996]; BTBW, 42.2 to 67.9% [Holmes et al. 1989, Wunderle 1995]), suggesting that resource abundance in coffee plantations is comparable to that in some natural forests.

Our skewed sex ratios are consistent with

findings that habitat segregation by sex is common in wintering Nearctic migrants and that males are more abundant in closed-canopy forests (Lynch et al. 1985, Lopez Ornat and Greenberg 1990, Wunderle 1992). In contrast, female AMREs and BTBW predominated in nearby sun coffee plantations (Wunderle and Latta 1996).

Male-biased sex ratios of migrants in shade

TABLE 7. Body condition ($\bar{x} \pm SE$, with n in parentheses) for three Nearctic migrant species captured during early, mid-, and late winter in 10 small (0.09 to 0.59 ha) and 4 large (4.25 to 8.70 ha) shade coffee plantations in the Dominican Republic during three winters. The index represents the residuals from the regression of body mass against principal components scores based on length of bill, wing chord, and tarsus. Positive values represent birds heavy for their structural size, and negative values represent birds light for their structural size.

	Males		Females	
	Small	Large	Small	Large
American Redstart				
Early winter	0.27 \pm 0.20 (13)	0.07 \pm 0.14 (19)	0.10 \pm 0.13 (13)	0.12 \pm 0.21 (13)
Midwinter	-0.29 \pm 0.15 (10)	-0.03 \pm 0.21 (12)	-0.28 \pm 0.17 (7)	0.04 \pm 0.20 (9)
Late winter	-0.38 \pm 0.24 (11)	0.16 \pm 0.06 (24)	0.02 \pm 0.21 (7)	-0.35 \pm 0.18 (8)
Black-and-white Warbler				
Early winter	0.19 \pm 0.16 (8)	-0.18 \pm 0.25 (13)	0.30 \pm 0.42 (9)	0.01 \pm 0.19 (9)
Midwinter	-0.11 \pm 0.21 (11)	-0.18 \pm 0.12 (9)	-0.16 \pm 0.12 (9)	-0.28 \pm 0.21 (11)
Late winter	0.36 \pm 0.41 (7)	0.38 \pm 0.35 (8)	0.31 \pm 0.24 (7)	0.02 \pm 0.25 (8)
Black-throated Blue Warbler				
Early winter	0.16 \pm 0.11 (33)	-0.07 \pm 0.01 (50)	0.20 \pm 0.19 (13)	-0.06 \pm 0.15 (19)
Midwinter	-0.01 \pm 0.03 (20)	-0.05 \pm 0.09 (36)	-0.13 \pm 0.14 (15)	0.04 \pm 0.10 (23)
Late winter	-0.20 \pm 0.13 (27)	0.10 \pm 0.11 (60)	0.30 \pm 0.17 (11)	-0.12 \pm 0.09 (30)

plantations are consistent with the contention that these plantations provide relatively high-quality winter habitat, particularly if males prevail in interference competition (Marra et al. 1993, Parrish and Sherry 1994). Although our finding that overwinter site persistence was higher in males than females (significantly in BTBW) is consistent with an explanation based on male dominance, previous studies of overwinter site persistence have failed to demonstrate a consistent relation between sex ratio skew and site persistence in the same habitat (Parrish and Sherry 1994, Wunderle 1995). Nonetheless, the absence of a relation between the proportion of females and plantation size indicates that females are not relegated to the smallest plantations and is consistent with the likelihood that habitat quality varies little, if at all, with plantation size.

Wandering individuals.—Values for the percentage of wanderer captures in coffee plantations (AMRE, 21%; BAWW, 12%; BTBW, 41%) are mostly lower than those found for wintering migrants in natural forests. For example, wandering BTBWs were present in three habitats in Puerto Rico but varied significantly from a minimum of 11 to 20% in tall-stature subtropical wet forest to a maximum of 47 to 57% in shrubby second-growth lower montane forest, with females wandering more frequently than males (Wunderle 1995). Similarly, Wallace (1998) found significant variation in the per-

centage of wanderers captured in three habitats in Cuba (BTBW, 46% in coastal scrub to 57% in coppice woodland; AMRE, 45% in undisturbed forest to 61% in coastal scrub; BAWW, 38% in the three habitats). The relatively low incidence of wanderers in our plantations may be associated with low mortality rates, because populations in habitats with a low incidence of wanderers relative to sedentary birds may have lower mortality rates than populations in habitats with a high incidence of wanderers (Rappole et al. 1989).

In our shade plantations, we observed wanderers attempting to establish territories from which they were displaced by the original occupant. Moreover, the disappearance of a sedentary individual frequently resulted in its replacement by a wandering individual for all three species (Wunderle and Latta unpubl. data). These observations indicate that wandering birds are displaced from plantations by sedentary individuals, which is consistent with the likelihood that plantations represent relatively high-quality habitat for migrants. In addition, the absence of a preponderance of wanderers in the smallest plantations suggests that habitat quality does not vary with plantation size.

Overwinter site persistence.—Overwinter site persistence is a measure of emigration and presumably mortality. The relatively high levels of overwinter site persistence indicate that rates

of overwinter emigration and mortality within these shade coffee plantations were relatively low, particularly for males. Little evidence exists for emigration of resident color-banded birds despite intensive searches and mist netting in plantations, although detection of long-distance (>0.5 km) wandering or location shifts following site abandonment was difficult with our sampling design. Marked birds were observed infrequently outside the plantation of origin, but in only three instances did birds (BTBW) abandon original home ranges for a nearby site outside the plantation (<50 m). Extensive netting in plantations failed to detect banded individuals once they disappeared from their original home range. However, wandering individuals were present throughout the winter, and they replaced individuals that disappeared from a site, suggesting that shifts in location occurred, as observed previously for wintering AMREs and BTBWs (Holmes et al. 1989, Wunderle 1995).

Mortality accounted for an unknown proportion of disappearances of overwintering migrants in plantations, although we suspect that predation was an important cause. We detected a variety of potential predators in the plantations, including mongooses (*Herpestes auropunctatus*), rats, and cats, but American Kestrels (*Falco sparverius*) and Sharp-shinned Hawks (*Accipiter striatus*) were probably the most important avian predators. Although kestrels were observed in plantations, they are known to prey on small birds only infrequently, in contrast to Sharp-shinned Hawks, which are primarily predators of small birds and were regularly netted and observed in the plantations. Moreover, the picked-apart remains of a dead AMRE and BTBW found in the plantations suggested raptor predation.

It is unlikely that food shortages contributed to mortality in these plantations. For example, severe dry periods that affect migrant survival by causing starvation (Poulin et al. 1992, 1993; Mayfield 1993) are rare in the subtropical moist zone where the plantations are situated. The absence of significant seasonal variation in body condition in the three species is consistent with the likelihood that food supplies did not decrease during winter. Also, foraging rates of the three species did not differ during winter, suggesting that winter food abundance did not decrease (Wunderle and Latta unpubl.

data). Finally, at least for BTBWs, abundance in plantations increased during winter, in contrast to an expected decline if food stress was an important regulatory factor. Thus, food supplies likely were adequate for overwinter survival in plantations.

It also seems unlikely that food abundance varied with plantation size, because surveys of invertebrate abundance on coffee leaves showed no differences between large and small plantations (Wunderle unpubl. data). However, it is unknown how abundance of canopy invertebrates changed with plantation size. All three migrant species were frequently observed foraging on plantation edges adjoining open pastures, as well as in isolated trees in pastures, suggesting that edges have little or no effect on food abundance for migrants. Moreover, body condition did not vary significantly with plantation size, suggesting that food abundance did not vary with plantation size.

Migrants in small plantations sometimes flew across open areas to forage in nearby trees in fields, hedge rows, and around buildings. Nearby scattered trees enabled migrants to use plantations that were too small to sustain a full home range, but flights from plantations to scattered trees were probably more costly in terms of time, energy, and predation risk than if all activities were confined to a plantation. Although we encountered Sharp-shinned Hawks in large and small plantations, it seems likely that predation risk was greater along plantation edges adjacent to fields and when individuals crossed open areas to forage outside a plantation.

Mortality and emigration rates, as measured by overwinter site persistence, were expected to be higher in plantations that were smaller than the average winter home range. Slight but consistent decreases in overwinter site persistence in small plantations relative to large plantations were consistent with this expectation. Although it was difficult to establish statistical differences between site persistence in large and small plantations, trends were consistent for all three species. For AMREs and BAWWs, differences in persistence were statistically significant, with lower persistence in small than in large plantations. It was noteworthy that decreases in site persistence in the smallest plantations were not more marked, suggesting that an abrupt edge with open field had only a

small effect on persistence in these forest-dwelling migrants.

Overall values of overwinter site persistence for the three species in small plantations (AMRE, 60.7%; BAWW, 61.1%; BTBW, 74.0%) fell within the range of site-persistence values known for more extensive native forest, particularly those with seasonally stable food supplies (Sherry and Holmes 1996, Wunderle 1995, Wallace 1998). Site-persistence values for males of the three species in small plantations (65.2 to 80.6%) fell within the mid- to high range observed in AMREs and BTBWs in natural forests (37.5 to 87.0%; Holmes et al. 1989, Wunderle 1995, Sherry and Holmes 1996). Similarly, persistence values for female BTBWs (57.1%) in small plantations fell within the range for females found in natural forests (44.8 to 62.5%; Holmes et al. 1989, Wunderle 1995). However, persistence values for female AMREs (40.0%, $n = 5$) and BAWWs (42.8%, $n = 7$) in small plantations were slightly below the lowest values recorded for female AMREs in natural forests (dry forest, 48%; Sherry and Holmes 1996). Site persistence of female AMREs and BAWWs deserves further study, but the overall persistence values of migrants in small plantations are consistent with values in more extensive forests elsewhere in the Caribbean.

Annual survivorship and annual return rates.—Minimum estimates of annual survivorship of migrants can be determined roughly by squaring values of overwinter site persistence (Holmes et al. 1989). This assumes that overwinter site persistence represents survivorship over a 6-month winter period, the birds survive the other half of the year at the same rate, and the probability of survival in the two periods is independent. With these assumptions in mind, we estimated annual survivorship rates of migrants from all plantations (AMRE, 0.44; BAWW, 0.42; BTBW, 0.58) and found that these values were within the range of estimates for annual survivorship of small passerines based on banding studies (Roberts 1971).

Annual survivorship based on overwinter site persistence was substantially higher than observed annual return rates in AMREs (0.44 vs. 0.34) and BTBWs (0.58 vs. 0.31) but not in BAWWs (0.42 vs. 0.40). In addition, annual return rates to coffee plantations were lower than those of AMREs (51.0%) and BTBWs (46.0%) to territories in Jamaican forests (Holmes and

Sherry 1992), although the value for BTBWs was within the range for this species in Puerto Rican forests (20.8 to 36.2%; Wunderle 1995, unpubl. data). A 50% annual return rate to winter sites may not be unusual for warblers (Holmes and Sherry 1992), suggesting that migrants in our plantations returned at a rate lower than expected.

Identifying factors that contribute to relatively low rates of annual return to plantations is difficult, partly because this measure includes survival during migration as well as on the breeding and wintering grounds. However, it is unlikely that plantation characteristics contributed to increased mortality during migration or on the breeding grounds. For example, body condition did not deteriorate during winter, although we do not know if spring departure was delayed in plantations (relative to natural forests) to enable birds to obtain adequate fat reserves for migration. Delayed departure could delay arrival on the breeding grounds, resulting in reduced breeding success (Marra et al. 1998). Nonetheless, it is unlikely that migrants were in poor condition when they departed from plantations in the spring.

The failure of some returning birds to settle in the same plantations in the next year may have contributed to the relatively low annual return rates. Some individuals (five BTBWs, three AMREs, two BAWWs) were found outside of their plantation of previous residence, suggesting that site shifts between winters occurred and that these shifts were more frequent between than within winters. Year-to-year shifts in the centers of winter territories (median ca. 28 m) are common in BTBWs and AMREs in Jamaican forests (Holmes and Sherry 1992). Site shifts of this magnitude could contribute to the loss of resident birds from previous sites or plantations, especially in small plantations.

Conservation implications.—We found that winter site fidelity in three Nearctic migrant species in shade coffee plantations was comparable to site fidelity found in some native tropical forests. In addition, the size of isolated plantations had only a small effect on site fidelity in these species, particularly if plantations were of sufficient size to sustain a winter home range. Plantation edges adjoining open farmland had little effect on site fidelity of these species. Abrupt forest edge adjoining

open farmland may in itself have little effect on site fidelity or survival of these migrants in some tropical forests. The high ratio of edge relative to forest interior characteristic of small fragments may not be as detrimental to these species in tropical forests as it is on the temperate breeding grounds. Our findings indicate that increasing tropical forest fragmentation (with its associated increase in forest edge) may not severely exacerbate the negative effects of habitat loss from tropical deforestation for these three species of migrants. However, this assumes that small forest fragments do not undergo ecosystem decay (Lovejoy et al. 1986), which eventually would reduce their suitability for use by migrants and residents alike.

Caution is required when extrapolating our findings on habitat patch size to other wintering migrant species and to other tropical habitats. Our study species may be especially insensitive to edge effects because they occur in a diversity of remnant Caribbean woodlands (Wunderle and Waide 1993). However, area effects in AMREs and BAWWs were suggested in the Virgin Islands (Askins et al. 1992). Therefore, future studies of winter site-fidelity in various tropical forest types and with different species of migrants are needed to insure that the absence of edge effects is not just a trait of the species or habitat we studied.

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LITERATURE CITED

- ARMITAGE, P. 1955. Tests for linear trends in proportions and frequencies. *Biometrics* 11:375–385.
- ASKINS, R. A., D. N. EWERT, AND R. L. NORTON. 1992. Abundance of wintering migrants in fragmented and continuous forests in the US Virgin Islands. Pages 197–206 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- BURKE, D. M., AND E. NOL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115:96–104.
- COCHRAN, W. G. 1954. Some methods of strengthening the common chi-square tests. *Biometrics* 10:417–451.
- DOBSON, F. S., AND W. T. JONES. 1986. Multiple causes of dispersal. *American Naturalist* 126:855–858.
- FAABORG, J. R., AND W. J. ARENDT. 1984. Population sizes and philopatry of winter resident warblers in Puerto Rico. *Journal of Field Ornithology* 55:376–378.
- FLEISS, J. L. 1981. *Statistical methods for rates and proportions*. John Wiley and Sons, New York.
- GAUTHREAUX, S. A. 1982. The ecology and evolution of avian migration systems. Pages 93–168 in *Avian biology*, vol. 6 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.
- GREENBERG, R. 1992. Forest migrants in non-forest habitat on the Yucatan Peninsula. Pages 273–286 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- GREENBERG, R., P. BICHIER, A. CRUZ ANGON, AND R. REITSMA. 1997a. Bird populations in shade and sun coffee plantations in central Guatemala. *Conservation Biology* 448–459.
- GREENBERG, R., P. BICHIER, AND J. STERLING. 1997b. Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. *Biotropica* 29:501–514.
- HARTSHORN, G., G. ANTONINI, R. DUBOIS, D. HARCHARIK, S. HECKADON, H. NEWTON, C. QUESADA, J. SHORES, AND G. STAPLES. 1981. The Dominican Republic, country environmental profile. United States Agency for International Development, McLean, Virginia.
- HOLMES, R. T., AND T. W. SHERRY. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection and conservation. Pages 563–578 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- HOLMES, R. T., T. W. SHERRY, AND L. REITSMA. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *Condor* 91:545–561.
- KRICHER, J. C., AND W. E. DAVIS. 1986. Returns and winter-site fidelity of North American migrants banded in Belize, Central America. *Journal of Field Ornithology* 57:48–52.
- LOPEZ ORNAT, A., AND R. GREENBERG. 1990. Sexual

- segregation by habitat in migratory warblers in Quintana Roo, Mexico. *Auk* 107:539–543.
- LOVEJOY, T. E., R. O. BIERREGAARD, JR., A. B. RYLANDS, J. R. MALCOLM, C. E. QUINTELA, L. H. HARPER, K. S. BROWN, JR., A. H. POWELL, G. V. N. POWELL, H. O. R. SCHUBART, AND M. B. HAYS. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in *Conservation biology: The science of scarcity and diversity* (M. E. Soulé, Ed.). Sinauer Associates Sunderland, Massachusetts.
- LYNCH, J. F., E. S. MORTON, AND M. E. VAN DER VOORT. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). *Auk* 102:714–721.
- LYNCH, J. F. AND D. F. WHIGHAM. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* 28: 287–324.
- MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- MARRA, P. P., T. W. SHERRY, AND R. T. HOLMES. 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: A removal experiment with American Redstarts (*Setophaga ruticilla*). *Auk* 110:565–572.
- MARTIN, T. E., AND D. M. FINCH (Eds.). 1995. *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York.
- MAYFIELD, H. F. 1993. Kirtland's Warblers benefit from large forest tracts. *Wilson Bulletin* 105: 351–353.
- MOHR, C. O. 1947. Table of equivalent population of North American small mammals. *American Midland Naturalist* 3:223–249.
- NUTTLE, T. 1997. Densimeter bias? Are we measuring the forest or the trees? *Wildlife Society Bulletin* 25:610–611.
- PARRISH, J. D., AND T. W. SHERRY. 1994. Ecological correlates of sexual habitat segregation in a wintering Neotropical migrant passerine: The importance of seasonality. *Auk* 111:38–49.
- PERFECTO, I., R. A. RICE, R. GREENBERG, AND M. E. VAN DER VOORT. 1996. Shade coffee: Disappearing refuge for biodiversity. *BioScience* 46:598–608.
- POULIN, B., G. LEFEBVRE, AND R. MCNEIL. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73: 2295–2309.
- POULIN, B., G. LEFEBVRE, AND R. MCNEIL. 1993. Variations in bird abundance in tropical arid and semi-arid habitats. *Ibis* 135:432–441.
- PLYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. *Identification guide to North American passerines*. Slate Creek Press, Bolinas, California.
- RAPPOLE, J. H., M. A. RAMOS, AND K. WINKER. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. *Auk* 106:402–410.
- RAPPOLE, J. H., AND D. W. WARNER. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pages 353–393 in *Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation* (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington D.C.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* No. 103.
- ROBBINS, C. S., B. A. DOWELL, D. K. DAWSON, J. COLÓN, F. ESPINOZA, J. RODRIGUEZ, R. SUTTON, AND T. VARGAS. 1987. Comparison of Neotropical winter bird populations in isolated patches versus extensive forest. *Acta Oecologica Oecologia Generalis* 8:285–292.
- ROBERTS, J. O. L. 1971. Survival among some North American wood warblers. *Bird-Banding* 42:165–183.
- SHERRY, T. W., AND R. T. HOLMES. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77:36–48.
- SHIELDS, W. M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* 101:780–789.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, New York.
- WALLACE, G. E. 1998. *Demography of Cuban bird communities in the nonbreeding season: Effects of forest type, resources, and hurricane*. Ph.D. dissertation, University of Missouri, Columbia.
- WARKENTIN, I. G., AND D. HERNÁNDEZ. 1996. The conservation implications of site fidelity: A case study involving Nearctic-Neotropical migrant songbirds wintering in a Costa Rican mangrove. *Biological Conservation* 77:143–150.
- WINKER, K., J. H. RAPPOLE, AND M. A. RAMOS. 1990. Population dynamics of the Wood Thrush in southern Veracruz, Mexico. *Condor* 92:444–460.
- WUNDERLE, J. M., JR. 1992. Sexual habitat segregation in wintering Black-throated Blue Warblers in Puerto Rico. Pages 299–307 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- WUNDERLE, J. M., JR. 1995. Population characteristics of Black-throated Blue Warblers wintering in three sites on Puerto Rico. *Auk* 112:931–946.
- WUNDERLE, J. M., JR. 1999. Avian distribution in Dominican shade coffee plantations: Area and habitat relationships. *Journal of Field Ornithology* 70:58–70.

- WUNDERLE, J. M., JR., AND S. C. LATTA. 1996. Avian abundance in sun and shade coffee plantations and remnant pine forest in the Cordillera Central, Dominican Republic. *Ornithología Neotropical* 7:19–34.
- WUNDERLE, J. M., JR., AND S. C. LATTA. 1998. Avian resource use in Dominican shade coffee plantations. *Wilson Bulletin* 110:271–281.
- WUNDERLE, J. M., JR., AND R. B. WAIDE. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. *Condor* 95:904–933.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewoods Cliffs, New Jersey.

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