

POPULATION STRUCTURE, TERRITORIALITY AND OVERWINTER SURVIVAL OF TWO MIGRANT WARBLER SPECIES IN JAMAICA¹

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Abstract. We studied the ecology and behavior of American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulescens*) on their wintering grounds in Jamaica during 3 years, 1986-1989. Winter densities were comparable to (American Redstart) or slightly greater than (Black-throated Blue Warbler) those recorded for these species in breeding areas. Males, females, first-year and older individuals of each species occurred within the same habitats and study areas, with no evidence of intraspecific habitat segregation. Individuals of both sexes occupied territories, which were maintained by displays, vocalizations (chip notes), and stereotyped agonistic interactions. Territories were defended against conspecifics of the same sex and frequently of the opposite sex, although those of males and females sometimes overlapped, especially in the Black-throated Blue Warbler. Both sexes of each species responded aggressively to playbacks of breeding song/chip tapes and to decoys. Territories were occupied throughout the winter period, with most individuals of both species remaining through the winter within <50 m of where they were captured, marked, and observed in October-early November. Overwinter survival was high: 80% of 124 redstarts and 66% of 53 black-throated blues color-marked in early winter (October-November) were still alive and present on territory in late winter (March-April). Individually marked birds disappearing during the winter were almost invariably replaced, usually by new (unmarked) individuals, indicating competition for territories and possibly the presence of floaters. This latter finding, coupled with those of strong overwinter site attachment and intense territorial behavior, suggests that events in winter are important in the population dynamics of these migrant species.

Key words: *Dendroica caerulescens*; *neotropical migrants*; *overwinter survival*; *Setophaga ruticilla*; *site attachment*; *winter territoriality*; *winter limitation*.

INTRODUCTION

Many migratory passerine birds that breed in temperate North America spend two-thirds of their annual cycle in tropical or subtropical habitats (Keast 1980). Some investigators have suggested that such migrants in winter occur mostly in secondary habitats, often exploit superabundant or ephemeral resources, and/or may in general not be fully integrated into tropical communities (e.g., Willis 1966, Karr 1976, Hutto 1980). Moreover, the theoretical arguments of Fretwell (1972) have led to the hypothesis that migrant bird populations may be most affected, i.e., limited, by events occurring in winter (Fretwell 1972, 1986; Terborgh 1980; Morse 1980; Alerstam and Hogstedt 1982; but see Cox 1985). These findings and hypotheses have led to a deduction being used in conservation arguments

that winter is an especially difficult season for migratory birds, that high mortality then is probably to be expected, and that population declines among long-distance migrant passerines may, for example, be due mostly to events in winter (Wallace 1986, Connor 1988). To date, however, information on the demography, especially the survival, of migratory passerines in their winter quarters, which is needed to test such hypotheses, has been lacking.

Although the general distribution and habitat associations of most migratory passerine birds in their neotropical winter quarters have been reasonably well documented (see Keast and Morton 1980, Rappole et al. 1983), their population ecology and behavior in winter, especially dispersion patterns and densities, aggressive behavior, age and sex ratios, and survivorship, have rarely been quantified. Rappole and Warner (1980) described the behavior of migrant species in Veracruz, Mexico, including aspects of territoriality and dispersion, Nisbet and Medway (1972) studied the dispersion and population

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ecology of *Acrocephalus orientalis* wintering in Malaysia, and Price (1981) documented territoriality and possible food limitation of *Phylloscopus trochiloides* in its winter quarters in India. Greenberg (1980, 1984), in perhaps the most detailed study of the socioecology of wintering migrants, considered the social relations and habitat exploitation patterns of two migrant species in Panama. Recently, Lynch et al. (1985) and Morton et al. (1987) described a pattern of habitat segregation between male and female Hooded Warblers (*Wilsonia citrina*) in the Yucatan, which could have important demographic implications. Although individual migrants have been shown to exhibit strong site fidelity to winter sites from one year to the next (Diamond et al. 1973, Loftin 1977, Faaborg and Arendt 1984, Kricher and Davis 1986), few studies have considered the survival of individuals through the winter season, and apparently none on a quantitative population basis (Greenberg 1986).

In this paper, we report on the socioecology of two migratory paruline warblers, the American Redstart (*Setophaga ruticilla*) and Black-throated Blue Warbler (*Dendroica caerulescens*), in their winter quarters in Jamaica. These two species were chosen because their ecology and behavior on the breeding grounds was relatively well studied (Black 1975; Holmes et al. 1986; Rodenhouse 1986; Sherry and Holmes 1988; Steele 1989; Holmes and Sherry, unpubl. data), but little was known of events or circumstances in winter that might affect their population biology. Jamaica was chosen as a study site because both species occur widely there (Lack 1976), and could be studied simultaneously. Using individually marked birds on four study sites, we asked the following questions: (1) What are the densities and dispersion patterns of these species populations in winter habitats? (2) Do age and sex classes segregate by habitat or do they co-occur in the same area? (3) What behavioral interactions maintain the observed dispersion patterns? (4) Do individuals persist in the same area through the winter? And, (5) can such persistence be used to estimate overwinter survival? Answers to these questions indicate the spatial and temporal responses of these migrant passerines to winter habitats, and provide a basis for understanding the winter socioecology and demography of these species and ultimately the importance of winter environments to their population dynamics.

WINTER DISTRIBUTIONS AND STUDY SITES

American Redstarts winter throughout the Greater Antilles and along the Caribbean coast of Mexico, Central America, and northern South America (Rappole et al. 1983). Black-throated Blue Warblers winter almost exclusively in the Greater Antilles, from Puerto Rico in the east to Cuba, Cayman Islands, and Jamaica in the west, although individuals occur occasionally on the mainland of Central and South America (AOU 1983).

Redstarts begin arriving in Jamaica in late August, but the main influx appears to be in mid- to late September (R. Sutton, pers. comm.). Black-throated blues arrive later, usually in early to mid-October (L. Salmon, pers. comm.). Both species occur widely and abundantly in Jamaica, with redstarts more common at low elevations and black-throated blues at mid- and higher elevations (Lack and Lack 1972, Lack 1976). In October 1986, we established three study sites (Rocklands, Copse, Luana Point) and, in October 1987, added a fourth (Paradise). These were located along a north-south transect between Montego Bay and Black River near the western end of the island. All study plots were flagged at 25-m intervals, so that sightings of individual birds could be mapped in detail. Habitat types follow the terminology of Asprey and Robbins (1953).

Rocklands was an 8-ha plot in a forested valley at 300 m elevation near Anchovy, 7 km south of Montego Bay, St. James Parish. It was located adjacent to the Rocklands Wildlife Sanctuary and to large tracts of similar habitat. The vegetation was second-growth dry limestone scrub forest, comprised mostly of dense stands of young trees (mostly 2–10 cm diameter at breast height [dbh] and 4–10 m tall), primarily logwood (*Haematoxylon campechianum*) with scattered larger trees (20–50 cm dbh, including *Ceiba pentandra*, red birch *Bursera simaruba*, *Terminalia latifolia*, and *Ocotea* spp.). The shrub layer was dense but patchy. Vines covered many of the trees and shrubs, often producing impenetrable tangles. During the 3 years of study, several small parts of this plot (each <1.5 ha) were cleared and burned for cultivation.

Copse was a 5-ha plot located within a 40-ha remnant of old-aged wet limestone forest on

Copse Mountain at about 450 m elevation, 5 km southwest of Rat Trap, Westmoreland Parish. This mountaintop forest was surrounded by pasture, and contained a diverse set of native tree species characteristic of wet limestone forest at mid-elevations, including *T. latifolia*, *Cedrela odorata*, *Ocotea* spp. Canopy height averaged 30–35 m, with occasional emergents >40 m. Ferns, small saplings, and shrubs (Melastomataceae, Rubiaceae) were common in the dense understory. Epiphytes, lianas, and vines were numerous, especially in several large tree-fall gaps.

The Luana plot was located along the south coast of Jamaica, about 13 km west of Black River near Luana Point, St. Elizabeth Parish. The study area was a 5.5-ha plot located within a narrow (100–150 m) but long (2 km) strip of woodland situated between the Caribbean Sea and an extensive mangrove swamp. The vegetation consisted mostly of logwood, occasional red birch, and a variety of other trees ranging to 15 m in height, and many shrubs and vines, which often formed dense thickets. Black (*Avicennia germinans*), white (*Laguncularia racemosa*), and occasional red (*Rhizophora mangle*) mangroves occurred along the inland side of the plot, while *Coccoloba uvifera* was a common tree along the coastal strand. Similar habitats were found along other margins of this and other mangrove swamps in Jamaica, but are local in occurrence along the shorelines (Lack 1976).

The fourth locality, Paradise, was also near the south coast about 6.5 km southeast of Savanna-La-Mar, Westmoreland Parish. It consisted of a 10.5-ha plot within an approximately 30-ha remnant patch of lowland coastal forest, which had been heavily (but selectively) cutover. The most common trees were burnwood (*Metopium brownii*), *Clusia* spp., red birch, and various palms, including *Sabal jamaicensis* and *Roystonea principes*, which provided a broken canopy at about 20–25 m, with occasional emergents to 30 m. Red mangroves and low shrubby vegetation occurred along one edge of the study area. Epiphytes and vines were numerous. The understory consisted of shrubs, small trees, and, on the southern half of the study area, dense patches of sawgrass (*Cladium jamaicense*).

The climate in Jamaica is subtropical, with mean monthly temperatures ranging between 23° and 27°C (Lack 1976). Rains are extensive in October and November, with the dry season be-

ginning in December or January and extending through March or early April. On 12 September 1988, Hurricane Gilbert caused extensive damage to many of our study areas. Cope and Paradise, the two more forested sites, were strongly affected, with many trees and large branches being snapped off and falling to the ground to form dense tangles of dead vegetation. Subsequently, with the increased light reaching the forest floor, the understory vegetation grew rapidly and by late March 1989, there were dense tangles of vines and shrubs on these two sites, which were often difficult to penetrate. The study areas at Rocklands and Luana Point were less severely affected, although occasional trees were broken off or uprooted and leaves were stripped from the vegetation.

METHODS

We conducted our study during three winter seasons 1986–1989. The study sites were visited three times each year: in “early winter” (23 October–7 November 1986, 19 October–5 November 1987, 18 October–6 November 1988), in “midwinter” (9–22 December 1986, 18–31 January 1988, 3–16 January 1989), and in “late winter” (17–31 March 1987, 22 March–4 April 1988, 16–29 March 1989). Within each of these sampling periods, we spent 3–5 days on each site, capturing, marking, censusing, and observing wintering migrants. Most individuals were captured and marked during the early winter trip, although new or previously unmarked birds were occasionally caught and marked during subsequent sampling periods. Upon locating a bird by sight or by hearing its chip note, we erected a mist net, placed a stuffed or clay decoy of the species next to the net, along with a loudspeaker connected to a remotely located tape recorder. We then broadcast a tape recording of mixed call notes and songs (recorded for each species on breeding sites). Although responses were variable, many birds were caught within 5–10 min. Once a bird was caught, it was often used as a live decoy to catch the next bird; no individuals were held for >45 min. Each bird was individually marked with a numbered aluminum and two colored plastic bands. Individuals of both species <1 year old (classified as HY = hatching-year birds prior to December 31 or as SY = second-year birds as of 1 January, U.S. Fish and Wildlife Service, Bird Banding Manual 1977)

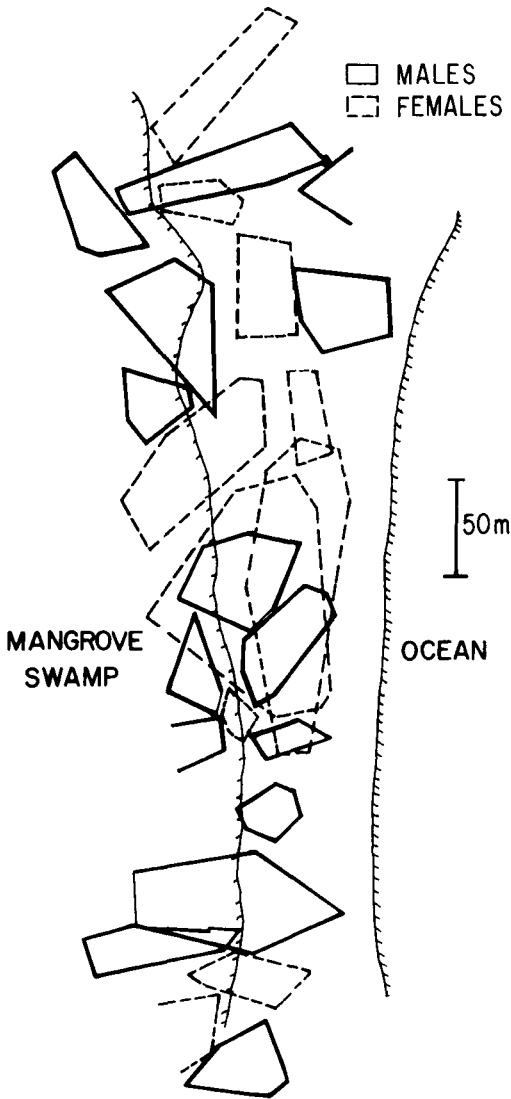


FIGURE 1. Territories of male and female American Redstarts on the Luana Point study site, Jamaica, 20-28 March 1987. Boundaries enclose all locations of observed individuals, most of whom were color-banded, and represent minimal areas occupied.

were distinguished from older birds (ASY = after second year) by having incompletely ossified skulls (early winter captures only) and/or by plumage characteristics using criteria described in the U.S. Fish and Wildlife Service Bird Banding Manual (1977) and by Pyle et al. (1987).

All captured birds were weighed on a Pesola balance to the nearest 0.1 g. Subcutaneous fat in the furcular region was scored as follows: 9 (no fat), 1 (trace), 2 (fat filling bottom of furculum),

3 (fat filling furculum), and 4 (fat mounded and spreading over breast muscle).

On each 4- to 5-day census period on each plot, we systematically and repeatedly traversed the study area, recording locations and movements of all marked and any unmarked birds on gridded maps. Minimal activity ranges or territory boundaries were determined by enclosing all observations of each individual. Call notes were often used to locate individuals, and each bird was visually observed in order to check for color bands, age, and sex. Behavior and occurrences of aggressive interactions were also recorded. Resightings of color-marked individuals in successive time periods provided data on site attachment and persistence and survival through the winter. Distances moved by individually marked birds during the winter were determined from the central points of their mapped activity ranges in successive sampling periods.

Mean values are given as \pm SD. Tests of statistical differences between means were made with Student's *t*-test and between proportions with Chi-square.

RESULTS

POPULATION STRUCTURE: DISPERSION PATTERNS, DENSITIES, AND AGE/SEX RATIOS

American Redstarts. Male and female redstarts of both age classes (HY/SY and ASY) occurred on all four study sites. Individuals of both sexes and age classes were interspersed, as illustrated by the pattern at Luana Point in March 1987 (Fig. 1). Male redstarts never overlapped each other in space, and most females occupied areas exclusive of other females. However, females occasionally overlapped other females and males (Fig. 1.) When this occurred, the two birds were rarely seen in close proximity, and when they were seen together, one quickly supplanted the other (see below). In male-female contacts, the male was usually the more aggressive and chased the female. In many cases, however, females defended areas against males and performed circle-chasing displays (see below). Although the data are insufficient for precise measurements, female redstarts appeared to occupy larger areas than did males, particularly when they overlapped with males (see Fig. 1). Yet, some female redstarts, like most males, occurred in very restricted areas where they were seen consistently at different seasons of the winter, often in the same tree(s).

TABLE 1. Densities and sex and male age ratios of American Redstarts and Black-throated Blue Warblers in early winter (late October–early November), midwinter (mid-December–January) and late winter (late March–early April) on the Jamaica study plots, 1986–1989.

	Density (number/10 ha)			Sex ratio (% males)			Male age ratio (% ASY)*		
	1986–1987	1987–1988	1988–1989	1986–1987	1987–1988	1988–1989	1986–1987	1987–1988	1988–1989
American Redstart									
Luana Point									
Early winter	— ^b	40.0	50.9	—	54 (22)	54 (28)	—	66 (9)	50 (15)
Midwinter	41.8	43.6	45.6	56 (23)	54 (24)	64 (25)	92 (12)	56 (9)	56 (16)
Late winter	<u>47.3</u>	<u>34.5</u>	<u>45.6</u>	<u>59 (27)</u>	<u>47 (19)</u>	<u>56 (25)</u>	<u>86 (14)</u>	<u>50 (6)</u>	<u>57 (14)</u>
Means	44.6	41.8	47.4	57.5	49.0	58.0	89.0	57.3	54.3
Paradise									
Early winter	—	24.8	22.8	—	62 (26)	50 (24)	—	85 (13)	75 (12)
Midwinter	—	26.7	23.8	—	54 (28)	60 (25)	—	73 (11)	73 (15)
Late winter	—	<u>31.4</u>	<u>21.0</u>	—	<u>39 (33)</u>	<u>55 (22)</u>	—	<u>44 (9)</u>	<u>75 (12)</u>
Means	—	27.6	22.5	—	51.7	55.0	—	67.3	74.3
Rocklands									
Early winter	15.7	16.3	16.3	82 (11)	77 (13)	54 (13)	88 (9)	89 (9)	100 (7)
Midwinter	15.4	13.8	10.0	70 (10)	73 (10)	100 (8)	100 (7)	86 (7)	88 (8)
Late winter	<u>15.0</u>	<u>11.3</u>	<u>11.3</u>	<u>75 (12)</u>	<u>78 (9)</u>	<u>89 (9)</u>	<u>89 (9)</u>	<u>100 (7)</u>	<u>75 (8)</u>
Means	14.9	13.8	12.4	78.3	76.0	81.0	92.3	91.7	87.7
Black-throated Blue Warbler									
Copse									
Early winter	30.0	32.0	36.0	83 (12)	56 (16)	50 (18)	38 (8)	88 (8)	36 (11)
Midwinter	30.0	34.0	40.0	73 (15)	53 (17)	65 (20)	42 (12)	86 (7)	33 (11)
Late winter	<u>26.0</u>	<u>30.0</u>	<u>36.0</u>	<u>77 (10)</u>	<u>67 (15)</u>	<u>65 (17)</u>	<u>50 (8)</u>	<u>86 (7)</u>	<u>33 (12)</u>
Means	28.7	32.0	37.3	77.7	58.7	56.7	43.3	87.3	34.0
Rocklands									
Early winter	—	13.8	10.0	—	45 (11)	25 (8)	—	—	—
Midwinter	17.5	15.0	8.8	43 (14)	50 (12)	14 (7)	—	—	—
Late winter	<u>11.3</u>	<u>11.3</u>	<u>10.0</u>	<u>44 (9)</u>	<u>22 (9)</u>	<u>50 (8)</u>	—	—	—
Means	12.5	12.5	9.6	43.5	39.0	29.7	—	—	—

* ASY = individuals > 1 year of age, see Methods.

^b Insufficient sample sizes.

Redstart densities at Luana, Paradise, and Rocklands ranged from 10.0 to 50.9 individuals/10 ha, varying among plots, seasons within the winter, and between years (Table 1). Densities were consistently highest at Luana (averaging about 44/10 ha), followed by Paradise (25/10 ha) and Rocklands (14/10 ha). In the wet limestone forest at Copse, redstarts occurred high in the canopy, and were difficult to lure into the understory for purposes of capturing and marking, and therefore to census. By using individual differences in plumage characteristics to separate birds, however, we estimated there were about 12, 14, and 18 redstarts/10 ha on the Copse study area in the winters of 1986–1987, 1987–1988, and 1988–1989, respectively. Compared to the preceding two winters, redstart densities in 1988–1989 were slightly lower at Paradise and Rock-

lands but higher at Luana and Copse, indicating little effect of the hurricane in September 1988.

These redstart densities at Paradise and Luana Point were considerably higher than those reported for the species in several Caribbean and one Mexican site (4–17/10 ha) by Bennett (1980) or in the Yucatan (0–6.5 redstarts/10 ha) by Waide et al. (1980). They are comparable, however, to those found in redstart breeding areas in North America. For example, redstart densities over a 16-year period in a northern hardwoods forest in New Hampshire ranged between 12 and 44 individuals/10 ha, \bar{x} = 29.4 (Holmes et al. 1986). Bennett (1980) reported breeding redstart densities of 13, 21, and 29 birds/10 ha, respectively, for sites in Tennessee, Maryland, and Washington.

Both sexes and age classes of redstarts occurred

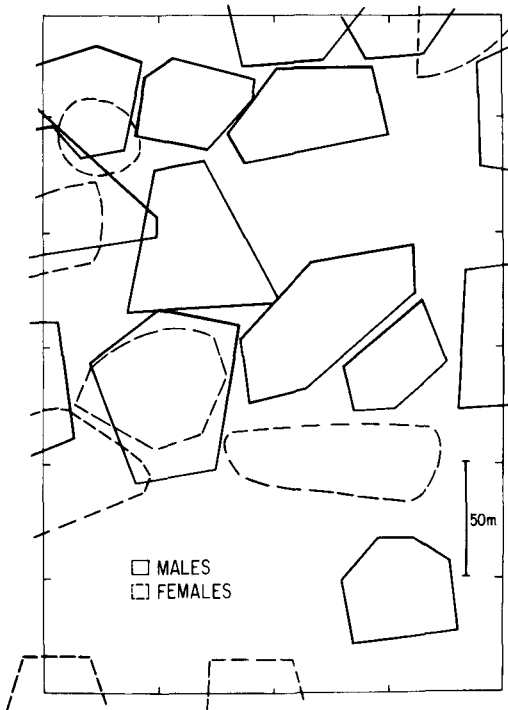


FIGURE 2. Territories of male and female Black-throated Blue Warblers on Copse Mountain study site, Jamaica, 27 October–4 November 1987. Boundaries enclose all locations of observed individuals, most of whom were color-banded, and represent minimal areas occupied.

on each study site. At Luana and Paradise, the numbers of males and females were nearly equal, while at Rocklands, the site with the lowest redstart density, males comprised about 75–80% of the individuals present in each season (Table 1). Age ratios were determined most accurately for males, because they could be aged visually by plumage in the field (see Methods). A greater proportion of older (ASY) redstarts occurred at Rocklands (88–92%) than at Paradise or Luana (54–74%), except for the latter site in 1986–1987 where they comprised 89% of the males (Table 1). Of 27 females caught and aged at Luana, 51.9% were ASYs, while 90% of those caught at Paradise were ASYs ($n = 10$). Thus, age structure of both male and female redstart populations varies considerably from place to place in the winter grounds.

Black-throated Blue Warbler. Like redstarts, Black-throated Blue Warblers were dispersed relatively evenly through the study plots, as illustrated by the pattern at Copse in early winter

1987 (Fig. 2). Male black-throated blues occupied home ranges exclusive of other males, and those of females were usually spatially separate from those of other females. When individuals of the same sex were seen in close proximity, which was rare, they were usually involved in aggression, often chasing (see below). Males and females, however, often had overlapping home ranges (Fig. 2). In fact, we frequently observed male and female black-throated blues foraging closely together (within 1–2 m) or moving through the same area within a short time of each other, without any sign of aggressive interaction between them. On four occasions in trying to capture either a male or a female, which had been observed nearby, we attracted and captured a bird of the opposite sex, indicating they had been present in the same local area or at least they had been drawn into the area by the playback and had not been driven off. We also caught two males in a single net in several instances, but these had been individuals observed to be chasing. Based on this largely anecdotal evidence, we suspect that activity ranges of male and female Black-throated Blue Warblers overlap considerably.

At the coastal plots, Black-throated Blue Warblers were uncommon; only one or two males were seen at Luana each winter, while three to four of each sex occurred on the Paradise study area. The species was more abundant at Copse and Rocklands, sites inland from the coast and at elevations > 300–400 m. Densities there ranged from 8.8 to 40 individuals/10 ha, averaging about 33/10 ha at Copse and 12/10 ha at Rocklands (Table 1). Densities at both sites remained relatively stable from early to late winter, although a slight overwinter decline occurred at both sites in 1986–1987 (Table 1). Black-throated blue density increased slightly at Copse in 1988–1989, despite extensive hurricane damage which occurred prior to their arrival in September 1988 (see Winter Distribution and Study Sites).

We are not aware of any comparable density data for wintering black-throated blues. However, the winter densities we report here for Jamaica are higher on average than those recorded for this species in the center of its north temperate breeding areas (e.g., $\bar{x} = 10.7 \pm 2.6$ SD individuals per 10 ha, range = 8–14, $n = 16$ years, in New Hampshire; Holmes et al. 1986).

As with redstarts, both male and female and ASY and HY/SY black-throated blues were found

on the same sites. Males dominated numerically at Copse (57–77%), but not at Rocklands (30–44%) (Table 1).

Age ratios were more difficult to obtain for Black-throated Blue Warblers because individuals of this species could not be aged by observation in the field; age determinations were therefore based entirely on birds captured on each plot and examined in the hand. For Copse, ASY males comprised 43, 87, and 34% of the male population in the three winters, respectively (Table 1). The increase in 1987–1988 reflected a high return of males marked in the previous season and the settling of relatively few HY/SY males. In the following year, fewer older males returned, and the study area was settled mostly by yearlings. At Rocklands, based on a very small sample size, ASY males comprised about 33% of the males present ($n = 6$). Of the females captured and aged by plumage and skull ossification (Pyle et al. 1987), 26.3% ($n = 19$) were ASYs at Copse and 14.3% ($n = 7$) at Rocklands. Thus, as for redstarts, age and sex ratios of wintering Black-throated Blue Warbler populations change considerably from site to site and year to year.

TERRITORIALITY

From the above data on population structure, it is clear that individual American Redstarts and Black-throated Blue Warblers occupy mutually exclusive intraspecific ranges, at least within sexes, indicating a territorial system. Here we describe the behavioral interactions between individuals which lead to the observed patterns of dispersion.

American Redstart. Localized activity and aggressive interactions between redstarts in winter, which suggested territoriality, have been described by Schwartz (1964) and Rappole and Warner (1980). The latter authors also reported that male and female redstarts responded to playbacks and that males exhibited a “wing droop” display at territorial boundaries. No other information seems to exist about the nature or frequency of behavioral interactions among individual redstarts in winter.

In Jamaica, redstarts of both sexes used a variety of stereotyped behavioral displays when interacting intraspecifically. Although song was not used by these wintering birds, both sexes uttered a species-specific “chip” note, probably the same as the “harsh chip” described by Ficken (1962). Such chip notes were heard frequently through-

out the day, but birds were often silent for long periods. At times, birds (both males and females) would chip repeatedly, every few seconds or so, in a surge of activity sometimes lasting 5–10 min. On occasion, two or more adjacent individuals would chip simultaneously. Such chip notes were also given in response to our playback tapes. In these cases, if a bird was nearby, it would almost invariably chip immediately, i.e., within 1–2 sec of the first broadcast redstart song. In addition, individuals of both sexes also uttered a thin “zeep” note in response to our vocalization playbacks, as well as other times, e.g., when we moved close to an individual foraging low in vegetation.

Redstarts giving a chip note, either spontaneously or in response to our vocalization playback, frequently assumed a stereotyped crouching posture, with the wings slightly outstretched and drooped, the tail noticeably fanned, head forward, and the bird generally having a sleeked appearance. Birds often appeared to be agitated in such circumstances, hopping and “pivoting” (Ficken 1962) relatively frequently (compared with before and after the display), with few if any feeding motions or attempts. This is the “wing-droop display” of Rappole and Warner (1980), and probably corresponds to the combined “head forward,” “wings out,” and “tail spread” displays described for redstarts in the breeding season by Ficken (1962).

On breeding grounds, male redstarts frequently contest territorial boundaries with a ritualized “circling” display (Ficken 1962, 1963). Identical behavior was employed by redstarts of both sexes and age classes in Jamaica. In this display, one individual first flies towards and circles, usually just in front of a second, perched bird. The second bird then takes flight and pursues the first back to a perch within its territory, at which point the second bird then circles in front of the first, and the pattern is repeated. Sometimes the birds circled and chased without either bird landing. In these displays that we observed in Jamaica, as in the breeding areas (Ficken 1962; Sherry and Holmes, pers. observ.), the birds were usually silent, although occasionally one or the other would give a chip note. Some circling sequences lasted for minutes at a time, others went on for up to an hour or more, and in several cases, the same two birds were observed circle chasing on two or more successive days.

These circling displays involved primarily older (ASY) males, but twice we observed the be-

havior between an ASY male and a female and between two females (all birds color-marked and sexes confirmed by inspection in the hand), and once between an ASY male and an HY male. These displays were observed most often in the early winter, probably due to the fact that birds were still establishing territories then, but they also took place in mid- and late winter. For instance, in late March 1987 at Luana Point, we watched an ASY male and a female circle-chase for 65 min on two different days.

Another indication of strong territorial antagonism between redstarts in winter was their response to simulated territorial intrusions. Most male and female redstarts responded quickly and aggressively to tape-recorded redstart song/chip notes and/or to the presence of a decoy. Birds usually began chipping immediately when the tape was played, and either began to move slowly through the foliage towards the playback location or, on occasion, fly directly to the nearest tree over the set-up, chipping actively.

Responses to the playbacks were variable, probably due to the location of the playback site relative to the territory of a bird, time of day or season, and whether or not a bird had previously heard playbacks or had recently encountered trespassers. In October 1986, in our search for possible study sites, we visited 11 different forested areas over a variety of mostly lowland or foothill areas throughout Jamaica that contained redstarts. Of 94 song/chip note playbacks, 81.9% resulted in at least one redstart and 22.3% in more than one bird appearing, 7.4% elicited circling displays among two or more contiguous birds, 5.3% elicited song responses, and 3.2% resulted in physical fights among respondents. These 94 playbacks involved entirely naive birds, i.e., previously unexposed to our simulated territorial intrusions. Also, our success in capturing redstarts appeared to be greater in early winter, suggesting that the aggressiveness of birds waned slightly over the winter period. However, redstarts in mid- or late winter often approached the experimental playback set-up, although they seemed less willing to come in as close as they did in early winter. Also, birds appeared to respond most aggressively to a live, caged bird, since on a number of occasions we quickly caught, using a live decoy, a particular redstart individual that had been unresponsive to our stuffed decoy on the same or previous days. To illustrate the effectiveness of a caged bird in eliciting ter-

ritorial responses, we captured 21 redstarts (as well as set up nets and decoys, and banded and measured birds) on our Paradise site on the mornings of 1 and 2 November 1987. Both males and females, and individuals of different ages (ASY and HY/SY), appeared to be equally responsive to the playbacks, although we did not quantify this behavior.

Black-throated Blue Warbler. Like redstarts, Black-throated Blue Warblers interacted aggressively with conspecifics. Again, song was not used (although song was heard several times in late winter), but birds uttered a species-specific call note, *ichuk*, lower pitched and distinctive from the redstart's but identical to that given by the species in the breeding season. Compared to redstarts, black-throated blues were less aggressive, although this may be due to the difficulty of observing interactions in this species in the denser shrub and lower strata of the habitats they occupied. We regularly saw a male and female foraging together within 1 m or less of each other, although we rarely saw two males foraging similarly. Prolonged agonistic interactions were seen twice. The first case involved two unbanded females and a banded male on the Copse study site on 28 October 1987. The display consisted of a flight, often but not always involving a circular pattern similar to that of the redstart's circle display, in which one bird appeared to initiate the display by flying past or starting out ahead of the other, thus inciting the second bird to follow in a chase. Both birds uttered soft chip notes throughout the duration of the flights. Sometimes the birds both landed after a circling flight; other times they continued chasing back and forth. The flights were generally horizontal (varying in height from 2–15 m above ground), and oriented in a variety of directions and locations, thus less stereotyped than the more aligned back-and-forth circling pattern characteristic of redstarts. Several times the birds foraged briefly between chases. We first encountered the two females chasing at 07:50 local time in an area <0.25 ha containing several contiguous tree-fall gaps along with regenerating low shrubs and vines. About 30 min later, the male appeared, and became involved in the chases, both being chased and doing the chases. Within a few minutes, one of the females disappeared and was not seen subsequently. By 09:37 the male and female were still interacting, but the male was largely the aggressor, flying at the female, who was primarily

feeding. We saw the male make 21 circling flights plus a variety of short (2–3 m) foraging flights during a 5-min period. When we returned again to the site at 11:15, only the male was seen in the vicinity. There was no physical contact between birds during this interaction. We have seen identical displaying behavior, sometimes lasting for several hours, between two female Black-throated Blue Warblers early in the breeding season in New Hampshire (Holmes and Sherry, unpubl. data). Such “circling” displays are known from a variety of other paruline warblers (Ficken and Ficken 1965), although not previously from individuals in winter quarters.

The second situation was a prolonged fight between two males at Copse on 30 October 1987. One (color-banded) male was observed constantly following a second, unbanded male, diving at it, chasing it from tree to tree in close pursuit, and giving loud chips when perched. Several bouts of aerial combat occurred, with the two birds fluttering together in the air as they descended towards the ground, their feet held up in either a defensive or aggressive fashion, and bills stabbing towards each other. The interaction between these two individuals lasted for at least 65 min, and when we returned 1 hour later, only the banded male could be found anywhere in the vicinity.

As with redstarts, both male and female Black-throated Blue Warblers often responded quickly to the playback of songs and chip notes, although the response did seem to wane more noticeably in this species as the season progressed. Females appeared to respond to male breeding songs and chips just as strongly as did males; also, the stuffed decoy we used was of a male, and females often came in chipping and approached the model closely. Thus, Black-throated Blue Warblers of both sexes responded aggressively to conspecifics, and used a variety of call notes and visual displays in these interactions.

SITE ATTACHMENT AND PERSISTENCE OF MIGRANT WARBLERS THROUGH THE WINTER

The extent to which birds remain in the same area throughout the winter is another indication of a territorial winter social system. To quantify degree of persistence in an area, we measured the distances between the centers of activity of individuals of both species from the time they were marked and their territories mapped in early

winter and when they were observed again in either midwinter or late winter (see Methods).

Between early winter and midwinter, male redstarts moved an average of 24 to 25 m and females 24 to 31 m, varying slightly with age (Table 2), although the differences were insignificant ($P > 0.1$). Distances moved between early and late winter averaged slightly longer (Table 2), with the only statistically significant difference being that HY/SY females moved further on average than did ASY males ($P < 0.01$). The longer average distance for HY/SY females was due largely to the influence of one yearling female that moved to opposite ends of the Luana plot (223 m) between October 1987 and late March 1988.

For Black-throated Blue Warblers, the mean distances moved by males and females between early winter and midwinter ranged from 27 to 57 m (Table 2), but these did not differ significantly ($P > 0.1$) between sexes or age classes. Between early and late winter, black-throated blues moved an average of about 18 to 74 m (Table 2), but the only statistically significant differences were that both HY/SY males and females moved significantly further than did ASY males ($P < 0.05$). In 1989, one HY/SY female shifted her center of activity 224 m between January and late March, and one yearling male moved 109 m, indicating that major changes in location do occasionally occur. Thus, as with redstarts, yearling black-throated blues were somewhat less committed than older birds to their sites, and at least a few individuals had a greater tendency to shift their locations over the course of the winter. Overall, these findings indicate that both sexes and age classes of American Redstarts and Black-throated Blue Warblers remained most of the winter in very localized areas, i.e., within < 50 m.

REPLACEMENT OF TERRITORIAL BIRDS THAT DISAPPEARED

Over the course of our study, 15 color-marked redstarts disappeared from our study plots between early winter and midwinter or between midwinter and late winter. Five of these were ASY males whose territories were found to be occupied later the same season by, respectively, (1) an unbanded ASY male, (2) an unbanded SY male (two records), (3) an unbanded ASY female, and (4) a neighboring banded ASY male who shifted his territory into the vacated area. Two

TABLE 2. Mean distances between the activity centers (=territories) of individually color-banded American Redstarts and Black-throated Blue Warblers between early winter and midwinter and between early and late winter in Jamaica. Data from three winter seasons (1986–1989) were combined.

	Distances between activity centers (m)			
	Males		Females	
	ASY ^a $\bar{x} \pm SD$ (n)	HY/SY ^b $\bar{x} \pm SD$ (n)	ASY $\bar{x} \pm SD$ (n)	HY/SY $\bar{x} \pm SD$ (n)
American Redstart				
Between early winter and midwinter ^c	23.9 ± 17.5 (50)	24.8 ± 18.9 (10)	30.7 ± 24.8 (22)	23.8 ± 7.4 (10)
Between early and late winter ^c	27.4 ± 18.3 (53)	37.1 ± 20.5 (9)	39.5 ± 21.7 (21)	51.8 ± 61.2 (10)
Black-throated Blue Warbler				
Between early winter and midwinter	27.7 ± 28.6 (13)	27.5 ± 24.7 (10)	57.3 ± 13.3 (4)	37.0 ± 26.9 (8)
Between early and late winter	21.9 ± 13.7 (13)	42.3 ± 35.6 (9)	17.7 ± 16.3 (3)	74.8 ± 86.4 (5)

^a ASY = individuals >1 year of age, see Methods.

^b HY/SY = individuals <1 year of age, see Methods.

^c See text and Table 1 for sample period dates.

SY males disappeared and were replaced, one by an unbanded female and the other by a neighboring banded ASY female. Six of the 15 were females, three of which were replaced by unbanded females, one by an unbanded ASY male, one by an unbanded HY male, and one by a neighboring banded ASY male who shifted into the area. Finally, an ASY and an SY male disappeared but were not replaced.

Similarly, 16 color-marked Black-throated Blue Warblers disappeared from the plots during the study. Four were males which were replaced by

(1) an unbanded male, (2) an unbanded female, and (3) a banded female whose territory may have previously overlapped that of the disappeared bird (two records). Six females disappeared and were replaced, two by unbanded males, three by unbanded females, and one by a banded male. The latter bird's territory may have previously overlapped that of the female before she disappeared. Six black-throated blues were not replaced (four females, two males), three of which disappeared between mid- and late winter, thus relatively late in the season.

TABLE 3. Overwinter site persistence/survival of American Redstarts and Black-throated Blue Warblers on Jamaican study sites, based on resightings of individuals color-marked in early winter or midwinter and subsequently observed within the same winter season. Data from 3 years, 1986–1987, 1987–1988, and 1988–1989 were combined for these analyses.

	Males			Females			Total
	ASY ^a	HY/SY ^b	All	ASY	HY/SY	All	
American Redstart							
Number marked in early winter	62	12	74	37	13	50	124
% present in midwinter	93.5	91.7	93.2	75.7	76.9	76.0	86.3
% present in late winter	88.7	75.0	86.5	70.2	69.2	70.0	79.8
Number marked in midwinter ^c	65	14	79	32	10	42	121
% present in late winter	95.4	85.7	93.6	93.8	90.0	92.9	93.4
Black-throated Blue Warbler							
Number marked in early winter	16	15	31	9	13	22	53
% present in midwinter	81.3	86.7	83.9	66.7	61.5	63.6	75.5
% present in late winter	75.0	80.0	77.4	55.6	46.2	50.0	66.0
Number marked in midwinter ^c	14	17	31	6	9	15	46
% present in late winter	92.9	82.4	87.1	83.3	77.8	80.0	84.8

^a ASY = individuals >1 year of age, see Methods.

^b HY/SY = individuals <1 year of age, see Methods.

^c Includes individuals marked in early winter and present in midwinter plus those newly marked in midwinter.

Thus, redstarts that disappeared from their territories during the winter were replaced about 90% of the time, while the comparable figure for black-throated blues was about 62%. In both species, the vacancies created by these disappearing individuals were filled mostly by unmarked individuals, or in a few cases by neighbors shifting their territories.

OVERWINTER SURVIVAL: POPULATION ESTIMATES

American Redstart. Of 124 redstarts of both sexes and ages marked in the early winter period, 86.3% were present on the study area in midwinter and 79.8% were still there in late March–early April (Table 3). Although the numbers of HY/SY individuals in the sample were low, first-year males disappeared at a greater rate than the older ASY males, while the rates were similar for the two female age classes (Table 3). Overwinter survival for both sexes and age classes of redstarts was higher between midwinter and late winter than between early winter and midwinter (Table 3). During the first half of the winter, females disappeared at a disproportionately greater rate than did males (Table 3).

Black-throated Blue Warbler. Black-throated Blue Warblers exhibited a lower rate of overwinter survival compared to redstarts (Table 3). For all sex and age categories combined, 75.5% of 53 black-throated blues marked in early winter were still present in midwinter, and 66.0% remained through late winter (Table 3). No clear age-related differences were evident, although SY females disappeared at a slightly greater rate than did ASY females (Table 3). Also, both sexes of Black-throated Blue Warblers disappeared more often between early winter and midwinter than between midwinter and late winter (Table 3), as found in redstarts.

WINTER MASS AND BODY CONDITION

American Redstart. Mean body mass of male redstarts changed over the winter season, with males in midwinter being significantly lighter than those present in late winter (Fig. 3). Mean body mass of female redstarts did not differ significantly ($P > 0.05$) over the winter (Fig. 3). Similar values and overwinter trends for redstarts wintering in Jamaica were reported by Diamond et al. (1977), although they did not report data separately for the two sexes. The mean mass of all males caught in Jamaica and weighed was $7.2 \pm$

0.3 g ($n = 86$) and of females 6.8 ± 0.4 g ($n = 44$), values which were both significantly ($P < 0.001$) lower than those of male and female redstarts on breeding grounds in New Hampshire (males = 8.6 ± 0.5 g, $n = 71$; females = 8.7 ± 0.6 g, $n = 80$; Holmes et al. 1986).

On the whole, redstarts captured in Jamaica throughout the winter were lean; no fat scores > 2 were recorded and most were 0 and 1. Mean fat scores for males in early, mid-, and late winter were 0.44 ± 0.54 ($n = 53$), 0.19 ± 0.40 ($n = 16$) and 0.22 ± 0.43 ($n = 18$), respectively. Males in early winter had significantly higher scores than in midwinter ($P < 0.005$) and in late winter ($P < 0.005$). Fat scores for female redstarts in early, mid-, and late winter were 0.43 ± 0.69 ($n = 37$), 0.50 ± 1.0 ($n = 4$), and 0.0 ± 0.0 ($n = 5$), respectively, with the only significant difference being between the early and late winter samples ($P < 0.05$).

Black-throated Blue Warbler. Male Black-throated Blue Warblers significantly increased in mass between early winter and midwinter (Fig. 3), with the trend continuing through late winter, although the latter difference was insignificant ($P > 0.05$). Females also appeared to increase in mass from early winter to midwinter (Fig. 3), although the difference here was not significant ($P > 0.05$). Mean mass for all males caught during the winter in Jamaica was 9.2 ± 0.6 g ($n = 52$) and for females, 8.8 ± 0.6 g ($n = 32$), values significantly lower ($P < 0.001$) than those of breeding males and females in New Hampshire (males = 9.8 ± 0.5 g, $n = 70$; females = 10.1 ± 0.9 g, $n = 55$; Holmes et al. 1986).

Fat scores for male Black-throated Blue Warblers averaged 0.45 ± 0.63 ($n = 29$) in early winter, 0.20 ± 0.41 ($n = 20$) in midwinter, and 0.20 ± 0.42 ($n = 10$) in late winter. Comparable scores for females were 0.32 ± 0.48 ($n = 19$), 0.0 ± 0.0 ($n = 4$), and 0.19 ± 0.41 ($n = 6$). Although a declining trend through the winter season is indicated in these data, differences were not statistically significant for either sex ($P > 0.1$).

DISCUSSION

POPULATION STRUCTURE

Based on global calculations, Terborgh (1980) predicted that densities of many migrant populations in their neotropical winter quarters should be several times greater than in breeding areas,

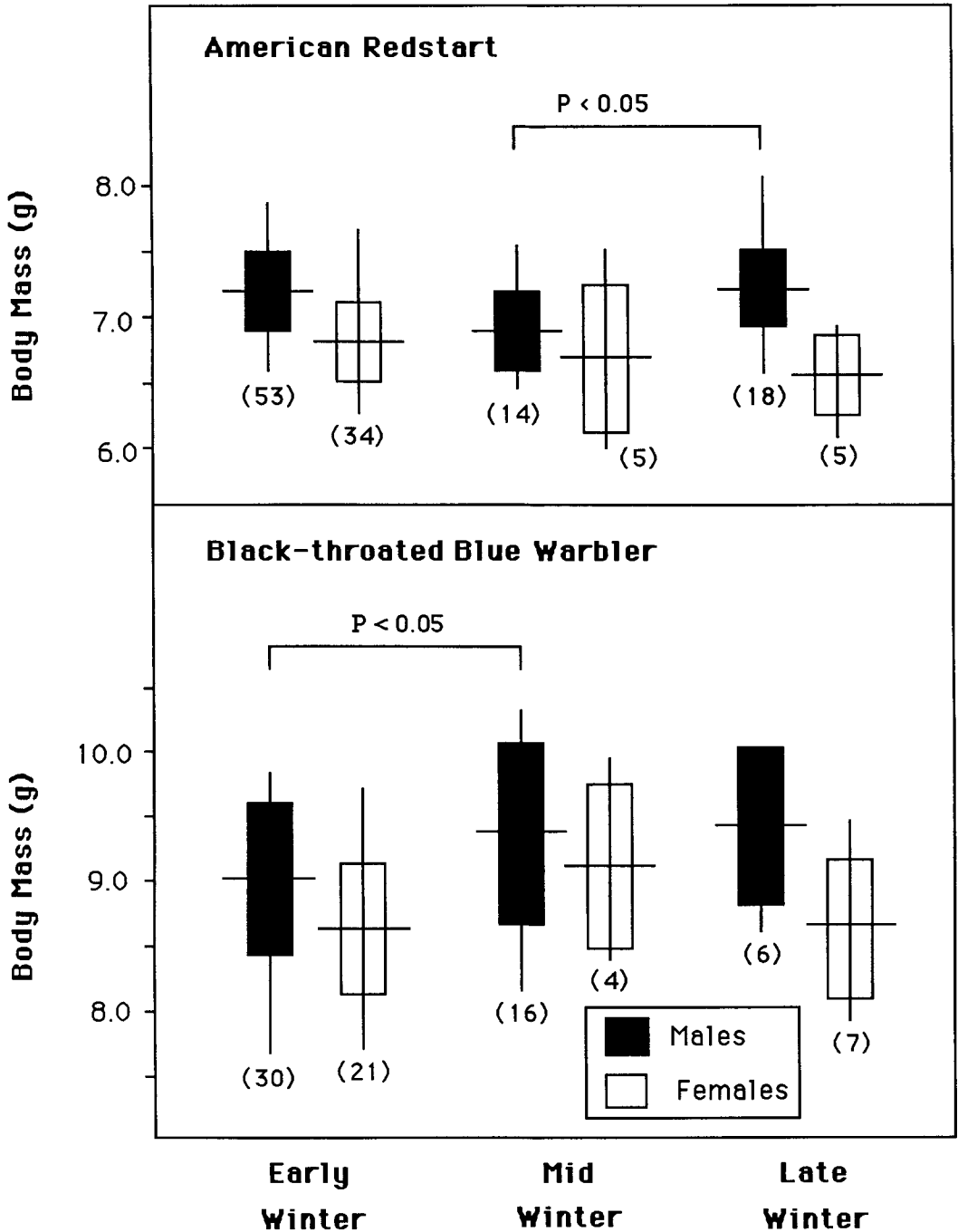


FIGURE 3. Body masses of male and female American Redstarts and Black-throated Blue Warblers in early (late October–early November), mid (mid-December–January) and late (mid-March–early April) winter in Jamaica. Horizontal bars = \bar{x} ; boxes = \pm SD; vertical lines = range; (n) = sample size.

largely because of more birds being concentrated into a smaller geographic area in winter. This was not upheld for American Redstarts in Jamaica whose densities were similar to those found in some parts of the breeding range, while winter densities of Black-throated Blue Warblers averaged about twice as high as those in their northern temperate breeding grounds. These two species in Jamaica appear to spread out over a wider range of habitats in winter (coastal forest scrub, mangroves, wet limestone forests, and agricultural and urban areas—Lack 1976; Holmes and Sherry, pers. observ.) than they do in summer (mainly deciduous forest), with the result that winter densities in any one habitat are not unusually high. Little quantitative or comparative information, however, seems to be available on habitat occupancy or breadth in winter and summer for these or any neotropical migrant passerine.

No segregation of sex or age classes was evident for either warbler species on our Jamaican sites, unlike that reported for Hooded Warblers in the Yucatan (Lynch et al. 1985) or suggested for Black-throated Blue Warblers in Haiti (Woods 1975). However, density and age-sex ratio differences between the Jamaican study sites for each species may reflect differences in habitat suitability. For instance, the high densities of redstarts at Luana may be related to the presence of a highly productive mangrove swamp, an hypothesis further supported by the presence at Luana of more older (ASY) male redstarts along the mangrove edge (Holmes, Sherry, and Reitsma, unpubl. data). However, even though redstarts occurred at relatively low densities in the second-growth vegetation at Rocklands, suggesting a lower quality site, most of the males there were ASYs (Table 1) which might be expected to occupy more preferred sites. Further studies of habitat suitability and selection of these warblers in winter are clearly needed, especially whether there is any age- or sex-related dominance involved in habitat selection and whether habitat selection is density dependent.

TERRITORIALITY

American Redstarts and Black-throated Blue Warblers in Jamaica both occupied and defended winter territories, using the same behavior as they do in the breeding areas, except for the absence of song. One noteworthy point, however,

was that females appeared to be just as defensive as males. In both species, but particularly redstarts, females displayed, chased, and fought with males, as well as with other females, and they were readily attracted to recordings of the male's breeding song and were drawn in close to male models, a characteristic which allowed us to capture and mark a large number of these females. In the northern temperate summer in New Hampshire, when we used the same tapes and decoys with breeding redstarts and black-throated blues, females rarely responded, and never approached such a playback set-up (Sherry and Holmes, unpubl. data). The fact that the winter activity ranges of males and females did overlap in some cases in both species, especially in the Black-throated Blue Warbler, suggests some subtle differences in the behavioral interactions between the sexes in their response to conspecifics, which we did not detect. Moreover, the observations of closely associating male and female black-throated blues suggest the occurrence of consort pairs, similar to that described for Canada Warblers (*Wilsonia canadensis*) wintering in Panama by Greenberg and Gradwohl (1980).

The occurrence of territorial behavior is usually interpreted as reflecting a selective force involved in the defense of some critical resource (Brown 1964). Winter territories also imply some resource is limiting (Ekman 1984, Nillson 1987), and their very existence is consistent with the idea that populations are limited during the winter, i.e., that individuals are competing for limiting resources. Since there is no evidence of any pairing or other reproductive behavior operating in winter, the most likely resources being defended are either a predator-free living space or food. Predation on small birds, especially in Jamaica, probably is infrequent, if it occurs at all. The only regularly-occurring bird-hunting raptor in Jamaica is the American Kestrel (*Falco sparverius*), which rarely hunts in forest habitats (Lack 1976); snakes are scarce; and the only mammalian predators are introduced (e.g., mongoose, *Herpestes auro-punctatus*, rats, feral cats), and would probably have little effect on small aerially active passerines such as warblers. Defense of a food resource is thus a likely possibility, although little is known about food abundance or availability for migrants in their winter quarters (Greenberg 1984, 1986). Price (1981) considered food as the most probable limiting resource for sylviid warblers wintering in India.

OVERWINTER SITE PERSISTENCE AND SURVIVAL: EMIGRATION VS. MORTALITY

The fact that 80% of the color-marked American Redstarts and 66% of the Black-throated Blue Warblers remained on our Jamaican study plots through the 5- to 6-month winter season suggests that mortality and/or movement during this time is relatively low. That birds do shift locations during the winter season was evidenced by new birds appearing on our study areas when residents disappeared and by recorded instances of color-marked individuals of both species making major shifts in location during a winter season. These replacements and local movements took place both between early winter and midwinter and between midwinter and late winter, indicating that floaters are present and/or that birds will shift locations throughout the winter.

Acknowledging that these long-scale movements do occur, but also assuming that they are relatively infrequent, we can use the measurements of overwinter persistence (Table 3) as minimal estimates of survival for these two species during the winter. If we consider these data to represent "survivorship" over a 6-month winter period and if birds survive through the other half of the year at the same rate, we can square these values to obtain rough estimates of annual survivorship, assuming the probability of survival in the two halves of the year is independent. Doing this with the data for these species in Jamaica (Table 3) produces annual survivorship estimates of 0.64 for redstarts and 0.44 for Black-throated Blue Warblers, values that fall within the range for small passerine birds calculated from band recovery data (Roberts 1971). Since an unknown proportion of the losses in these wintering warbler populations is due to emigration or at least local movement, we suggest that overwinter survival in these two warbler species in Jamaica may in fact be relatively high compared to that occurring during other parts of the year. This would be particularly true for the redstart. Additional insight into survivorship of these species will come from measurements of their year-to-year return rates in both their winter and breeding grounds, data which we are now in the process of gathering (Holmes and Sherry, unpubl.).

The timing of disappearance of these migrant warblers varied through the winter season. More individuals of both warbler species disappeared between early winter and midwinter than be-

tween midwinter to late winter (Table 3). This could be due to more unsettled individuals being on the study areas in early winter (Nisbet and Medway 1972, Price 1981), more jockeying for territories and therefore more local movement, or to higher mortality in the early part of the winter. Migration for both species appeared to be completed by the time we began our fieldwork in mid-October, and we have no evidence of birds moving through the area after that time, although such movement would be difficult to detect. Individuals, however, may still have been establishing and/or contesting territories at that time, as evidenced by the aggressive interactions which were observed most frequently in the early winter time period.

Food shortages seem least likely in early winter, since this corresponds to the wetter part of the season when insects appeared to be relatively more abundant (Holmes and Sherry, pers. observ.). The significant lower body masses and fat scores of male redstarts in midwinter, however, indicate that they may encounter more stressful conditions as the winter progresses. A similar trend of declining weights during the winter was shown for sylviid warblers in the paleotropics (Nisbet and Medway 1972, Price 1981). In contrast, Black-throated Blue Warblers showed a different pattern, in which both males and females increased in weight over the winter (Fig. 3). This might be related to the fact that they were studied in moister forests at slightly higher elevations, where feeding conditions may be different from those in the lower, drier areas where redstarts were more common. Also, we observed Black-throated Blue Warblers in Jamaica feeding frequently on fruits and nectar, resources that may stay relatively constant through the winter, especially in the cooler and wetter climate at mid- and higher elevations. Redstarts, in contrast, fed exclusively on insects, which may undergo more of a change related to the January–March dry season (Lack 1976), particularly in the lower elevation sites. Finally, our data for warblers in Jamaica are derived almost exclusively from territorial individuals in "good" habitat which might be expected to maintain relatively good body conditions as compared, for instance, to floaters or birds in more marginal areas. Although the significantly lower winter masses of both sexes of these two species in Jamaica, compared to breeding areas, may be due in part to the lack of gonadal development, they may reflect, as Lima

(1986) predicts for northern temperate wintering birds, a response to scarce food supplies or a period of high predation risk. In any case, they suggest that winter may be a stressful time for these migrant birds in their winter quarters.

In conclusion, the following evidence from this study is consistent with the hypothesis developed by Lack (1976), Fretwell (1972, 1986), Price (1981), and others that winter is a potentially stressful time for these migrant bird populations: (1) the occurrence of intense territoriality indicating competition for limiting (possibly food) resources, (2) replacements of disappeared color-marked birds with unbanded individuals that were apparently floaters, (3) low weights in winter, relative to those in summer, and (4) seasonal declines in fat scores and weights (at least in redstarts). Inconsistent with the idea, however, are the findings that individual birds persist ("survive") at relatively high rates through the winter and that Black-throated Blue Warblers appear to increase in weight during the winter. Furthermore, these and other differences between the two warbler species suggest that they may differ in the degree to which they are affected by winter events. Some of these differences may be related to the habitats they occupy (or in which we studied them) and to the available food supplies: the redstart was dependent on small flying insects in the lower elevation, drier sites, and black-throated blues fed on insects and small fruits in moister forests at mid-elevations. Also, the more frequent syntopy of male and female Black-throated Blue Warblers indicates a less exclusive territorial system, suggesting that even within a particular social system, such as territoriality, subtle variants may occur with important implications for population processes such as competition between sexes. Further considerations of the frequency and degree of overlap between the sexes in winter and of the possible significance of intrasexual exclusion and intersexual overlap in these two species are needed, especially with regards to resource availability and limitation.

It is clear that more demographic data from other populations and species obtained on a larger geographic scale, and coupled with similar information from these same species populations in their temperate breeding grounds, will be necessary to evaluate the relative importance of winter vs. breeding season events in affecting the population dynamics and regulation of these and other migratory passerines.

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