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Sexual habitat segregation in wintering Black-throated Blue Warblers in Puerto Rico

Abstract. Sexual habitat segregation by Black-throated Blue Warblers (*Dendroica caerulescens*) wintering in Puerto Rico appears to be related to the canopy height and successional stage of montane forests. A stepwise discriminant function analysis was based upon altitude and 13 vegetation variables measured at warbler capture sites in three study areas. Female capture sites differed from those of males by having smaller trees, more foliage at 0–2 m and 4–6 m above the ground, and less foliage at 12–15 m above the ground. Using a classificatory discriminant function analysis with four vegetation variables it was possible to classify correctly 60 of 64 warbler capture sites in three study areas. Thus female Black-throated Blue Warblers were most common in the younger, shrubby-sapling stages at high altitude and males were most common in the older, taller forests of lower altitude. Forests of intermediate canopy height and age had an equal mix of males and females. The possibility that the observed habitat segregation is maintained by behavioral dominance and/or intrinsic "preferences" is discussed.

Sinopsis. La segregación sexual de habitat de *Dendroica caerulescens* invernantes en Puerto Rico parece estar relacionada con la altura del dosel y el estadio sucesional de los bosques montanos. Se realizó un análisis de función discriminante STEPWISE basado en altitud y 13 variables de vegetación medidas en sitios de captura de *D. caerulescens* en tres áreas de estudio. Los sitios de captura de hembras difirieron de aquellos de los machos por tener árboles mas pequeños, mas follaje a 0–2 m y 4–6 m por encima del suelo y menos follaje a 12–15 m. Usando un análisis clasificatorio de función discriminante con cuatro variables de vegetación fue posible clasificar correctamente 60 de 64 sitios de captura de *D. caerulescens* en tres áreas de estudio. Así, las hembras fueron mas comunes en los estadios arbustivos mas jóvenes en elevaciones altas y los machos en los bosques mas maduros y altos de elevaciones bajas. Bosques con edades y alturas de dosel intermedias tuvieron

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una mezcla proporcional de ambos sexos. La posibilidad de que la segregación de hábitat observada sea mantenida por dominancia conductual y/o "preferencias" intrínsecas es discutida.

Competition theory has provided potential mechanisms for explaining variation in migration patterns and nonbreeding distributions of birds (e.g., Salomonsen 1955, Cox 1968, Lack 1968, Fretwell 1972, 1980, Gauthreaux 1978, 1982). Despite the attractiveness of these theories, little current evidence indicates that competition is important in determining winter distributions within or among migrant species (Greenberg 1986). Evidence for past or present intraspecific competition on the wintering grounds includes geographic separation, habitat segregation, territoriality, dominance hierarchies, and foraging differences. Some of these patterns, such as geographic separation, might indicate past competition between sex or age classes which no longer occurs on the wintering grounds. Other patterns, such as habitat segregation and foraging differences, might also indicate past competition, which now might be completely or partially extant. Evidence for current competition includes intraspecific territoriality or dominance hierarchies on wintering grounds.

The level of documentation of the evidence for intraspecific competition on the wintering grounds is highly variable. For example, geographic separation of sex or age classes has been demonstrated for waterfowl (e.g., Bellrose et al. 1961, Nichols and Haramis 1980), raptors (e.g., Belopol'skij 1972, Mead 1973, Mueller et al. 1977), shorebirds (e.g., Myers 1981), woodpeckers (Howell 1953), finches (King et al. 1965, Ketterson and Nolan 1976, Balph 1977), tanagers (Pearson 1980), and blackbirds (Dolbeer 1982, James et al. 1984). However, factors other than intraspecific competition could explain these distributions (e.g., Myers 1981, Gauthreaux 1982, Ketterson and Nolan 1983, Greenberg 1986). Foraging differences between sexes within the same habitat have been well documented for many species (e.g., Pitelka 1950, Kilham 1965, Selander 1966, Storer 1966, Morse 1968, Williamson 1971, Peters and Grubb 1983). Intraspecific territoriality is common and widespread among various wintering migrants ranging from raptors, shorebirds, woodpeckers, hummingbirds, to a variety of passerines (e.g., Rappole and Warner 1980, Greenberg 1985, Myers et al. 1979). Also, dominance relationships have been documented among wintering migrants, particularly within social species (see Gauthereaux 1978, for review), but the ecological importance of these relationships as an indicator of intraspecific competition (i.e., whether they produce reduced fitness in subordinates) remains controversial (e.g., Ketterson and Nolan 1983).

Only a few examples of intersexual habitat segregation have been found for migrant passerines wintering in the tropics. In Malaysia, overwintering Oriental Reed Warblers (*Acrocephalus orientalis*) display habitat segregation by sex (Nisbet and Medway 1972). Females were most common in Phragmites swamps, which were similar in structure to the reed beds used on the breeding grounds, but males were most abundant in scrub habitats. In the Yucatan Peninsula of Mexico, wintering male and female Hooded Warblers (*Wilsonia citrina*) segregated on the basis of habitat structure (Lynch et al. 1985). Female Hooded Warblers were found mostly in open low vegetation whereas males occupied the closed-canopy forests of moderate to tall stature. In Haiti, field observations and netting results indicated that female Black-throated Blue Warblers (*Dendroica caerulescens*) were most abundant in montane regions while males were most abundant in lowland forests (Woods 1975).

My preliminary observations of Black-throated Blue Warblers throughout Puerto Rico indicated that males occupy tall-stature montane forests and woodlands and that females occur in brushy (sapling stage) low-stature secondary woodlands in montane regions. Montane areas with intermediate stature forests contained both males and females. To test the hypothesis that the sexes of wintering Black-throated Blue Warblers occupy different habitats in Puerto Rico, I quantified altitude and vegetation characteristics in the sites where the birds were captured or observed.

Study areas

Three study areas were selected where different sex ratios of wintering Black-throated Blue Warblers had been observed. These three areas (El Verde, Palo Hueco, and Carite) are still in use as part of an ongoing study of Black-throated Blue Warbler demography and population ecology. Two other localities (Cedro and Big Tree Trail) were used for transect samples to verify observations made on the three intensive study areas. These two localities were selected because of their vegetation characteristics and altitude, without prior knowledge of warbler sex ratios.

EL VERDE. The El Verde Field Station is located in the Luquillo Experimental Forest in eastern Puerto Rico. Warblers were captured over an area of about 25 ha around the field station. The forest at El Verde is classified as subtropical wet forest in the Holdridge system and is a broad-leaved evergreen forest (Odum and Pigeon 1970, Ewel and Whitmore 1973, Brown et al. 1983). The study area is approximately 350 m in elevation (range 312–472 m) with moderately sloping topog-

raphy. The dominant tree, tabonuco (*Dacryodes excelsa*) comprises as much as 35% of the forest canopy (Wadsworth 1951), but species in the genera *Sloanea, Inga, Sapium, Alchorneopsis, Manilkara, Guarea, Cecropia,* and *Didymopanix* are also common. Three tree strata include: a discontinuous upper canopy layer (at 24 m), a second continuous canopy (at 20 m), and a sparsely vegetated, open understory (foliage height profiles in Wunderle et al. 1987).

PALO HUECO. The study area (about 23 ha) at approximately 515 m elevation is 1.2 km southwest of El Verde in the Luquillo Experimetal Forest. The slightly sloping area is within the lower montane wet forest zone in the Holdridge system and was originally a broad-leaved evergreen forest (Ewel and Whitmore 1973). The site has been extensively disturbed by man, and presently consists of a heterogenous mix of native secondary forest, brushy edge and field, and an overgrown plantation of *Callophylum brasiliense.* The western boundary along highway 186 is a brushy mix of dense fern thickets, bamboo, and diverse second-growth trees and saplings, particularly *Cecropia* and *Didymopanix,* as well as numerous shrubs in the Melastomatacea, Piperacea, and Rubiacea. Remnant second-growth forest is scattered along the east and southern boundaries and contains a mix of trees in the genera *Cyrilla, Buchenavia, Micropholis, Ocotea, Magnolia, Tabebuia, Dacryodes, Inga,* and *Ficus.* The remnant secondary forest has a relatively closed canopy at 15–20 m with several indistinct layers below, including a thick understory of shrubs, palms, and ferns.

CARITE. The Carite study area (38 ha) is located approximately 33 km to the southwest of the Palo Hueco area in the Sierra de Cayey in southeastern Puerto Rico. It has a mean elevation of 720 m (range 640–768 m) with variable topography. The area lies within the lower montane wet forest zone of the Holdridge system and was originally broad-leaved forest (Ewel and Whitmore 1973). It is covered with a patchwork of abandoned farmland and partially cut forests which has resulted in a scattered mix of dense thickets of ferns and razor grass (*Scleria canescens*), shrubby edges, sapling thickets, and patches of secondary palm and broadleaf forest. The ridges and upper slopes are shrubby with widely scattered trees of the genera *Cecropia, Didymopanix, Micropholis, Ocotea, Ormosia, Alchornea, Buchenavia, Tabebuia,* and the palm *Prestoea montana.* These trees form a closed canopy (15–20 m) in the stream valleys. Shrubs in the Melastomatacea, Piperacea, and Rubiacea are abundant throughout the area. The brushy edge and sapling areas of Carite resemble those of Palo Hueco.

BIG TREE TRAIL TRANSECT. The 500-m transect was situated on the Big Tree Trail, located at approximately 518 m in the Luquillo Experimental Forest. This area was selected because it represented tall-stature, mature forest at a relatively high altitude. The tabonuco (*Dacryodes excelsa*) forest along the trail is similar in structure and composition to the El Verde forest.

CEDRO TRANSECT. The 600-m transect was located at approximately 508 m elevation along a dirt road running east, 3 km from the town of Cedro in the Sierra de Cayey. The area was selected because it represented short-stature, brushy, second-growth woodland at an altitude lower than Carite. The transect ran through the bottom of a valley, surrounded by overgrown farmland. Trees here were generally of lower stature than those of Palo Hueco, but the species composition appeared similar.

Methods

Black-throated Blue Warblers were located and captured with tape recordings played on a Sony TCM 5000 tape recorder as described in Holmes et al. 1989. The tapes consisted of a mixture of primary song (LP record by Borror and Gunn, no date) and aggressive "chip" notes recorded in Carite in October 1988. Once a responsive individual was found, the tape recorder was turned off and a 12-m mist net was set-up within the birds' area of activity. A speaker was placed on the ground, under the middle of the net, and operated remotely by a hidden observer located 6 m from the net. Songs and call notes were played at a natural rate with variations in volume until the focal bird was captured or until 1–2 hr had passed without success. In addition to the songs, a mount of a male Black-throated Blue Warbler, placed on a 1.5-m upright stick alongside the net was used for the last 80% of the captures (total captures = 64). Both sexes responded readily to the recordings alone or to the mount and recordings together.

Birds were captured with playback during all daylight hours almost every morning from 21 October 1988 through 31 March 1989. However, 64% of the captures occurred during October and November when the warblers appeared to be most responsive to song. We attempted to capture all birds encountered, and occasionally (27% of 64 birds) we returned to a site, following an earlier failure, to capture a specific individual. Eleven birds (six males; five females) were impossible to capture and thus were not marked. Once an individual was captured, the capture site was marked with colored plastic flagging and the locality indicated on a map. For each captured warbler, we obtained standard measurements and banded it with three plastic color bands and an aluminum U.S. Fish and Wildlife Service band.

In addition to captures of individual warblers by playback in the three study areas we ran transects with playback to locate Black-throated Blue Warblers along the

Big Tree Trail (4 February 1989) and in Cedro (7 February 1989). The transects represent an independent test of the sexual habitat segregation observations made on the three study areas. Trails or dirt roads were used to pass through each habitat in a relatively straight line. The observer walked slowly through the habitat with a tape playback of warbler song and calls. When an individual responded to the recording, the location where the bird was first observed was indicated with flagging and then marked on a map. Each transect was terminated after a predetermined, arbitrary number of individuals ($n = 8$) were located.

From 13 to 28 April 1989, we returned to the sites where individuals had been observed along the two transects and to the capture sites of each bird on the other three study areas to measure altitude and vegetation features. We established the center of each vegetation plot 15 m from the site of initial observation along the transect or 15 m from the capture site in the direction from which the bird approached the playback, as noted earlier when first encountered. An altimeter was used to take altitude readings in the center of each plot. From the center, four 8-m radius transects were established in the N, S, E, W compass directions. Vegetation features measured within each 0.02-ha circular plot were:

1. Shrub density at breast height was counted along two radial transects by an observer counting all vertical woody stems (< 3 cm diameter) touching his outstretched arms. The number of deciduous shrubs (i.e., broadleaf), palms, and ferns was recorded separately.

2. We measured the diameter at breast height (dbh) of all saplings and standing trees with diameters greater than 3 cm. Trees were classified as either standing dead, palm, broadleaf, or tree fern.

3. Canopy height of the 10 highest canopy trees extending over each plot was measured with a range finder.

4. We measured foliage height profiles by using a method modified after that of Schemske and Brokaw (1981). Profiles were determined at 20 points (every 1.6 m) along north-south and east-west transects in each plot. A 3-m vertical pole, marked at 0.5-m intervals, was placed at each point to record the intervals in which vegetation touched the pole. For height intervals above 3 m we sighted along the pole into the canopy and counted the presence of vegetation in estimated height intervals in meters (3–4, 4–6, 6–8, 8–10, 10–12, 12–15, 15–20, and 20–25). We recorded only the presence or absence of a leaf contact in each height category and not the total number of contacts per category. Therefore for each height category a maximum of 20 touches could be obtained, because each height class was sampled at 20 points along the transects within each plot.

Information from these measurements was summarized for discriminant function analysis into: shrub density of broadleaf stems (< 3 cm dbh); total broadleaf stems > 3 cm dbh; mean dbh of the five largest trees; mean canopy height; and number of points with the presence of at least one broadleaf contact in the height classes of 0–2 m, 2–4 m, 4–6 m, 6–8 m, 8–10 m, 10–12 m, 12–15 m, 15–20 m, and 20–25 m. Emphasis was placed on the structure of broadleaf plants because this is the most commonly used substrate for foraging (Wunderle, unpubl.).

The first level of analysis consisted of a stepwise discriminant function analysis (Tabachnick and Fidell 1983) using SAS software version 6.03 (SAS Institute Inc. 1988). Each vegetation plot at the capture site of 64 birds in the three study areas was classified apriori as either "male" or "female" based on the gender of the bird at the capture site. We then used the stepwise procedure to indicate which vegetation variables contributed most to the differentiation of the two habitat classes. Once the habitat variables with the greatest discriminatory power were identified, they were then used in a classificatory discriminant analysis (Tabachnick and Fidell 1983) to classify habitats as "male" or "female." This procedure permitted the identification of "incorrectly" classified sites (capture sites or transect sites), thus providing an indication of the ability of the discriminant function to correctly describe male and female habitat.

Results

Captures of Black-throated Blue Warblers indicated significantly different ($\chi^2 = 21.22$, d.f. = 2, $P < 0.001$) sex ratios in the three study areas: 83% females in Carite ($n = 24$); 50% females in Palo Hueco ($n = 20$); and 15% females in El Verde ($n = 20$). The eight warblers located using playback along the Cedro transect were females; on the Big Tree Trail transect eight males were encountered.

Of the 64 warblers captured in the three study sites, 49 (77%) were observed again during the winter months. Of those observed again, 37 (76%) were found within 50 m of their original capture site. Maps of locations of these individuals indicated that these birds were mostly inhabiting exclusive areas (with the exception of some overlap between male and female habitat use discussed below). In addition, their consistent aggressive behavior (i.e., chases and "chip" notes) within a relatively limited area impliess that these birds were territorial, as documented for Black-throated Blue Warblers in Jamaica (Holmes et al. 1989). However, 12 (seven males, five females) of the re-sighted birds were found in different parts of the study area at distances greater than 100 m from the original capture site. Seven of these birds were observed more than once in wide-

TABLE 1 Summary of the stepwise discriminant function analysis on 64 capture sites of males (n = 31) and females (n = 33) with 14 original variables

Variable	Step	Partial r^2	F statistic	P
Mean dbh of five largest trees	1	0.574	83.679	0.0001
Foliage class 0–2 m	2	0.251	20.464	0.0001
Foliage class 12–15 m	3	0.199	14.933	0.0003
Foliage class 4–6 m	4	0.081	5.167	0.0270
Altitude	5	0.012	0.705	0.4047
Shrub density	5	0.011	0.636	0.4285
Canopy height	5	0.002	0.101	0.7514
Foliage class 2–4 m	5	0.001	0.048	0.8275
Foliage class 6–8 m	5	0.001	0.020	0.8891
Foliage class 8–10 m	5	0.003	0.186	0.6681
Foliage class 10–12 m	5	0.002	0.130	0.7200
Foliage class 15–20 m	5	0.022	1.302	0.2585
Foliage class 20–25 m	5	0.001	0.048	0.8269
Total stems	5	0.006	0.342	0.5607

ly scattered localities throughout the study area. Such birds could not be predictably relocated, and were generally found outside known territories. These birds were usually silent, were never observed chasing conspecifics and were probably nonterritorial floaters. This analysis is based upon the capture sites of all 64 warblers and thus includes the habitats used by both territorial and floater individuals.

The results of the stepwise discriminant function analysis were consistent with my previous field observations of habitat segregation by sex. The analysis found that four of the original 14 variables (1 altitude and 13 vegetation) had significant discriminatory power (Table 1). Female capture sites differed from those of males by having smaller trees (mean dbh of five largest trees, $\bar{X}$ = 19.3 cm vs. $\bar{X}$ = 29.4 cm), more foliage in the 0–2-m and 4–6-m height classes ($\bar{X}$ = 12.7 vs. $\bar{X}$ = 7.7, and $\bar{X}$ = 13.3 vs. $\bar{X}$ = 5.7), and less foliage in the 12–15-m height class ($\bar{X}$ = 3.4 vs. $\bar{X}$ = 14.1). Differences in foliage height profiles of male and female capture sites were apparent in Carite and Palo Hueco, but not in El Verde (Fig. 1).

Using a classificatory discriminant function analysis with these four variables alone it was possible to classify correctly 60 of the 64 capture sites in the three study areas. Two of the misclassified sites were in Palo Hueco where one male capture site was classified as a female site and one female site classified as a male site. In El Verde, two female capture sites were incorrecly classified as male sites. When all 14 of the original variables were used to construct a discriminant function, all 64 capture sites were correctly classified.

To test the 4-variable discriminant function I used it to classify independently male and female sites on the Cedro and Big Tree transects. Fifteen of the 16 activity sites along the two transects were correctly classified. One male on the Big Tree transect was incorrectly classified. All of the transect birds were classified correctly by the 14-variable discriminant function.

Black-throated Blue Warblers might spatially segregate based on altitude alone, whereby females predominate at higher altitudes (i.e., Carite) and males at lower altitude (i.e., El Verde). Observed habitat differences between the sexes might then reflect the relationship between vegetation and altitude. Indeed, significant (P < 0.05) positive correlations were found between altitude and individual variables such as shrub density (r = 0.51), total stems (r = 0.81), and the 2–4-m (r = 0.65), 4–6-m (r = 0.75), 6–8-m (r = 0.79), 8–10-m (r = 0.47) foliage classes, whereas significant negative correlations existed between altitude and individual variables such as canopy height (r = -0.81), mean dbh of the five largest trees (r = -0.67), and the 12–15-m (r = -0.67), 15–20-m (r = -0.74), 20–25-m (r = -0.61) foliage classes. Nevertheless, several results indicate that the sexes are not segregated on the basis of altitude alone. In the Palo Hueco area where male and female capture sites showed no significant differences in altitude (t = 0.406, P = 0.689), 90% of the sites were properly classified by the discriminant function analysis using only four vegetation variables. Furthermore, accurate discrimination of male and female sites using only vegetation variables was possible from sites along the two transects in which mean altitude did not differ significantly (t = 1.838, P = 0.087). Thus, it appears that male and female Black-throated Blue Warblers in our study sites segregated

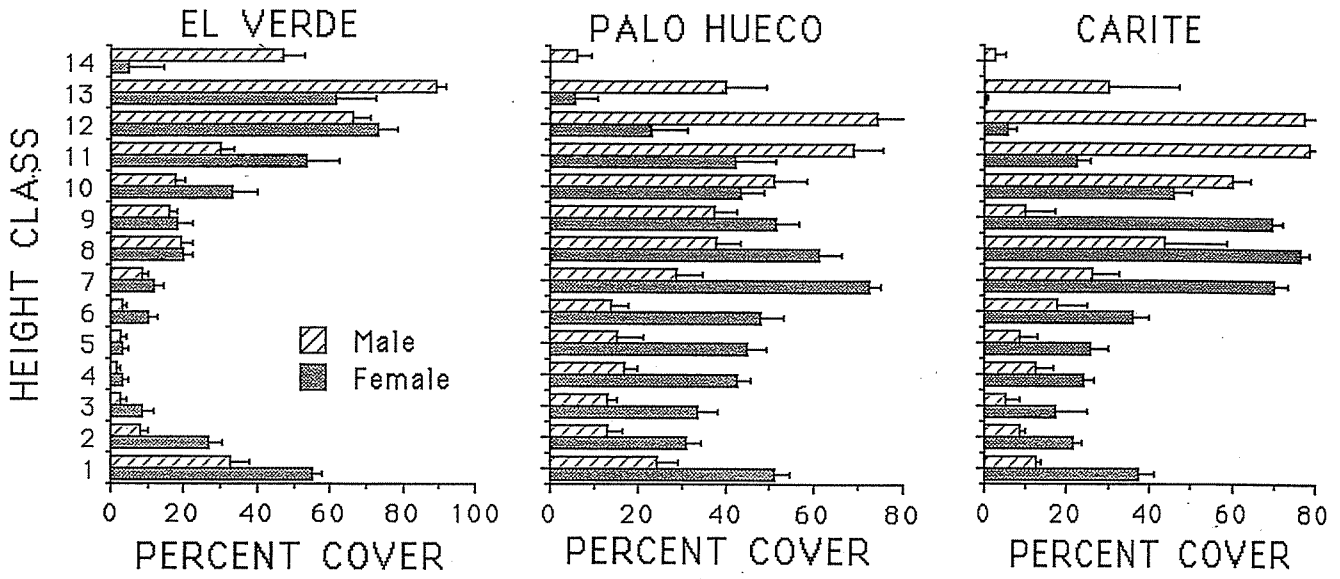

FIGURE 1. Foliage height profiles from capture sites of male and female Black-throated Blue Warblers in El Verde (n = 3 females, n = 17 males), Palo Hueco (n = 10 females, n = 10 males), and Carite (n = 20 females, n = 4 males), Puerto Rico. Percent cover represents percentage of sample points with live vegetation present in a given height interval. Height intervals in meters: *1* = 0–0.5, *2* = 0.5–1.0, *3* = 1.0–1.5, *4* = 1.5–2.0, *5* = 2.0–2.5, *6* = 2.5–3.0, *7* = 3.0–4.0, *8* = 4.0–6.0, *9* = 6.0–8.0, *10* = 8.0–10.0, *11* = 10.0–12.0, *12* = 12.0–15.0, *13* = 15.0–20.0, *14* = 20.0–25.0.

mostly on the basis of vegetation structure. However, because many of these characteristics (e.g., tree size and foliage height profiles) also vary with altitude, females will probably predominate at high altitude (because of low stature vegetation) whereas males predominate at low altitude (because of high stature vegetation) in undisturbed locations.

Discussion

There are two alternative hypotheses regarding the proximate mechanisms responsible for the maintenance of intersexual habitat segregation on the wintering grounds. The behavioral dominance hypothesis suggests that the behaviorally dominant sex excludes the subordinate sex from the preferred habitat (Lynch et al. 1985). The other, an intrinsic hypothesis, proposes that females and males each have an intrinsic "preference" for the different habitats in which they are found (Morton et al. 1987). These two hypotheses are not necessarily mutually exclusive. This study was not designed to test either of these hypotheses, but some observations are consistent with an intrinsic hypothesis and others are consistent with a behavioral dominance hypothesis, possibly indicating that a complex mechanism is responsible for Black-throated Blue Warbler habitat segregation.

Observations and preliminary results from El Verde appear to be consistent with the intrinsic preference hypothesis. For example, in El Verde males spent most of their time in the uppermost canopy and only infrequently came down to within a meter of the ground in gaps (i.e., openings in the canopy). Although males were sometimes captured in treefall gaps and a powerline opening, they were never captured in the forest understory during a one-year netting study in El Verde (Wunderle et al. 1987). Only with song playback were we able to attract males down from the canopy into the understory at El Verde. The absence of Black-throated Blue Warblers in the El Verde forest understory can probably be attributed to the relative absence of broadleaf foliage in the first 10 m from the ground (e.g., Fig. 1). This absence of understory foliage most likely explains the absence of females, which are known to forage primarily in the lower foliage strata on both the breeding grounds (mean foraging height = 3.3 m, Holmes 1986) and on the wintering grounds in Puerto Rico (Wunderle, unpubl. data). Thus, if females "prefer" the lower foliage strata, they would be absent from habitats lacking such strata.

Further evidence from El Verde, consistent with the intrinsic hypothesis, is the similarity of sex ratios among transients or floaters (defined as individuals never recaptured or resighted) and territorial individuals. After the passage of Hurricane Hugo on September 1989, we initiated a general netting program in El Verde following the methods of Wunderle et al. (1987). Twenty-four 12-m nets were opened for two days at two

or three week intervals (October 1989–April 1990) in the center of the study site. We captured and color-banded 27 individuals, of which 15 individuals were transients or floaters. Of these transient/floaters 80% were males as compared to 83% of territorial individuals ($n = 12$) recordered during November 1989. Thus, males established territories at El Verde in approximately the same proportions as nonterritorial warblers moving through the forest—a finding consistent with an intrinsic habitat preference explanation. If males were always dominant to females, then females should be more common among the transient/floaters than among territory holders at El Verde, a prediction that was not supported by the data.

These observations do not refute the importance of behavioral dominance as a proximate explanation for sexual habitat segregation in Puerto Rico. The evidence for dominance based on morphology is mixed. For example, the significant difference ($t = 2.25, P = 0.03$) in average body weight of males (9.8 g + 0.4 SE, $n = 33$) and females (9.5 g + 0.3 SE, $n = 31$) in October–December was so slight (3%) that it probably has little or no effect on the outcome of aggressive interactions. Yet Black-throated Blue Warblers of all ages are sexually dichromatic throughout the year, and such plumage differences can be important in dominance relationships (Rohwer 1975, 1977). Studies in Jamaica (Holmes et al. 1989) and in Puerto Rico (Wunderle, unpubl. data) show that dominance interactions might be common. For example, these warblers are highly territorial, within and between sexes, although aggressive interactions appear to be greater within than between sexes. Males and females fight using highly stereotyped displays. Also, I found three territories (two in El Verde, one in Palo Hueco) that were initially occupied by females but in the second year were occupied by males. Yet females and males often have overlapping territories and sometimes forage in close proximity. Age too, is likely to be important in these dominance relationships, because juveniles are commonly displaced by older birds, at least within the same sex (Wunderle, unpubl. data). Consistent with the complexity of these dominance interactions is an explanation suggested by Sherry (pers. comm.) in which females tend to be outcompeted for preferred habitat and/or microhabitat on average, but some females (older?) hold their own against some males. Other females coexist with males by deferring to male dominance with very localized (microhabitat) segregation while maintaining high overlap of territories spatially.

Behavioral dominance might reinforce sexual habitat preferences if males tend to be dominant in habitats with high foliage strata and females dominate in habitats with low foliage strata. The overlap of male and female terriories might occur only when both "male" and "female" strata occur together. Therefore, if the strength of an aggressive response is related to the strength of a preference for a foraging site (e.g., vegetation strata) then habitat segregation might become more marked. A test of this hypothesis requires observations of males losing a disproportionate number of territorial interactions in "female" habitat and females losing a disproportionate number in "male" habitat. Presently, such data are unavailable for any of the species known to show habitat segregation.

Sexual habitat segregation spreads Black-throated Blue Warblers across several habitats in montane regions and presumably reduces the likelihood of intraspecific competition. It is probable that the diets of males and females differ in their corresponding habitats. Dietary preferences might actually drive the segregation, but which is the cause and which is the effect is currently unknown. Diet differences occur in the three study sites (Wunderle, unpubl. data). Females commonly fed on the abundant melastome fruits in Carite whereas in El Verde the abundance of small fruits is limited and males rarely fed on fruit. Thus sexual habitat segregation might produce (or be a result of) dietary differences, which in turn might have differential effects on dispersion patterns, social behavior, and survivorship of males and females.

Habitat segregation between male and female Black-throated Blue Warblers might be difficult to detect in areas with forests of intermediate stature with a wide range of foliage height strata. Studies in such forests are likely to find an equal mix of males and females. This might be why habitat segregation was not found in Jamaica on the sites intensively studied by Holmes et al. (1989), or in surveys of migrants (Waide, Wunderle, and Lodge, unpubl. data) in a diversity of Jamaican habitats during the winter 1987–88. However, a survey in Jan. 1989 by Waide, Wunderle, and Lodge following Hurricane Gilbert showed a preponderance of females in montane forests in the Blue Mountains. Additional surveys of migrants by the same workers were conducted in a diversity of habitats in the Dominican Republic, and failed to detect habitat segregation in this species. In these cases, male and female habitat segregation might not have been detected because only intermediate stature forests were surveyed and not the extremes of "female" or "male" habitats. Also, tall-stature forest, in which males are expected to predominate, is now rare in the Caribbean region as a result of deforestation.

Finally, the observed pattern of habitat segregation may exist only under certain population densities relative to the availability of male and female habitats. If density-dependent habitat selection occurs on the wintering grounds, then reduction or elimination of the favored habitat of one sex could force the displaced sex into the remaining habitats. If the displaced sex moved

into habitats occupied by the opposite sex, the pattern of habitat segregation would disappear. This too, might contribute to differential mortality depending on the behavioral dominance relationships of the sexes. For example, if the displaced sex was behaviorally subordinate, it would likely suffer higher mortality. However, if the displaced sex were dominant it might, in turn, displace some of the subordinate sex from the remaining habitat and contribute to higher mortality of subordinates.

Rangewide changes in land use, such as deforestation or reforestation, might upset existing patterns of sexual habitat segregation. In Puerto Rico, the land area covered by natural forest has been increasing in the past 30 years from a minimum of 6% of the island in the 1940s to a current level of approximately 32% (Birdsey and Weaver 1982). Thus, Black-throated Blue Warblers overwintering in Puerto Rico might have passed through a habitat and population bottleneck in the past and now find a more equitable mix of male and female habitats which permits or drives habitat segregation. However, deforestation is currently the norm throughout the rest of this warbler's Caribbean wintering grounds, and in these areas individuals of the displaced sex (males, in the case of Black-throated Blue Warblers) are likely to flood the habitat of the other sex. This process could obscure or eliminate sexual habitat segregation.

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NOTE ADDED IN PROOF: Lopez and Greenberg (1990) have recently documented sexual segregation by habitat in five species of migrant warblers wintering in Mexico. In these cases, males were most common in the mature stages of succession and females most common in the earlier stages.

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FRONT COVER: The habitat photograph on the cover, by Jan Erik Pierson, is of Henri Pittier National Park in northern Venezuela, where numbers of migrants overwinter, including Olive-sided Flycatchers, Golden-winged Warblers, Blackburnian Warblers, Cerulean Warblers, American Redstarts, Northern Waterthrushes, and Ovenbirds. The Common Yellowthroat, photographed by Barth Schorre, is a bird of marsh borders and shrublands that winters throughout Central America.