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POPULATION CHARACTERISTICS OF BLACK-THROATED BLUE WARBLERS WINTERING IN THREE SITES ON PUERTO RICO

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ABSTRACT.—I studied ecology and behavior of wintering Black-throated Blue Warblers (*Dendroica caerulescens*) at three sites on Puerto Rico over four years. The site with tall mature forest and relatively few fruiting understory plants had warbler populations characterized by: a predominance of males; relatively early fall arrival of returning adults; high site fidelity; large home ranges; low density of sedentary birds; few wandering individuals; high overwinter persistence of sedentary birds; and an invertebrate-rich diet. In contrast, the shrubby second-growth site with an abundance of fruiting plants had warbler populations characterized by: a predominance of females; relatively late arrival of returning adults compared to juveniles; low site fidelity; small home ranges; high density of sedentary and wandering birds; low overwinter persistence of sedentary birds; and a nectar- and fruit-rich diet. At the third site, the population traits fell within these extremes. Some site variation is attributable to sex differences in site persistence, wandering, and home-range size, which appear as population differences only because sex ratios vary among sites. However, differences in abundance and seasonality of fruit and nectar may further contribute to site differences in overwinter persistence of sedentary birds, wandering, home-range size, and density. *Received 26 April 1994, accepted 27 January 1995.*

THE IMPORTANCE OF EVENTS on the wintering grounds in the annual cycle of migratory species is suggested by the theoretical arguments of Lack (1968), Fretwell (1972, 1986) and others (Morse 1980, Terborgh 1980, Alerstam and Hogstedt 1982; but see Cox 1985). For Nearctic migrants, events on the tropical or subtropical wintering grounds could be especially important because many migrants spend over one-half the year there (Keast 1980). Moreover, high rates of deforestation on the tropical or subtropical wintering grounds (Lanly 1982) indicate that events there may have an even greater impact on Nearctic migrants in the future (Rappole and Powell 1986). However, despite indications that events on the wintering grounds may be important to the annual cycle of Nearctic migrants, and likely to become more so, only recently have workers focused on the behavior and demographic information needed to evaluate the importance of these events.

Relatively few studies of wintering migrant passerines have considered basic socioecological and demographic characteristics including aggressive behavior, dispersion patterns, densities, sex and age ratios, overwinter site persistence, and annual return rates, and most of these have been conducted at only one wintering locality (e.g. Nisbet and Medway 1972, Rappole and Warner 1980, Price 1981, Greenberg 1984, Staicer 1992). Only those of Holmes et al. (1989), Rappole et al. (1989), Winker et al. (1990), and Mabey and Morton (1992) have described these characteristics at more than one location. These studies have documented population differences among sites, many of which are presumed to correspond to resource variation. For example, sexual habitat segregation may reflect resource differences that together with sex differences contribute to demographic and behavioral variation among wintering migrant populations (Lynch et al. 1985, Lopez and Greenberg 1990, Parrish and Sherry 1994).

The Black-throated Blue Warbler (*Dendroica caerulescens*) shows sexual habitat segregation in parts of its winter range (Woods 1975, Sliwa 1991, Wunderle 1992) and, as a consequence, may show other behavioral and demographic

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differences among wintering sites. The species winters mostly in the Greater Antilles in various montane habitats, including montane broadleaf and pine forests, shrubby second growth, and coffee plantations, but occupy lowland habitats as well (Wunderle and Waide 1993). On Puerto Rico, females are most common in the younger, shrubby-sapling stages, and males are most common in the older, taller forests (Wunderle 1992).

I studied Black-throated Blue Warbler populations wintering in three Puerto Rican sites using individually marked birds to document site differences in sex and age ratios, pattern of fall arrival, prevalence of wanderers and sedentary birds, home-range size, home-range density, overwinter site persistence, annual return rates, diet and fruit abundance, and body condition. These traits were quantified to determine the extent of population variation among wintering sites with different sex ratios and to identify some of the factors associated with variation in these population characteristics. My study and similar ones in Jamaica (Holmes et al. 1989, Holmes and Sherry 1992) help to elucidate the extent of variation in the winter ecology of Black-throated Blue Warblers, thus providing information needed to assess the role of the wintering grounds in this species' population dynamics.

STUDY SITES AND METHODS

Three sites on the Caribbean island of Puerto Rico were selected where different sex ratios of wintering Black-throated Blue Warblers had previously been recorded. These sites have been described in detail in Wunderle (1992), and only a brief description is provided here.

The El Verde site surrounds the El Verde field station in the Luquillo Experimental Forest in eastern Puerto Rico at an altitude of 350 m. The broad-leafed evergreen forest here is classified as subtropical wet forest in the Holdridge system (Brown et al. 1983). Prior to the arrival of Hurricane Hugo on 18 September 1989, a closed canopy existed at 20 to 24 m, with an open understory. Shortly after the hurricane, Walker (1991) found that 56% of the trees in his El Verde plots were defoliated, and some trees were uprooted (9%) or had trunks snapped (11%), but overall tree mortality was low (7%). Vegetation recovery was well underway by the 1990-1991 field season, when the forest was characterized by a relatively dense understory of saplings and shrubs with a broken, but vegetated canopy.

Palo Hueco is located 1.2 km southwest of El Verde at 515 m in the Luquillo Experimental Forest. The site is within the lower montane wet forest zone in the Holdridge system and was originally a broad-leafed evergreen forest (Ewel and Whitmore 1973). The site has been extensively disturbed by humans, and presently consists of a heterogeneous mix of native secondary forest, brushy edge and field, and an overgrown plantation of *Callophylum brasiliense.* Hurricane damage to the site was milder than that observed in El Verde and consisted primarily of branch breakage with very few uprooted trees or snapped tree trunks (unpubl. data).

Carite is located 33 km to the southwest of Palo Hueco at 720 m in the Sierra de Cayey in southeastern Puerto Rico. The site lies within the lower montane wet zone of the Holdridge system and was originally broad-leaved forest (Ewel and Whitmore 1973). It is now covered with a patchwork of abandoned farmland and partially cut forests, resulting in a scattered mix of dense thickets of ferns, shrubby edges, sapling thickets with patches of secondary palm, and broadleaf forest (canopy 15-20 m) in ravines. Carite suffered less hurricane damage than the other sites, with damage consisting of some limb breakage in the canopy and partial defoliation of trees on ridge tops (unpubl. data).

Each site was studied for at least three complete winters, although the field seasons at Palo Hueco did not correspond with those at the other sites due to a late start there. Both El Verde and Carite were studied during the entire winters (11 October-8 April) of 1988-1989, 1989-1990, and 1990-1991, with visits in the winter of 1991-1992 to locate returning birds to document annual return rate and overwinter site persistence. With the exception of the 1988-1989 winter, when Palo Hueco studies were initiated on 5 December 1988 and ended on 9 April, Palo Hueco was visited during the period of 11 October through 8 April in the winters of 1989-1990, 1990-1991, and 1991-1992. To determine overwinter site persistence of sedentary birds, home-range positions were mapped during six- to nine-day visits to each site during "early winter" (1-25 November), "midwinter" (21 January-6 February), and "late winter" (20 March-7 April).

Black-throated Blue Warblers were captured in mist nets (12 m, 30-mm mesh, 4 shelves), either with or without the use of tape-recorded playbacks of conspecific vocalizations. The tape-playback method, devised by Holmes et al. (1989) and Sliwa and Sherry (1992), was used in all years primarily from October through December, with only a few playback captures occurring in other months. Nets operated in the absence of playback also were run at all sites. At Palo Hueco and Carite, nets were run in long lines (20-38 nets per line) through the center of the study site for intervals of 2.0 to 2.5 days. Netting sessions without playback were conducted at Palo Hueco during the following periods: 3-7 April 1989, 22-24 January 1990, 26-29 March 1990, 22-26 October 1990, 28 January-

1 February 1991, 26–30 March 1991, 28 October–1 November 1991, 27–31 January 1992, and 30 March–3 April 1992. At Carite, netting sessions in the absence of playback occurred: 17–22 March 1989, 5–8 February 1990, 27 October–3 November 1990, 28 January–5 February 1991, and 26 March–3 April 1991. Prior to the hurricane, netting in the absence of playback was mostly ineffective in capturing warblers in El Verde (Wunderle et al. 1987). However, in the aftermath of Hurricane Hugo, 24 isolated 12-m nets were opened for two days at two- or three-week intervals (October–April 1990), and proved effective in capturing warblers (Wunderle 1995).

Once an individual was captured, the capture location was marked with colored plastic flagging and the locality indicated on a map. For each captured warbler, my assistants and I obtained standard measurements and weighed each individual with a Pesola balance to the nearest 0.1 g. Following the methods of Holmes et al. (1989), we scored subcutaneous fat in the furcular region as follows: 0 (no fat), 1 (trace), 2 (fat filling bottom of furculum), 3 (fat filling furculum), and 4 (fat mounded and spreading over pectoralis). Birds were sexed on the basis of plumage coloration and aged using the methods of Pyle et al. (1987), which were verified by examining the extent of skull ossification for individuals captured in October. 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; U.S. Fish and Wildlife Service, Bird Banding Manual 1977). 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.

To establish the relative arrival dates of different sex and age classes of warblers on the study sites, visits were alternated so that sites received equivalent visitation effort from 11 October to 26 December in 1989 and 1990. Black-throated Blue Warblers were absent or nearly so (observed zero to four individuals per site in 1989) from the sites during the first week of October and most did not begin to arrive until the second week of October. During the October–December visitation period, each site was visited for a minimum of two days each week. Assuming that 11 October represents the first field visit and subsequent visits are numbered consecutively from that date, the distributions of visitation dates ($\bar{x}$ = 20, 19, 10 November for El Verde, Palo Hueco, and Carite, respectively) did not differ significantly among the three sites (Kruskal-Wallis statistic = 4.19, df = 2, $P = 0.12$). The age and sex of arriving birds was confirmed by mist-net capture or by the sighting of returning marked birds. The earliest date by which an individual's sex and age was determined is designated as the confirmation date, which is used to compare relative arrival of birds of different sex and age classes at the three sites. Thus, the confirmation date was established by first observing a marked bird (i.e. returning ASY birds) or by net capture (unbanded HY/SY or ASY birds, and banded ASY birds). Confirmation usually occurred within a week of a bird's arrival.

The terms sedentary and wanderer are used to describe the spatial behavior of warblers in this study, as used by Rappole et al. (1989) and Winker et al. (1990). Sedentary birds are defined here as individuals that were observed two or more times on different days within 50 m of the first sighting, in contrast to wanderers that never were resighted within 50 m of a previous sighting. The term territory or territorial is used only in those instances where defense of an area by chasing was observed.

To determine the percentage of sedentaries relative to wanderers, transect censuses were run in the three sites from 15 November to 31 January during the winters of 1989–1990 and 1990–1991. All warblers were counted and mapped during slow morning walks of 2- to 3-h duration along trails of varying length (El Verde, 650 m; Palo Hueco, 550 m; Carite, 470 m) that passed through the middle of each site. Transects passed through the home ranges of known sedentary individuals, as determined during intensive searches before and after each transect count (see below). In addition, immediately following each transect count (late morning and afternoon), a search was made for each bird to obtain additional sightings and confirm its status.

During each visit to a site, the location of all warblers was noted in relation to conspicuous landscape features on a field map. Recording the position of birds was facilitated by series of trails throughout the sites, as well as grids of trails with plastic flagging (at 20-m intervals) in areas where the vegetation was especially thick and obvious natural features were absent. Observations recorded on field maps were transferred to a larger more detailed map (1:1500 scale) based on surveys obtained with a compass and hip chain. Home-range size was determined in November because this was the period during which sedentary birds were most conspicuous and, hence, home-range boundaries most accurately mapped. Home-range size was determined for individuals observed for a total of at least 2 h over four or more different days. Additional observations of an individual beyond these minimal times did not increase my estimates of the individual's home-range size (unpubl. data). Intensive mist netting at Carite and Palo Hueco confirmed the accuracy of home-range boundaries determined from field observations in these sites. However, mist netting was not as intensive in El Verde and was used to confirm only a few home-range boundaries. Therefore, it is possible that some home-range sizes in El Verde were actually larger than estimated by field observations. Home-range size was calculated by drawing straight lines between the outermost points where the bird was observed, thereby producing a polygon enclosing all locations where the bird was

TABLE 1. Percentage of Black-throated Blue Warblers resighted in week following capture within 50 m of location where captured in mist nets with or without playback, and number of captures (in parentheses) using the two methods at three sites on Puerto Rico. All captures made 11 October through 23 December 1989-1992.

	Males		Females	
	ASY	HY/SY	ASY	HY/SY
		El Verde		
Playback	75.0 (12)	65.2 (23)	100.0 (1)	50.0 (6)
Nonplayback	66.6 (6)	58.8 (17)	0.0 (0)	100.0 (1)
		Palo Hueco		
Playback	33.3 (6)	62.5 (8)	33.3 (3)	35.0 (20)
Nonplayback	30.0 (10)	40.9 (22)	38.9 (18)	37.2 (43)
		Carite		
Playback	0.0 (0)	45.5 (11)	16.6 (6)	37.0 (27)
Nonplayback	50.0 (6)	37.5 (8)	31.3 (16)	29.3 (41)

observed. Areas of these polygons were determined by a computer digitizer. Although birds were captured and studied over relatively large areas at each site (25 ha at El Verde, 23 ha at Palo Hueco, 38 ha at Carite), studies of home-range density were restricted to smaller portions of each study site (17.4 ha at El Verde, 9.5 ha at Palo Hueco, 9.9 ha at Carite).

Foraging observations were made throughout the winters of 1989-1990, 1990-1991, and 1991-1992 while walking slowly through the sites. Diet information was gathered after observing a foraging individual for a 10-s interval before recording the first food item as invertebrate, flower, or fruit. It was not possible to distinguish whether flowers were probed for invertebrates or for nectar. Only one feeding behavior was recorded for a given individual on a given day. An effort was made to obtain diet information from as many different individual warblers as possible; 16 individuals were observed more than once, but always on different days.

Fruiting phenology was monitored throughout the winter in belt transects along trails in Palo Hueco and Carite. At each site, two 50-m portions of trail were randomly selected along trails where the two mist-net lines were operated periodically. Fruiting shrubs (Melastomataceae, *Miconia racemosa* and *M. tetrandra*) were monitored in one meter strips on both sides of the trail. Each *Miconia* plant was individually inspected and the abundance of ripe fruit per plant classified in one of four categories: (0) 0-4 fruits; (1) 5-15 fruits; (2) 16-25 fruits; (3) 26-35 fruits; and (4) 36-45 fruits. Fruit-density estimates were then derived by adding the midpoints of these estimation categories for each fruiting *Miconia* in the belt transect. Phenology was assessed at weekly to biweekly intervals from 12 October through 7 April in 1989-1990, 1990-1991, and 1991-1992.

The analysis involved various statistical tests described in Sokal and Rohlf (1981). Homogeneity of variances was tested with Bartlett's test before an analysis of variance (ANOVA) was used. A two-way ANOVA with replication was used to compare: home-range size among sites and between sexes; home-range density among sites and among years; percentage of sedentary birds among sites and within sex; and body mass among sites and winter periods. A row-by-column test of independence, with a *G*-statistic, was used to test for independence of: sex and age ratios among capture methods; site fidelity among sites; sex and age ratios among sites; over winter site persistence among sites; annual return rate among sites and between sexes; diet type and site; sex and diet type; and diet type and season. A linear regression was used to describe the change in estimated fruit density in relation to winter date. A log-linear model was used to examine the interaction among sex and age class, and territorial status. Nonparametric tests such as the Mann-Whitney *U*-test and Kruskal-Wallis test, were used to compare distributions of confirmation dates that were not normally distributed. In addition, Kruskal-Wallis tests were used to compare fat scores among winter periods at a site and among sites during the same winter period. A probability of type I error of 0.05 or less was accepted as significant, but greater values are shown for descriptive purposes. Standard deviations are used to describe variation around the mean.

RESULTS

Capture methods compared.—Sex and age ratios of Black-throated Blue Warblers captured using tape-recorded playbacks did not differ significantly from those obtained by netting without playbacks at the same sites (Table 1; three sites individually, $G = 1.44$ to 5.84, df = 3, all $Ps > 0.05$). In addition, the likelihood of finding marked birds within 50 m of initial capture in the week following capture did not differ with capture method for males (Table 1; three sites individually, $G = 0.004$ to 0.63, df = 1, $Ps > 0.05$) or females (Table 1; three sites individually, $G = 0.03$ to 0.12, df = 1, $Ps > 0.05$). Similarly, the likelihood of finding a marked individual within 50 m of initial capture in the week following capture did not differ with capture methods for ASY birds (Table 1; three sites individually, $G = 0.20$ to 1.34, df = 1, $Ps > 0.05$) or HY/SY birds (Table 1; three sites individually, $G = 0.04$ to 0.74, df = 1, $Ps > 0.05$). Thus, the response to conspecific vocalizations was not restricted to one sex or age class (also see Sliwa and Sherry 1992), or to individuals showing site fidelty. Therefore, results from the two methods were pooled in subsequent analyses.

Arrival.—Males and females were first detected on the sites at about the same dates, based on my earliest confirmation dates (males, $\bar{x}$ = 12 November ± 24.5 days, $n = 21$; females, $\bar{x}$ = 14 November ± 26.0 days, $n = 31$). The distribution of confirmation dates did not differ significantly between the sexes (Mann-Whitney $U = 480.50$, df = 1, $P = 0.57$). Even within a site there was no evidence to suggest differential arrival dates for the sexes ($P > 0.05$).

Age differences in earliest confirmation dates were found at Carite, where the distribution of earliest confirmation dates differed significantly between age classes (Mann-Whitney $U = 250.0$, df = 1, $P = 0.002$). Here, HY/SY birds ($\bar{x}$ = 31 October ± 8.3 days, $n = 50$) were present earlier than ASY birds ($\bar{x}$ = 11 November ± 17.7 days, $n = 19$). Similarly, for Palo Hueco, the data available suggest that HY/SY birds ($\bar{x}$ = 8 November ± 25.1 days, $n = 33$) were present earlier than ASY birds ($\bar{x}$ = 20 November ± 24.2 days, $n = 20$), although the difference was not quite significant (Mann-Whitney $U = 228.0$, df = 1, $P = 0.06$). Age differences in arrival were not apparent at El Verde (HY/SY, $\bar{x}$ = 3 November ± 16.8 days, $n = 49$; ASY, $\bar{x}$ = 4 November ± 17.1 days, $n = 30$), where the distributions of earliest confirmation dates were not significantly different (Mann-Whitney $U = 726.0$, df = 1, $P = 0.93$).

Returning ASY birds were not detected simultaneously at the three sites, as evidenced by significant differences among sites in the mean of the earliest confirmation dates of returning marked birds (Kruskal-Wallis statistic = 6.12, df = 2, $P = 0.04$). On average, marked ASY birds returned earliest to El Verde ($\bar{x}$ = 5 November ± 16 days, $n = 12$), somewhat later to Palo Hueco ($\bar{x}$ = 12 November ± 21 days, $n = 12$), and later yet at Carite ($\bar{x}$ = 22 November ± 14 days, $n = 10$).

Likelihood of remaining at capture location.—Many captured birds did not remain in the vicinity of the capture location (i.e. site fidelity within 50 m of capture location in week following capture), and either disappeared or did not show consistent site fidelity. The likelihood that an individual would remain after initial capture in October and November varied significantly among the sites ($G = 18.34$, df = 2, $P < 0.001$). During this period, captured birds were most site faithful at El Verde (63% of 65 captures), moderately faithful at Palo Hueco (47% of 49 captures), and least faithful at Carite (28% of 76 captures). This pattern persists ($G = 15.34$, df = 2, $P < 0.001$) considering all captures regardless of capture month (El Verde, 62% of 69 captures; Palo Hueco, 39% of 130 captures; Carite, 34% of 116 captures).

Within a site, the likelihood that an individual would remain after an initial October-November capture did not differ significantly between sexes ($Ps > 0.05$). Although not significant, males tended to have a higher likelihood of remaining at El Verde (67% of 54 male captures; 45% of 11 female captures), Palo Hueco (69% of 13 male captures; 50% of 28 female captures), and Carite (38% of 16 male captures; 21% of 70 female captures). Within a sex, the likelihood that an individual would remain after the initial October–November capture did not differ with age ($Ps > 0.05$) as found in males (77% for ASY; 58% for HY/SY), and females (33% for ASY; 31% for HY/SY).

Some of the October–November disappearances of captured birds may be attributed to aggressive displacement by returning territorial individuals. For example, in nine cases marked HY/SY birds were displaced aggressively in October or early November by marked ASY individuals returning to a location occupied in the previous winter (six males by four males and two females; three females by one male and two females). In these instances, the HY/SY individuals were sedentary for at least 4 to 15 days, during which time they were heard giving chip notes and observed chasing other conspecifics. When the original ASY territorial occupant of the previous year returned, chases and intense chipping occurred between the two

TABLE 2. Sex and age numbers (percentages in parentheses) of Black-throated Blue Warblers obtained from birds observed on fixed home ranges (sedentary) and captured by mist nets in October and November at three sites in Puerto Rico.

	Males			Females		
	ASY	HY/SY	All	ASY	HY/SY	All
			El Verde			
Sedentaries						
1988-1989	6	6	12	1	1	2
1989-1990	7	7	14	0	2	2
1990-1991	6	11	17	0	1	1
Sedentary total	19 (39.5)	24 (50.0)	43 (89.6)	1 (2.1)	4 (8.3)	5 (10.4)
Total net sample	32 (37.6)	40 (47.1)	72 (84.7)	3 (1.2)	10 (11.8)	13 (15.3)
			Palo Hueco			
Sedentaries						
1988-1989	—	—	—	—	—	—
1989-1990	4	1	5	3	4	7
1990-1991	3	4	7	4	4	8
1991-1992	4	4	8	2	7	9
Sedentary total	11 (27.5)	9 (22.5)	20 (45.5)	9 (22.5)	15 (27.5)	24 (54.5)
Total net sample	15 (18.1)	17 (20.5)	32 (39.6)	18 (21.7)	33 (39.8)	51 (61.5)
			Carite			
Sedentaries						
1988-1989	1	1	2	2	8	10
1989-1990	1	2	3	3	3	6
1990-1991	2	5	7	4	6	10
Sedentary total	4 (10.5)	8 (21.1)	12 (31.6)	9 (23.6)	17 (44.7)	26 (68.4)
Total net sample	4 (4.7)	16 (18.6)	20 (23.3)	13 (15.1)	53 (61.6)	66 (76.7)

birds for varying intervals (15 min to > 1.5 h), often over several days (two to four days) before the HY/SY individual finally departed. In two cases at El Verde, we found the displaced HY/SY individuals (both males) as sedentary birds on home ranges at 75 and 160 m, but in the other instances the displaced individuals disappeared from the site. However, in most cases in which an individual disappeared from an October-November capture locality, aggressive interactions were not detected.

Sex/age ratios.—Wunderle (1992) previously described significant sex-ratio differences among the sites; the pooled October-November samples (Table 2) further support these site differences for both sedentary birds ($G = 26.89$, df = 2, $P < 0.001$) and net samples ($G = 72.30$, $P < 0.001$). Year-to-year variation in sex ratios of both sedentary birds and birds in net samples was nonsignificant ($Ps > 0.05$). Although not significant ($Ps > 0.05$), females tended to be slightly more prevalent than males in total mist-net captures compared with samples of sedentary birds at a site (El Verde, 10.4 vs. 15.3%; Palo Hueco, 54.5 vs. 61.4%; Carite, 68.4 vs. 76.7%).

Sex-ratio skews also were apparent at an even smaller geographic scale, as illustrated by the total captures obtained from two net lines in Palo Hueco. The ends of the two net lines were separated by 35 m; one line passed to the southeast through relatively tall forest (15- to 20-m canopy), and the other to the west through shrubby, short, young second-growth woodland (12- to 15-m canopy). Despite the proximity of the two net lines, significantly ($G = 14.22$, df = 1, $P < 0.001$) more males were captured in the tall forest (61.8%, 21/34) than in the shrubby young second growth (25.7%, 27/105).

Although age ratios within a sex varied among the sites (Table 2), the differences were not significant ($Ps > 0.05$) for either sex as found in samples from nets and sedentary individuals. For all sites combined, HY/SY birds made up a significantly ($G = 4.48$, df = 1, $P = 0.03$) higher proportion of birds in nets (67%) than on sedentary home ranges (55%). At Carite, given the sex of the bird, significantly ($G = 7.45$, df = 2, $P = 0.03$) more HY/SY birds were present in samples from nets than on sedentary home ranges. In other words, a higher proportion of juveniles than adults were moving through or around Carite than were remaining sedentary. Although this pattern was suggested at Palo Hueco, it was not significant ($P > 0.05$).

Home-range size and density.—The size of November home ranges of sedentary birds differed significantly among the sites (two-way ANOVA, $F = 15.95$, df = 2 and 2, $P < 0.001$) and between sexes ($F = 12.37$, df = 1 and 2, $P < 0.01$). Average home-range sizes were largest at El Verde and smallest at Carite, and the average male home-range was larger than the average female home-range at a site (Table 3).

TABLE 3. Home-range size (ha) of sedentary Black-throated Blue Warblers in November (1989–1992) at three sites on Puerto Rico ($\bar{x}$ ± SD, with n in parentheses).

Site	Male	Female
El Verde	0.31 ± 0.08(30)	0.26 ± 0.04(9)
Palo Hueco	0.20 ± 0.06(9)	0.19 ± 0.07(18)
Carite	0.24 ± 0.07(12)	0.15 ± 0.04(23)

As expected, sites with the smallest home ranges had the highest home-range densities (Carite, $\bar{x} = 13.2 \pm 3.1$ home ranges/10 ha; Palo Hueco, $\bar{x} = 13.1 \pm 2.5$) relative to the site with the largest home ranges (El Verde, $\bar{x} = 7.3 \pm 1.9$ home ranges/10 ha). These site differences in home-range density (Table 4) were significant (two-way ANOVA, $F = 25.33$, df = 2 and 4, $P < 0.001$). In addition, home-range density varied among years (two-way ANOVA, $F = 0.023$, df = 2 and 4, $P = 0.023$), with the lowest densities in the 1989–1990 field season in the aftermath of Hurricane Hugo. Home-range densities also declined through the course of a winter, particularly at Palo Hueco and Carite, so that fewer sedentary individuals were present at the sites in late winter than early winter.

Sedentary vs. wandering birds.—The density of sedentary birds did not provide a complete measure of the number of warblers present at the study sites because wanderers were observed throughout the winter at all sites. However, transect surveys pooled for the period of 15 November through 31 January indicated significant differences (two-way ANOVA, $F = 26.68$, df = 2 and 2, $P = 0.001$) among sites in the percentage of sedentaries versus wanderers. Wanderers most frequently were encountered at Carite and least frequently at El Verde (Table 5). Sex differences also were apparent, as the percentage of sedentary birds was significantly higher for males than females (two-way ANOVA, $F = 7.75$, df = 1 and 2, $P = 0.03$).

Wandering birds still were present at Palo Hueco and Carite by late winter, as evidenced by newly captured birds that never were resighted, despite extensive searches. For example, at Palo Hueco during late winter: 9 of 20 captures in 1989–1990 were new, one of which was resighted; 4 of 9 captures in 1990–1991 were new, none of which were resighted; and 3 of 10 captures in 1991–1992, none of which were resighted. Similarly, at Carite during late winter, 6 of 12 captures in 1988–1989 were new, one of which was resighted, and 5 of 13 captures in 1990–1991 were new, none of which were resighted. Thus, at these two sites at least, wandering birds were present for the entire winter.

Overwinter site persistence.—The sites differed significantly ($G = 7.45$, df = 2, $P = 0.02$) in site persistence or disappearance of sedentary birds from early to late winter (Table 6). For all sex and age categories combined, 67.9% of the 53 sedentary birds present on home ranges in early winter were still present in late winter at El Verde in contrast to 47.7% of 44 sedentaries at Palo Hueco and 42.2% of 45 sedentaries at Carite. If the posthurricane year (1989–1990) is excluded, the proportion of birds still present in late winter is considerably higher at El Verde

TABLE 4. Densities (territories/10 ha) of Black-throated Blue Warbler territories in early winter (late October–late November), midwinter (late January–early February), and late winter (late March–early April) at three sites in Puerto Rico.

	1988–1989	1989–1990	1990–1991	1991–1992
El Verde				
Early winter	9.2	10.9	8.6	—
Midwinter	6.3	5.2	6.9	—
Late winter	7.5	4.6	6.9	—
Mean	7.7	6.9	7.5	—
Palo Hueco				
Early winter	12.7	14.7	13.7	13.7
Midwinter	16.9	10.5	14.8	12.7
Late winter	15.8	10.5	12.7	8.4
Mean	16.4	11.2	14.1	11.6
Carite				
Early winter	14.0	11.0	19.0	—
Midwinter	12.0	14.0	16.0	—
Late winter	12.0	8.0	13.0	—
Mean	12.7	11.0	16.0	—

TABLE 5. Mean number (± SD) of sedentary and wandering Black-throated Blue Warblers observed along transects at three sites on Puerto Rico during two winters (15 November–31 January).

		Males			Females			
Year	n[a]	Sedentary	Wanderer	Percent sedentary	Sedentary	Wanderer	Percent sedentary	Total percent sedentary
El Verde								
1989–1990	7	4.8 ± 2.2	0.8 ± 0.9	89.0 ± 15.6	1.3 ± 0.5	0.5 ± 0.6	71.3 ± 20.9	80.1 ± 19.5
1990–1991	6	5.7 ± 1.5	0.5 ± 0.6	95.3 ± 8.0	1.0 ± 0.0	0.3 ± 0.6	83.3 ± 28.9	89.3 ± 20.1
Palo Hueco								
1989–1990	6	2.3 ± 1.5	1.2 ± 1.1	56.5 ± 32.6	1.8 ± 0.8	2.2 ± 1.3	49.8 ± 26.7	53.2 ± 28.6
1990–1991	11	1.5 ± 1.0	0.6 ± 0.7	62.7 ± 38.3	2.9 ± 1.8	1.4 ± 0.7	64.4 ± 15.2	63.5 ± 28.4
Carite								
1989–1990	6	1.4 ± 1.7	1.0 ± 1.2	50.0 ± 50.0	1.6 ± 0.9	2.8 ± 1.3	36.0 ± 13.8	43.0 ± 35.4
1990–1991	5	1.0 ± 0.8	0.5 ± 0.6	62.5 ± 47.8	3.0 ± 1.6	3.8 ± 1.7	43.0 ± 14.1	52.7 ± 34.3

[a] Number of transect censuses.

(77% of 35 individuals), and only slightly different at Palo Hueco (40.6% of 32 individuals) and Carite (45.7% of 35 individuals). The hurricane had the greatest effect on the El Verde vegetation (Wunderle 1995), and it is not surprising that birds disappeared from the heavily damaged areas (only 50% of 18 sedentaries remained in late winter 1990). Finally, no consistent or statistically significant differences ($P >$ 0.05) in overwinter site persistence were found between sexes or age classes within a sex.

Some of the differences among sites in overwinter persistence of sedentary birds may be attributable to home-range abandonment by sedentaries rather than mortality, particularly at Carite. For example, six marked sedentary females (four Carite, two Palo Hueco) were not found on their original home ranges in late

TABLE 6. Overwinter site persistence of Black-throated Blue Warblers on three Puerto Rican study sites based on resightings of individuals color banded in early or midwinter, and subsequently observed in the same winter. Data for El Verde and Carite include years 1988–1989, 1989–1990, 1990–1991, and 1991–1992. Palo Hueco data include only entire winters of 1989–1990, 1990–1991, and 1991–1992, and midwinter to early winter in 1988–1989.

	Males			Females			
	ASY	HY/SY	All	ASY	HY/SY	All	Total
El Verde							
No. present in early winter	24	24	48	1	4	5	53
Percent present in midwinter	79.2	95.8	87.5	100.0	100.0	100.0	88.7
Percent present in late winter	75.0	62.5	68.8	0.0	75.0	60.0	67.9
No. present in midwinter[a]	19	24	43	1	4	5	48
Percent present in late winter	94.7	66.6	79.1	0.0	75.0	60.0	77.1
Palo Hueco							
No. present in early winter	11	9	20	9	15	24	44
Percent present in midwinter	72.7	77.7	75.0	100.0	86.7	91.7	84.1
Percent present in late winter	18.2	44.4	30.0	66.6	60.0	62.5	47.7
No. present in midwinter[a]	9	10	19	10	16	26	45
Percent present in late winter	22.2	70.0	47.4	70.0	75.0	73.1	62.2
Carite							
No. present in early winter	8	8	16	12	17	29	45
Percent present in midwinter	62.5	87.5	75.0	66.6	88.2	79.3	77.8
Percent present in late winter	25.0	50.0	37.5	33.3	52.9	44.8	42.2
No. present in midwinter[a]	5	8	13	9	28	37	50
Percent present in late winter	40.0	50.0	53.8	44.4	80.0	54.1	52.0

[a] Includes individuals marked in early winter and present in midwinter plus those newly marked in midwinter.

TABLE 7. Percentage of Black-throated Blue Warblers returning in early winter (October-November 1989-1992) to home ranges occupied in previous March (number in parentheses) for three sites on Puerto Rico.

	Males			Females			
Site	ASY	HY/SY	All	ASY	HY/SY	All	Total
El Verde	40.0 (15)	62.5 (16)	51.6 (31)	0.0 (0)	0.0 (3)	0.0 (3)	47.1 (34)
Palo Verde	62.5 (8)	50.0 (8)	56.3 (16)	25.0 (8)	36.4 (11)	31.5 (19)	42.9 (35)
Carite	50.0 (2)	62.5 (8)	50.0 (10)	25.0 (4)	37.5 (16)	35.0 (20)	40.0 (30)

winter despite extensive searches, yet they were found on their original home ranges in the following winter. In addition, three marked sedentary females (two Carite, one Palo Hueco) were observed well outside (>100 m) their original home ranges in late winter at new localities where they did not consistently remain. This behavior was not found at El Verde, where birds were neither observed outside their original home-range sites, nor were missing birds resighted in the following year. These observations at Palo Hueco and Carite are consistent with the possibility that some individuals abandon their home-range sites in certain habitats in late winter and wander to other areas.

Annual site return.—The annual site-return rate is defined as the proportion of individuals that returned in early winter to the home ranges on which they were observed previously in late winter (Table 7). This rate did not differ among sites ($G = 0.36$, df = 2, $P = 0.84$), although significant differences ($G = 4.69$, df = 2, $P = 0.03$) were found between males (53% returned) and females (31% returned). Within a sex, no significant differences were found between the return rates of HY/SY birds and ASY birds ($Ps > 0.05$).

Feeding observations.—As previously noted by Holmes et al. (1989), Black-throated Blue Warblers frequently fed on flowers and fruits, in addition to invertebrates. The 144 flowers probed by warblers included flowers of *Inga vera* (19%), *Hirtella rugosa* (19%), *Prestoea montana* (17%), *Schefflera morototoni* (15%), *Casearia sylvestris* (12%), *Palicourea riparia* (5%), *Marcgravia sintenissi* (3%), and several species in the Melastomatacea (12%). The 153 fruits consumed by warblers included fruits from *Miconia racemosa* (68%), *M. tetrandra* (20%), *Urera baccifera* (5%), *Casearia sylvestris* (4%), and *Palicourea riparia* (3%). Fruits of *M. racemosa* were particularly favored by Black-throated Blue Warblers, as evidenced by the fact that the warblers accounted for 84% of 173 fruits consumed by five bird species. Fruits usually were crushed or mashed in the bill, and the skin and larger seeds dropped while the juices and pulp were consumed.

The proportion of nectar and fruit consumed relative to invertebrates was highest at Carite and lowest at El Verde (Table 8). This difference was significant for both males ($G = 95.42$, df = 2, $P < 0.001$) and females ($G = 60.71$, df = 2, $P < 0.001$). At Carite, females consumed a higher proportion of nectar and fruit relative to invertebrates than males ($G = 19.25$, df = 1, $P < 0.001$). However, this sex difference in diet was not significant at Palo Hueco ($G = 0.39$, df = 1, $P = 0.53$) and El Verde samples were inadequate to test.

Ripe melastome fruits were present in the phenology transects throughout the year at Carite, although melastome fruits here declined during the course of the winter (Fig. 1). This seasonal decline in melastome fruits at Carite was significant ($F = 16.25$, $P = 0.001$, $R^2 = 0.44$) as evident in the equation

$$Y = 254 - 0.87\,\bar{x}, \qquad (1)$$

TABLE 8. Summary of diet observations of Black-throated Blue Warblers at three sites on Puerto Rico during winters of 1989-1992. Numbers in parentheses represent first food item identified after following a foraging warbler for 10 s.

	Percent of diet		
Sex	Invertebrate	Nectar	Fruit
	El Verde		
Male	98.4 (358)	1.1 (4)	0.1 (2)
Female	100.0 (30)	0.0 (0)	0.0 (0)
	Palo Hueco		
Male	90.9 (110)	0.1 (1)	8.3 (10)
Female	88.6 (140)	5.1 (8)	6.3 (10)
	Carite		
Male	78.4 (240)	8.2 (25)	13.4 (41)
Female	64.3 (360)	19.6 (110)	16.1 (90)

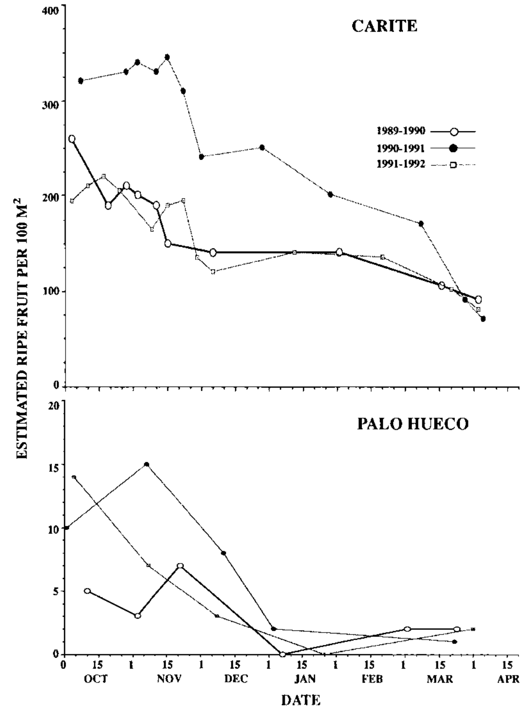

Fig. 1. Estimated abundance of ripe melastome fruits (*Miconia* sp.) in strip transects in Carite and Palo Hueco on Puerto Rico during three winters.

where Y predicts the estimated ripe fruit per 100 m^2 and x refers to the number of days after 12 October. Consistent with this seasonal decline in fruit abundance was a significant (G = 24.82, df = 1, P < 0.001) decrease in the proportion of melastome fruits in warbler diet in October (37 fruits:96 invertebrates) versus the proportion in March and April (8 fruits:128 invertebrates). Melastome fruits were never abundant at Palo Hueco, as found in the transect (Fig. 1) and virtually absent from El Verde (three plants along 300 m of trail).

Body mass and fat.—Male Black-throated Blue Warblers showed no significant body-mass variation among the three sites (two-way ANOVA, F = 0.69, df = 2 and 4, P = 0.50), nor among the three winter periods (F = 0.42, df = 2 and 4, P = 0.66). However, females showed significant (F = 8.33, df = 2 and 4, P < 0.001) variation in body mass among the sites, with the lightest birds found in Palo Hueco (Table 9). Female body mass did not vary significantly among the three winter periods (F = 0.29, df = 2 and 4, P = 0.74).

Fat-score variation was complex in both sexes (Table 9). For example, males showed significant variation in fat scores among sites only in early winter, when fat scores were highest at Palo Hueco and lowest at El Verde (Kruskal-Wallis statistic = 9.52, df = 2, P = 0.01). Male fat scores increased during the winter at El Verde (Kruskal-Wallis statistic = 7.27, df = 2, P = 0.03) and Carite (Kruskal-Wallis statistic = 137.29, df = 2, P < 0.001). Females also showed an increase in fat scores during the winter at Carite (Kruskal-Wallis statistic = 32.98, df = 2, P < 0.001), but differed from males by showing a seasonal increase at Palo Hueco (Kruskal-Wallis statistic = 8.20, df = 2, P = 0.02). Females also showed significant variation in fat scores

TABLE 9. Mean and standard deviation (with n in parentheses) of body mass (g) and fat scores of Black-throated Blue Warblers captured in early winter (1–25 November), midwinter (21 January–6 February), and late winter (20 March–7 April) at three sites on Puerto Rico, 1989–1992. Fat scores cover range from 0–4 based on the quantity of subcutaneous fat in furcular region.

	Body mass			Fat score		
Sex	Early winter	Mid-winter	Late winter	Early winter	Mid-winter	Late winter
			El Verde			
Males	9.6 ± 0.5 (53)	9.5 ± 0.4 (9)	9.7 ± 0.3 (7)	0.7 ± 0.7 (53)	1.2 ± 0.4 (9)	1.5 ± 1.3 (7)
Females	9.4 ± 0.4 (11)	9.6 ± 0.2 (9)	9.2 ± 0.4 (7)	0.8 ± 0.9 (11)	1.3 ± 0.5 (9)	1.1 ± 0.7 (7)
			Palo Hueco			
Males	9.9 ± 0.5 (13)	9.6 ± 0.5 (16)	9.8 ± 0.4 (22)	1.3 ± 0.4 (13)	1.2 ± 0.7 (16)	1.4 ± 0.6 (22)
Females	9.0 ± 0.5 (31)	8.9 ± 0.5 (28)	8.8 ± 1.6 (40)	1.1 ± 0.6 (31)	1.4 ± 0.6 (28)	1.2 ± 0.8 (40)
			Carite			
Males	9.6 ± 0.7 (17)	9.8 ± 0.5 (12)	9.4 ± 0.5 (7)	1.1 ± 0.7 (17)	1.3 ± 0.5 (12)	1.9 ± 0.9 (7)
Females	9.4 ± 0.5 (44)	9.4 ± 0.5 (22)	9.5 ± 0.4 (27)	0.7 ± 0.7 (44)	1.3 ± 0.6 (22)	1.9 ± 0.6 (27)

among sites in early (Kruskal-Wallis statistic = 44.29, df = 2, $P < 0.001$) and late winter (Kruskal-Wallis statistic = 14.68, df = 2, $P = 0.001$). Thus, both sexes showed seasonal increases in fat scores at two sites and variation in fat scores among sites during at least one winter period.

DISCUSSION

The relatively tall mature forest at El Verde with relatively few fruiting understory plants supported a Black-throated Blue Warbler population characterized by: a predominance of males; relatively early fall arrival of returning ASY birds; high site fidelity; large home-range size; low density of sedentary birds; few wandering individuals; high overwinter site persistence of sedentary birds; and an invertebrate-rich diet. In contrast, shrubby second growth with an abundance of fruiting plants at Carite supported a population characterized by: a predominance of females; relatively late arrival of returning ASY birds relative to both other sites and earlier-arriving HY birds; low site fidelity; small home-range size; high density of sedentary birds; low site persistence of sedentary birds; and a nectar- and fruit-rich diet. Despite these site differences, no consistent patterns in body condition were found among the sites, and annual return rates did not vary among the sites. Some site variation is attributable to sex differences in site persistence, wandering, and home-range size that result in population differences only because sex ratios vary among sites. However, differences in abundance and seasonality of fruit and nectar may further contribute to site differences in overwinter persistence of sedentary birds, wandering, home-range size, and density.

Individuals of both sexes displayed site persistence and defended small areas by using a combination of call notes, visual displays, and chases directed at intruding conspecifics as previously described by Holmes et al. (1989). Although chases between the sexes (both male by female and female by male) were sometimes observed, my assistants and I also saw single males and single females foraging within only a few meters of each other without any agonistic response, an association never encountered within a sex, as also noted by Holmes et al. (1989). Complete overlap of individual home-range sometimes was found between the sexes, but never between males, and only occasionally between females. Male home ranges never overlapped by more than 20%. In contrast, some female home ranges in dense vegetation in Palo Hueco and Carite overlapped each other by as much as 70%. In addition, some females showed site persistence without evidence of territorial defense, while all sedentary males displayed some territorial defense (i.e. call notes, and chases).

Wandering behavior of males and females also was observed during which call notes occasionally were heard; in these situations, no site persistence was observed. Curiously, wandering individuals of both sexes responded to playback of Black-throated Blue Warbler songs and call notes, suggesting that wanderers may maintain individual distance by use of vocalizations. Some wanderers may represent "floating" individuals displaced from suitable habitat by territorial birds and, therefore, forced to move widely in search of undefended sites. This is supported by the fact that several territories that became vacant in early winter and mid-winter were replaced by new individuals, which may have come from the ranks of the wanderers (see also Holmes et al. 1989). However, it is possible that, for some, wandering is a feeding response to widely dispersed fruit and nectar resources, which may not be economically defended within a territory. Thus, territoriality and wandering were characteristic of both sexes, although the latter was more common in females.

Competition via behavioral dominance may occur in Black-throated Blue Warblers wintering on Puerto Rico, although much of the evidence indicates that it is more strongly age related than sex related. For example, evidence for age-related behavioral dominance comes from observations of aggressive displacements in early winter of HY individuals by ASY individuals returning to their territories of the previous winter. Displacement by dominant territorial ASY birds may cause HY/SY birds to wander more than ASY birds, thus accounting for the higher proportion of HY/SY birds (relative to ASY birds) in net samples than in samples of sedentary birds, particularly in Carite. Also, the colonization of hurricane-damaged sites by HY/SY birds in the year following disappearance by ASY birds is consistent with an adult dominance explanation. In contrast, the occasional home-range overlap of sedentary male and female Black-throated Blue Warblers indicates the absence of aggression between the sexes. Furthermore, some sedentary females displayed no aggression even though their home ranges overlapped those of both males and females. In the few cases where displacements between individuals of the opposite sex were detected between known-age individuals, they were all age related, with the ASY bird displacing the HY/SY bird of the opposite sex. However, females were more frequent than males as wanderers, which would be expected of subordinate individuals displaced by territorial individuals.

Despite the greater tendency of females to wander, those females that displayed site fidelity showed overwinter site-persistence rates comparable to males at the same site. However, the sexes differed in annual return rates, with males showing more year-to-year site fidelity than females. Whether this difference is a result of differential survival or movement to other sites is unknown.

The sexes also differed in diet, at least in Carite where females consumed a higher proportion of nectar and fruit relative to invertebrates than did males in Carite. However, it is unknown whether this difference in diet reflects an actual sex difference in food preference or variation in food availability in the habitats in which the sexes reside. The differences in home-range sizes of the sexes may result from food-supply variation between the different habitats occupied by the sexes (see below).

The relatively high consumption rate of fruit at Carite was associated with an abundance of fruiting plants. Here, the October–April fruiting season of *Miconia racemosa* and the relatively high rate at which its fruits are consumed by Black-throated Blue Warblers indicate a potentially important role for migrants in seed dispersal, as suggested for other migrants (Greenberg 1981, Blake and Loiselle 1992). Fruiting in this melastome was highly asynchronous, so that an infructescence contained only a few ripe fruits on any particular day, but a single plant produced some ripe fruit daily for a five- to six-month period. Several marked birds were observed regularly visiting specific *Miconia* plants within their respective home ranges on different days during the winter. Although fruit production in Carite declined over the winter and the proportion of fruit consumed by warblers showed a corresponding decline, some frugivory still occurred in late winter.

The earlier appearance of HY birds in Carite relative to ASY birds may be attributed partially to high fruit and nectar abundance. HY individuals may be displaced from other areas by older territorial birds and, therefore, concentrate in fruit- and nectar-rich sites before settling or wandering elsewhere. However, it is not obvious why ASY birds would be so late in returning to their former home ranges in Carite, as compared to HY birds and returning ASY birds at the other two sites. Although birds arriving from the north might first be expected to appear in El Verde in the north, then Palo Hueco, and finally Carite in the south, the 35-km maximum distance between sites seems too small to detect arrival differences. Returning ASY birds in Carite initially may wander (consuming fruits and/or nectar?) before settling on their former home ranges. Support for the possibility of early-season wandering comes from the sightings or recaptures of eight marked birds that initially were captured in early winter and only detected again in the following early winter. The earlier arrival of returning ASY birds at El Verde indicates that there may be an advantage to early occupancy of previous home-range sites, particularly at a site where food supply may be seasonally constant and overwinter site persistence relatively high.

The higher abundance of fruit and flowers may contribute to the smaller home-range sizes of sedentary birds and the higher density of sedentary and wandering birds at Carite compared with El Verde. Some fruiting and flowering plants were not defended by territorial individuals because they were situated outside territories in inappropriate habitat (i.e. fern thickets) and, in other instances, defense appeared to be ineffective, particularly when several birds were simultaneously visiting widely dispersed fruiting/flowering plants. In addition, fruiting and flowering plants often were common in dense shrubby vegetation, where intruders may be undetected by territorial birds.

Black-throated Blue Warblers at El Verde fed primarily on insects and spiders, resources that might be expected to be seasonally constant in a nonseasonal wet subtropical forest. The predictability of this food source may contribute to the relatively high overwinter site persistence typical of Black-throated Blue Warblers at El Verde. Here the overwinter persistence rate of 68% (77% in nonhurricane years) is consistent with previously published values for Black-throated Blue Warblers in Jamaica (66%; Holmes et al. 1989). However, these values were mostly higher than those for overwinter site persistence in Palo Hueco (48%) and Carite (42%), where seasonal declines in fruit or nectar abundance may have contributed to site abandonment by sedentary birds. The fact that some of the sedentary birds missing in late winter were found in the following year in early winter indicates that site abandonment occurs and that overwinter site persistence is not always an accurate measure of winter survival in some habitats.

Densities of sedentary birds in El Verde, which averaged 6.9 to 7.7 birds per 10 ha, were especially low. Such low warbler densities and correspondingly large home-range sizes may result from low food-resource levels. Not only are understory fruit and flower densities low in El Verde, but it is likely that insect densities also are low. The high densities of lizards and frogs characteristic of El Verde (e.g. Drewry 1970, Reagan 1986) may depress insect densities, as experimentally demonstrated for *Anolis* lizards by Dial (1992), thereby limiting populations of insectivorous birds. The higher densities and smaller average home-range sizes at Palo Hueco and Carite are not surprising given both the greater abundance of fruit and flowers, and the likelihood of higher insect densities characteristic of early second growth (e.g. Janzen 1973). However, despite the potentially higher food supplies in second-growth vegetation at Palo Hueco and Carite, the mean density values (11.2–16.0 birds per 10 ha) were only slightly above those measured in Jamaica by Holmes et al. (1989) at one site (9.6–12.5 birds per 10 ha) and well below those at another (28.7–37.3 birds per 10 ha). This latter site is forested with low fruit and flower abundance (R. T. Holmes pers. comm.), suggesting that Jamaican forests may differ considerably from Puerto Rican forests in invertebrate abundance.

My findings are consistent with previous studies of sexual habitat segregation in which tall forests have a predominance of males and shrubby second growth a predominance of females (Lynch et al. 1985, Lopez and Greenberg 1990). Tall forests may have less seasonal variation in food supplies than shrubby sites, as demonstrated by Parrish and Sherry (1994). Seasonal variation in fruit and nectar in the diets of Black-throated Blue Warblers in Carite is consistent with seasonal variation in shrubby sites, and as discussed previously, it is likely that food supply (mostly invertebrates) is more constant in the tall forest in El Verde. Here, male densities of Black-throated Blue Warblers were low and territories large relative to sites with female predominance, suggesting low food densities where males predominate in contrast to American Redstarts (*Setophaga ruticilla*) in which sites with a predominance of males were characterized by high population density, small territory size, and high insect densities relative to sites with a predominance of females (Parrish and Sherry 1994). Thus, male territory size and densities may vary relative to those of females, depending on food density, but males settle primarily in habitats with the least seasonal variation in food supply. The reason males settle in such habitats may be because this allows earlier premigratory fattening and northward departure in spring (Parrish and Sherry 1994). Early male arrival on the breeding grounds may be advantageous in male-male competition for females and facilitate selection of optimal breeding territories (Ketterson and Nolan 1983, Francis and Cooke 1986).

No consistent patterns of variation in measures of body condition were found among the Puerto Rican sites. Male body mass did not vary significantly among the sites in contrast to female body mass, which varied significantly among the sites. Both sexes showed significant differences among sites in fat scores in early winter and females also showed differences among sites in late winter. This variation in body condition did not provide an indication of survival differences among the sites. However, fat scores, but not mass, varied with season, showing an overall increase during the winter at two sites for males and females (only at Carite did both sexes show increases). Thus, the birds were able to put on fat during the course of the winter, which suggests they were not food stressed during this period. A similar indication that Black-throated Blue Warblers were not food stressed during the winter was found in Jamaica, where body mass increased in males with a suggestive trend in females (Holmes et al. 1989).

Hurricane Hugo provided an opportunity to document the effect of a major habitat disturbance on wintering warbler populations. The storm's mid-September passage over the island occurred before the mid-October arrival of Black-throated Blue Warblers. At El Verde, the site of the most vegetation damage, the return rate of previously banded warblers in the hurricane's aftermath was comparable to other years. Returning warblers inhabited previously occupied locations despite considerable damage, including defoliation, downed trees, and broken branches. However, at the damaged sites, banded birds remained for only a couple of months before disappearing, presumably abandoning their original home-range site for less damaged places elsewhere. Abandonment by returning birds and the absence of settlement by newly arriving birds at damaged places, may have contributed to the low territory densities detected on all sites in the winter after the hurricane. However, a year after the hurricane (1990-1991), territory densities returned to normal. At El Verde, the abandoned places were recolonized in the following year (1990-1991) by HY/SY individuals. This pattern of year-to-year variation in age ratios also was noted in Jamaica, especially in the aftermath of a hurricane (Holmes et al. 1989).

One expected posthurricane effect, which was not found in El Verde, was an increase in the proportion of females as a consequence of the conversion of mature forest to second-growth vegetation. This expectation arose from previous findings (Wunderle 1992) that female capture sites differed from those of males by having smaller trees, more foliage at 0-2 and 4-6 m above the ground, and less foliage at 12-15 m above the ground. Thus, it was expected that the structural changes in the vegetation resulting from the hurricane should favor colonization by females, as found in Hooded Warblers (*Wilsonia citrina*) in the aftermath of a hurricane in Yucatan (Morton et al. 1993). However, this was not the case, as the El Verde sex ratio was still skewed towards males in the four years after Hugo (unpubl. data). These observations indicate that female Black-throated Blue Warblers are not selecting winter habitats on the basis of the vegetation variables correlated with their capture sites described in Wunderle (1992).

Sexual habitat segregation may indicate competition between the sexes, or at least the presence of competition sometime in the species' evolutionary history. Behavioral dominance could play a decisive role in excluding one sex from the highest-quality habitat(s), resulting in lower overwinter survival of the subordinate sex, as demonstrated by Marra et al. (1993) for the American Redstart. However, given time and the appropriate circumstances, the subordinate sex may evolve adaptations to the habitat(s) to which it was displaced, thereby alleviating intersexual competition. This may have occurred in Hooded Warblers, a species in which the sexes select different habitats on the basis of the physical structure of the vegetation (Morton 1990, Morton et al. 1993), rather than by exclusion of one sex by the other from a preferred habitat (Morton et al. 1987, Marra et al. 1993). In Black-throated Blue Warblers, behavioral dominance appears to play a limited role in segregation of the sexes, particularly given the presence of overlapping home ranges of sedentary individuals of the opposite sex. Females were less likely to show territorial defense and site fidelity, and more likely to wander than males, possibly as a result of their heavy reliance on fruit and nectar. Whether the behavioral and diet differences of the females result in lower overwinter survival is unknown. The ability to utilize nectar and fruit in addition to invertebrate prey facilitates habitat segregation, and may have arisen as a result of intersexual competition. Moreover, this broad diet may buffer Black-throated Blue Warblers from severe population declines resulting from extensive deforestation on its Caribbean wintering grounds, of which approximately 21% now remains forested (Wunderle and Waide 1994).

In summary, some of the findings of my study are consistent with those of Holmes et al. (1989) from Jamaica in supporting the hypotheses of Lack (1968), Fretwell (1972, 1986), and others that events on the wintering grounds are critical to the annual cycle of Nearctic migrants. For example, both studies found territorial defense, which indicates that resources (food) are potentially limiting, and replacement of marked territorial birds with unmarked birds, which indicates that certain individuals (floaters) are excluded by territorial defense. At one Puerto Rican site, low site-persistence rates and a high proportion of wanders may indicate low survival rates (e.g. Rappole et al. 1989, Winker et al. 1990). Inconsistent with the idea of winter as a potentially stressful time are the findings in both Jamaica and Puerto Rico of high overwinter site persistence or survival of Black-throated Blue Warblers for at least one site and the absence of deterioration in body condition (i.e. mass and fat) during the winter. However, my study differed from that of Holmes et al. (1989) in the range of habitats studied, which accounts for demographic and ecological differences. Presently, it is not known whether these population differences result in differential survival among wintering habitats. Low overwinter site persistence and wandering in a fruit/flower-rich habitat may be due to displacement by territorial birds, resulting in lower winter survival of wanderers. However, one cannot yet eliminate the possibility that these traits represent adaptations to high fruit and flower abundance without resulting in lower winter survival rates.

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