RESEARCH ARTICLE

Vertical sexual habitat segregation in a wintering migratory songbird

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ABSTRACT

Sexual habitat segregation during the wintering period is a widespread phenomenon and has important implications for the ecology and conservation of migratory birds. We studied Black-and-white Warblers (*Mniotilta varia*) wintering in second-growth scrub and old-growth mangrove forest in Jamaica to quantify sexual habitat segregation and explore whether patterns of habitat occupation have consequences on physical condition. We used this information along with a body size analysis and simulated territorial intrusions to assess whether behavioral dominance or habitat specialization was responsible for habitat segregation. Based on standardized capture data, we found that females were more abundant than males in both scrub and mangrove forests. Foraging observations, however, suggested vertical segregation within each habitat, with females foraging primarily near the ground and males in the mid-canopy and canopy, indicating that our sex ratio estimates may be biased. Using 2 measures of body condition, we show that males were in better body condition than females, regardless of habitat. We found that males were on average slightly larger than females, and home range analysis and simulated territorial intrusions indicated that males were more territorial than females. We argue that the observed vertical sexual habitat segregation is likely caused by behavioral dominance rather than habitat specialization. Winter body condition is known to carry over to affect migration timing, reproductive success, and annual survival in other songbirds, and therefore sexual habitat segregation may have important implications for year-round population dynamics in Black-and-white Warblers.

Keywords: Black-and-white Warbler, body condition, *Mniotilta varia*, nonbreeding, sexual habitat segregation, vertical segregation, wintering

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LAY SUMMARY

- Female Black-and-white Warblers were partially excluded from the middle and upper parts of the forest canopy by more dominant males.
- This vertical habitat segregation may have resulted in poor body condition in females compared to males.

Segregación vertical de hábitat por sexos en un ave canora migratoria invernante

RESUMEN

La segregación del hábitat por sexos durante el período invernal es un fenómeno generalizado y tiene implicancias importantes para la ecología y conservación de las aves migratorias. Estudiamos a *Mniotilta varia* invernando en matorrales secundarios y manglares maduros en Jamaica para cuantificar la segregación de hábitat por sexos y explorar si los patrones de ocupación de hábitat tienen consecuencias sobre la condición física. Luego usamos esta información junto a un análisis de tamaño del cuerpo y a intrusiones territoriales simuladas para evaluar si la dominancia comportamental o la especialización de hábitat fue responsable de la segregación de hábitat. Basados en datos de captura estandarizados, encontramos que las hembras fueron más abundantes que los machos en los matorrales y los manglares. Las observaciones de forrajeo, sin embargo, sugirieron una segregación vertical dentro de cada hábitat, con las hembras forrajeando principalmente cerca del piso y los machos en la mitad del dosel y en el dosel, indicando que nuestra estimación del cociente de sexos puede estar sesgada. Usando dos medidas de condición corporal, mostramos que los machos estuvieron en mejor condición corporal que las hembras, independientemente del hábitat. Encontramos que los machos fueron en promedio un poco más grandes que las hembras, y los análisis del rango de hogar y de las intrusiones territoriales simuladas indicaron que los machos fueron más territoriales que las hembras. Argumentamos que la segregación vertical de hábitat por sexos observada está probablemente causada por dominancia comportamental

más que por especialización de hábitat. Se sabe que la condición corporal de invierno tiene efectos sobre la fecha de migración, el éxito reproductivo y la supervivencia anual en otras aves canoras; por ende, la segregación de hábitat por sexos puede tener implicancias importantes para las dinámicas poblacionales de todo el año en *M. varia*.

Palabras clave: condición corporal, invernada, *Mniotilta varia*, no reproductivo, segregación de hábitat por sexos, segregación vertical

INTRODUCTION

Migratory bird populations can theoretically be limited during any part of the annual cycle (i.e. breeding, migratory, wintering; Sherry and Holmes 1995, Runge and Marra 2005). However, determining where and when limiting factors operate is complicated because migratory birds occur over large geographic areas and occupy multiple habitats as they complete their twice annual migration. A growing body of research on the wintering grounds suggests that rainfall-mediated food availability is the major limiting factor for migratory bird populations during the winter, at least in the Caribbean (Strong and Sherry 2000, Latta and Faaborg 2002, Sherry et al. 2005, Brown and Sherry 2006, Studds and Marra 2007, Smith et al. 2010, Studds and Marra 2011, Rockwell et al. 2012, Cooper et al. 2015, Rockwell et al. 2017). Despite this increased emphasis on the importance of the wintering period and calls for incorporating the full annual cycle into our ecological and conservation thinking (Marra et al. 2015), the wintering period is still poorly understood for all but a few species.

One of the dominant patterns among migratory birds is for females and males to segregate into different wintering habitats (reviewed by Catry et al. 2006, Bennett et al. 2019). Two basic mechanisms have been hypothesized to explain sexual habitat segregation: habitat specialization and behavioral dominance (Lynch et al. 1985, Marra 2000). In the former, innate differences between the sexes lead to habitat segregation, while in the latter males are dominant to females and actively exclude them from high-quality habitats. Strong evidence for the habitat specialization hypothesis is limited to Hooded Warblers (*Setophaga citrina*), where observational and experimental evidence suggests that females prefer shrubby woodlands and old fields and males prefer second-growth and mature forests (Lynch et al. 1985, Morton 1990). Bennett (2018) found strong support for the behavioral dominance hypothesis in Golden-winged Warblers (*Vermivora chrysoptera*), but perhaps the strongest evidence comes from American Redstarts (*Setophaga ruticilla*). Analysis of fall arrival patterns, in addition to playback and removal experiments, has shown that dominant older male American Redstarts largely exclude subordinate females and younger males from a high-quality mangrove forest in Jamaica (Marra et al. 1993, Marra 2000). Wunderle (1992, 1995) suggested that the 2 hypotheses may not be mutually exclusive and found mixed support for both hypotheses in Black-throated Blue Warblers (*Setophaga caerulescens*) wintering in Puerto Rico.

If birds segregate into different habitats based on innate habitat preferences, then there should be no immediate negative consequences because each sex should be well adapted to its preferred habitat. In contrast, if sexual habitat segregation arises through behavioral dominance, subordinate individuals may face negative consequences because they are forced into low-quality habitats. For example, Studds and Marra (2005) showed conclusively that behavioral dominance results in subordinate American Redstarts having decreased body condition and delayed departure on spring migration, which can carry over into the breeding season to affect reproductive success (Marra et al. 1998, Tonra et al. 2011) and natal dispersal (Studds et al. 2008). Subsequent correlational (Studds and Marra 2007, 2011) and experimental work (Cooper et al. 2015) confirmed that food was the limiting resource driving competition over space and resulting in consequences on body condition and migration timing. Not only can sexual habitat segregation result in negative consequences for subordinates, but if ignored, can lead to ineffective wintering ground conservation as well (Bennett et al. 2019). Sexual habitat segregation thus may have important consequences at both the individual and population level, and yet, we do not know if and why it occurs in many species.

Here, we investigate sexual habitat segregation and its consequences in Black-and-white Warblers (*Mniotilta varia*) wintering in Jamaica. The Black-and-white Warbler is an insectivorous, long-distance migratory songbird that winters in the southeastern United States, Central and South America, and the West Indies and breeds across much of eastern North America (Kricher 2020). The species is known to occupy a wide variety of habitats during the winter, ranging from coastal successional scrub to mature cloud forests (Hutto 2020, Kricher 2020). Previous evidence of sexual habitat segregation in Black-and-white Warblers is mixed. Two multi-habitat studies in Cuba and Mexico show biased sex ratios in some habitats but not others (Lopez-Ornat and Greenberg 1990, Wallace et al. 1996), and of 2 single-habitat studies, one found no sex ratio bias in shade coffee plantations in the Dominican Republic (Wunderle and Latta 2000) and another found a highly female-biased sex ratio in dry forest in Puerto Rico (Faaborg and Arendt 1984). Studies of sexual habitat segregation in this species do not exist from Jamaica, and the

potential consequences of habitat segregation have not been studied.

We studied Black-and-white Warblers in 2 Jamaican forest types, second-growth scrub forest (hereafter scrub) and old-growth black mangrove forest (hereafter mangrove). Our objectives were to determine (1) the degree to which Black-and-white Warblers exhibit sexual habitat segregation, (2) if there are consequences of habitat segregation on overwinter body condition, and (3) if this segregation is caused by habitat specialization or behavioral dominance. We predicted that because of its greater ability to support insect populations throughout the winter (Studds and Marra 2007, 2011), mangrove habitat would be preferred by both sexes. However, we predicted that male Black-and-white Warblers would be larger and more aggressive than females and that dominant males would at least partially exclude females from mangrove habitat. We also predicted that we would find corresponding differences in body condition based on habitat and sex.

METHODS

Study Site
This research was conducted within the Font Hill Nature Preserve (18.0391°N, 77.9411°W), located on the south coast of Jamaica in St. Elizabeth Parish. The primary research was conducted from January 10 through April 10 in 2009 and 2010, but we also used a long-term standardized banding dataset (2008–2017) to examine sex-based differences in habitat occupation and body size. The study period was divided into mid-winter (January 10–February 15) and late winter (March 15–April 10). These periods correspond with previous studies at these sites that have been used to document important seasonal declines in rainfall, food availability, and body condition in American Redstarts (Studds and Marra 2007, 2011).

Research was conducted on 2 scrub plots and 3 mangrove plots. Each plot ranged in size from 5 to 7 ha and was gridded with an alphanumeric system at least every 50 m and usually every 25 m. The scrub forest consisted of relatively dense understory vegetation and a 5–15 m tall canopy. During the study period, the scrub forest remained dry and never had standing water. The dominant tree species in the scrub forest was logwood (*Haematoxylon campechianum*) with other facultatively deciduous species such as *Bursera simaruba* and *Crescentia alata*. Scrub plots had a dense understory comprised of juvenile canopy species and *Bromelia pinguin*, intermixed with vine tangles. Canopy trees in scrub typically retain their leaves through the end of the mid-winter period (January 10–February 15) and shed their leaves by the beginning of the late-winter period (March 15–April 10). The mangrove sites were relatively undisturbed and had a canopy

height of 9–15 m with little to no ground vegetation except for mangrove saplings and pneumatophores from older mangroves. The mangrove forest was dominated by black mangrove (*Avicennia germinans*) with red mangrove (*Rhizophora mangle*) in wetter areas and white mangrove (*Laguncularia racemosa*) on drier margins. Mangrove trees retain most of their leaves throughout the dry season, providing shade in the understory, and in typical years mangrove habitats remain flooded year-round by 0.3–2 m of brackish water. However, water levels were low in both 2009 and 2010 because of low levels of precipitation in those years (Cooper 2014).

Field Methods
Black-and-white Warblers were captured using passive mist netting as part of a standardized long-term banding effort that consisted of running 10 passive nets for 2 consecutive days (30 min before sunrise until 1300 hr) in each of 4 plots (2 scrub, 2 mangrove). For this banding effort, 2 adjoining mangrove plots were combined so that banding effort was equalized between the 2 habitats. Net locations were consistent each year, with nets placed north/south and east/west on consecutive days in the same plot. Nets were run for 2, 8-day periods (4 days in each habitat per period) that began January 15 and March 15 each year from 2008 to 2017. In 2009 and 2010, we supplemented this banding effort by running 5–12 additional passive nets daily during our mid- and late-winter periods (see above). After capture, we individually marked birds by attaching one United States Geological Survey metal band and 2 plastic color bands. We then measured unflattened wing chord and tail length using a wing rule, and bill, tarsus, and tail lengths using digital calipers. Finally, we weighed each bird to the nearest 0.1 g using a digital scale. Each bird was then sexed using plumage characteristics (Pyle 1997).

At least once every 3 days throughout the season, we attempted to relocate banded individuals and map their home ranges. After encountering an individual, we noted its band combination and followed the individual while recording movements until it was lost from sight or stopped moving for >5 min. Observers recorded individual bird movements on paper maps that had a grid corresponding to the physical grid on each plot. The mapping effort was too low to obtain complete home range maps of all plots in all years. While mapping, we also recorded any time that we observed one individual physically displace another through an aggressive interaction (i.e. fights, chases, etc.).

To quantify foraging behavior, we carried out detailed foraging observations on a subset of color-banded individuals in each habitat (scrub: ♀ = 10, ♂ = 11; mangrove: ♀ = 9, ♂ = 9) in March and April of 2010. All observations were conducted within 4 hr of sunrise using continuous recording focal animal sampling (Martin and Bateson 1993).

To avoid bias toward conspicuous behaviors, recording began after the first attempted prey attack was made for each individual. While following an individual with binoculars, foraging behaviors were narrated into a digital recorder. A foraging sequence was stopped if the bird was lost from sight or if it changed from foraging to other behaviors (e.g., preening or interactions with other birds). If the individual was re-sighted within 30 s or switched back to foraging behaviors, observations continued. Observation of foraging bouts <30 s were discarded to avoid bias toward infrequently used behaviors. Prey attacks were characterized as surface (e.g., glean), sub-surface (e.g., probe), or aerial (e.g., sally-strike) attacks, and each time an individual carried out a foraging maneuver, we recorded the foraging height relative to the ground and the horizontal location relative to the trunk of the tree. For vertical positions, we split the forest into 3 equal height categories that were relative to the canopy height at the location of the foraging attempt: understory (including the ground), mid-canopy, canopy. Similarly, the horizontal position was divided into thirds depending on the bird's location on the tree relative to the trunk: inner (including the trunk), middle, and outer (end of branches). Foraging maneuvers that occurred on the ground were not assigned a horizontal location. To ensure consistent position estimates, a single observer (M.A.T.) carried out all foraging observations.

We tested for evidence of territoriality by conducting simulated territory intrusions using conspecific playback directed at a subset of color-banded individuals in 2009 and 2010 (scrub ♀ = 10, ♂ = 22; mangrove ♀ = 9, ♂ = 18). Using the mapping data (see above), we identified the approximate center of each focal individual's home range and confirmed that each individual used this area at least 5 times on separate days. Playbacks were only initiated when the individual was re-sighted within this central location. While maintaining visual observation of the individual, we concealed a speaker on the ground and then observed behavior from a concealed location >15 m away (following Marra 2000). The playback was always initiated with the focal individual in sight. Because chip notes are the most common vocalization during the wintering season, we began each playback session with 15 s of chip notes followed by a mix of songs and chips for a total of 5 min of playback. Before the playback was started, we estimated the distance of the focal bird to the speaker. During the playback, we scored the bird's aggressive response on a scale from 1 to 4 (1 = no response; 2 = occasional chips and remains in the vicinity but always >5 m away; 3 = obviously agitated with few close approaches within 5 m of the speaker; 4 = highly agitated with multiple approaches within 2 m of the speaker and spends most of playback sequence inside 3-m radius of the speaker; modified from Marra 2000). Intermediate values (1.5, 2.5, and 3.5) were also used when behaviors were intermediate between

categories. No playbacks were conducted within 150 m of each other during the same day to avoid prior exposure to neighbors.

Data Analysis

To estimate the sex ratio in scrub and mangrove, we counted the number of birds of each sex captured during our standardized long-term banding program (2008–2017). To avoid double-counting individuals, we only included the first capture of any given individual each year. We first used a chi-square goodness of fit test to determine if the sex ratio in each habitat was equal when pooled across all years. We then used a Fisher's exact test to see if habitat-based differences in sex ratios were consistent across all years.

We estimated the size, shape, and location of home ranges using our mapping data for color-banded individuals that were observed at least 30 independent times. Due to difficulties re-sighting individuals and insufficient mapping effort, we were only able to determine home range overlap in 2010, and only on most of one of the 2 scrub plots and a continuous area that included portions of 2 of the 3 mangrove plots. An individual location was considered independent each time a bird moved 10 m or more during a mapping bout or the observation was collected at least an hour from its previous encounter. These independent points were compiled on summary maps for each individual. We digitized these summary maps using a graphics tablet (Wacom, Kazo, Japan) and Photoshop Elements (Adobe Systems, San Jose, California, USA) and then georeferenced locations in ArcGIS 9.3 (ESRI, Redlands, California, USA) using GPS positions (≤0.5 m) collected at each grid point with a Trimble Pathfinder ProXRT Receiver (Trimble, California). We calculated the area of each home range using the 95% minimum convex polygon method (Mohr 1947). To estimate the overlap of individual home ranges, we digitized regions of overlap and estimated the area overlapped by all same- and opposite-sex neighbors separately. We then used an analysis of variance (ANOVA) to explore differences in proportional overlap by habitat and sex.

We observed 661 foraging attempts during 132 min of foraging observations. To explore sex-based differences in foraging, we used Fisher's exact test to compare sex-based differences in vertical and horizontal foraging locations. If a significant difference was found, we then carried out a post-hoc analysis to determine which pairwise differences were significant.

We tested for differences in structural body size between females and males because larger body size has been shown to allow individuals greater access to resources, which may be an indicator of dominance-mediated habitat segregation. To increase sample sizes, we used all banding data available from 2008 to 2017, and to avoid double-counting individuals, we only used the first capture of each

TABLE 1. Sex ratio (male:female) by habitat for Black-and-white Warblers (*Mniotilta varia*) wintering in Jamaica, 2008–2017.

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Total
Scrub	10:27	3:19	4:14	4:10	6:18	4:17	12:14	12:13	6:13	11:19	72:164
Mangrove	6:14	8:16	4:8	3:13	5:5	5:11	3:6	7:5	8:12	5:10	54:100

individual. To test for body size differences, we used the scores from a principal component analysis based on wing chord and tarsus length (Marra 2000) as the dependent variable in an ANOVA with the predictor variables habitat, sex, and an interaction effect. To determine sex-based differences in territoriality, we compared the response scores from our simulated territorial intrusion experiment using an ANOVA with the predictor variables habitat, sex, and an interaction effect. In both cases, the year was not included because of the small sample sizes within groups in some years.

To determine if there were consequences of habitat segregation, we looked at sex- and habitat-based differences in body condition in 2 ways, following Marra and Holmes (2001). First, for individuals that were caught in both mid- and late winter in the same year, we calculated change in mass (±0.1 g) over the season (scrub: ♀ = 27, ♂ = 10; mangrove: ♀ = 11, ♂ = 6). We then used an ANOVA to determine how a change in mass varied by habitat, sex, and the interaction effect. Second, because we could not capture all individuals in both seasons each year, we also calculated mass controlled for body size as an estimate of body condition for all individuals captured during late winter (scrub: ♀ = 88, ♂ = 32; mangrove: ♀ = 65, ♂ = 37). To do this we regressed body mass over the scores from a principal components analysis based on wing chord and tarsus. We found that mass increased linearly with this body size estimate, and we then used the residuals from this regression as an estimate of body condition (Marra and Holmes 2001). We used this body condition estimate as the dependent variable in an ANOVA that incorporated habitat, sex, and the interaction effect. Only birds from 2010 and 2011 were used in these analyses and we pooled those 2 yr together because of small numbers (<5) of individuals in some groups. All ANOVAs were carried out in SPSS Statistics 26 (IBM). Chi-square and Fisher's exact tests were carried out in the base *stats* package, and post-hoc tests for Fisher's exact test were carried out in the package *RVAideMemoire* (Hervé 2020) for program R (R Core Team 2020). All means are reported ± 1 standard error.

RESULTS

Abundance and Sex Ratios in Scrub and Mangrove Forests
From 2008 to 2017, we captured significantly more Black-and-white Warblers in scrub ($n = 236$) than in mangrove

habitat ($\chi^2 = 17.2$, df = 1, $P < 0.001$; $n = 154$). Across all years, we captured 2.3× more females than males in scrub habitat (164 ♀, 72 ♂) and 1.9× more females than males in mangrove habitat (100 ♀, 54 ♂; Table 1). Sex ratios in both habitats were found to be significantly female biased (scrub: $\chi^2 = 35.9$, df = 1, $P < 0.001$; mangrove: $\chi^2 = 35.9$, df = 1, $P = 0.002$), but the sex ratio of captured birds did not statistically vary between habitats (Fisher's exact $P = 0.38$) or among years (scrub: Fisher's exact $P = 0.20$, mangrove: Fisher's exact $P = 0.72$).

Sex- and Habitat-Based Differences in Space Use
We had sufficient data to estimate home range size for 20 females (10 scrub, 10 mangrove) and 14 males (9 scrub, 5 mangrove) in 2010. We found that home range size (scrub ♀: 1.3 ± 0.2 ha, mangrove ♀: 1.8 ± 0.2 ha, scrub ♂: 0.6 ± 0.1 ha, mangrove ♂: 1.1 ± 0.3 ha) differed by both sex ($F_{1,30} = 11.39$, $P < 0.001$) and habitat ($F_{1,30} = 5.99$, $P = 0.02$), with no interaction ($F_{1,30} = 0.30$, $P = 0.86$; full model $F_{3,30} = 6.97$, $P = 0.001$, $r^2 = 0.35$). Females had larger home ranges than males regardless of habitat, and home ranges were larger in mangrove than in scrub. Horizontal overlap by same-sex conspecifics was significantly greater in females (83 ± 5%) than in males (37 ± 10%; $F_{1,30} = 18.46$, $P < 0.001$), but the effects of habitat ($F_{1,30} = 0.08$, $P = 0.77$) and the habitat × sex interaction were not significant ($F_{1,30} = 0.04$, $P = 0.84$; full model $F_{3,30} = 6.30$, $P = 0.002$, $r^2 = 0.33$). Overlap by opposite-sex conspecifics was complete in all cases and therefore there were no sex- or habitat-based differences.

Foraging Observations
We observed 661 foraging attempts by 39 individuals (scrub: ♀ = 10, ♂ = 11; mangrove: ♀ = 9, ♂ = 9), and nearly all were gleans or probes on woody branches ($n = 637$, 96%) with foraging attempts rarely occurring on the ground ($n = 24$, 4%). We found that female and male vertical foraging locations differed significantly in both scrub (Fisher's exact $P < 0.001$) and mangrove habitat (Fisher's exact $P < 0.001$). In both habitats, females more frequently foraged in the understory and less frequently in the mid-canopy or canopy than males (Figure 1; all pairwise Fisher's exact $P < 0.001$). In contrast, horizontal foraging position did not differ significantly by sex in scrub (Fisher's exact $P = 0.54$). In mangrove, females tended to forage more frequently toward the tips of the branches than males, but the difference was not significant (Fisher's exact $P = 0.10$).
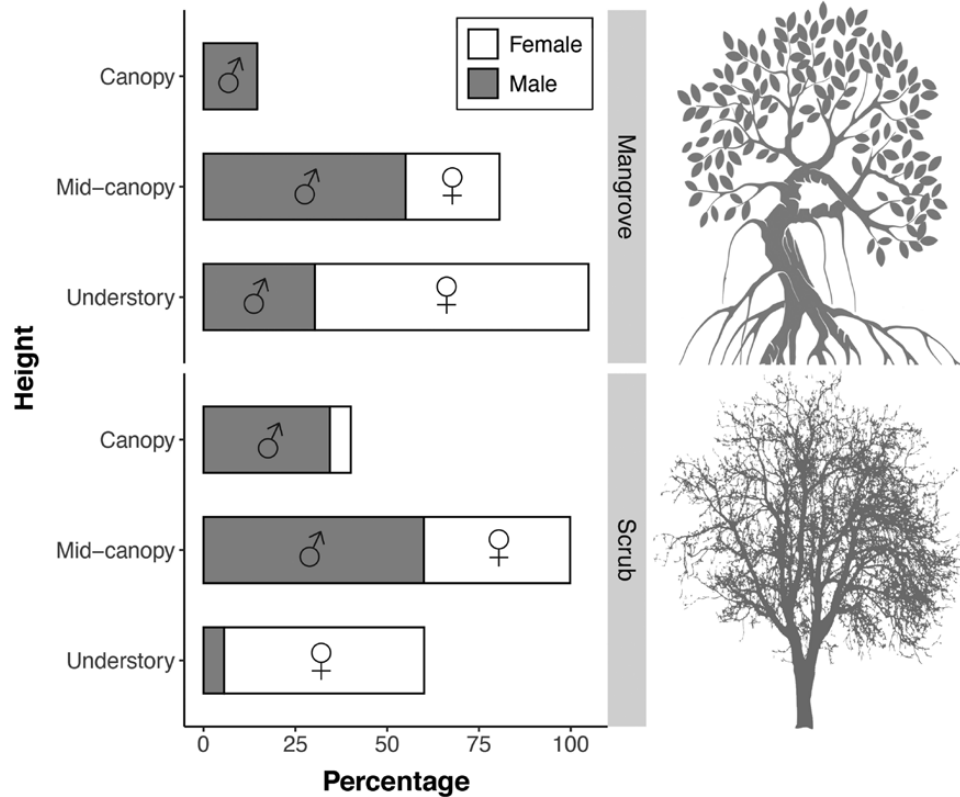
FIGURE 1. Percentage of foraging maneuvers observed in the understory, mid-canopy, and canopy for female (white) and male (shaded) Black-and-white Warblers in scrub and mangrove habitats. The size of the bars within each height category indicates the percentage of time spent foraging at that height by each sex relative to other height categories. Thus, percentages total to 100% within each sex and habitat. For example, 75% of foraging maneuvers by females in mangrove occurred in the understory, 25% occurred in the mid-canopy, and 0% occurred in the canopy.

Simulated Territorial Intrusions

Regardless of habitat, females showed almost no behavioral response to simulated territorial intrusions, with only one of 19 females (5.3%) chipping in response to the playback. In contrast, 33 of 40 (83%) males exhibited a more aggressive behavioral response. Males frequently chipped and approached the speaker closely and occasionally sang. Accordingly, we found that playback response score was significantly lower in females ($\bar{x}$ = 1.0 ± 0.3) than in males ($\bar{x}$ = 3.0 ± 0.2; $F_{1,55}$ = 57.5, P < 0.001), with no effect of habitat ($F_{1,55}$ = 0.9, P = 0.35) or a habitat × sex interaction ($F_{1,55}$ = 0.6, P = 0.46; full model $F_{3,55}$ = 20.4, P < 0.001, r^2 = 0.50). During hundreds of hours of mapping home ranges and making foraging observations, we rarely observed aggressive encounters within or between sexes. However, anecdotally, male displacement of females (n = 10) was much more common than other opposite- or same-sex displacements (♀–♂ = 0, ♀–♀ = 2, ♂–♂ = 2).

Body Size and Condition

We found that females had smaller bodies than males ($F_{1,457}$ = 21.1, P < 0.001) and there was no habitat difference ($F_{1,457}$ = 2.4, P = 0.12) or a habitat × sex interaction ($F_{1,457}$ = 0.2, P = 0.66). However, the full model explained less than 5% of the overall variation in body size ($F_{3,457}$ = 21.1, P < 0.001, r^2 = 0.04). We also found that change in mass from mid-winter to late winter differed by sex ($F_{1,50}$ = 4.6, P = 0.04) and habitat ($F_{1,50}$ = 8.6, P = 0.01), with no interaction effect ($F_{1,50}$ = 0.6, P = 0.46, full model $F_{3,50}$ = 4.57, P = 0.01, r^2 = 0.17). Across both habitats, females lost on average 0.5 ± 0.1 g of body mass, while males only lost 0.1 ± 0.1 g of mass (Figure 2). Regardless of sex, individuals in scrub habitat lost more mass ($\bar{x}$ = 0.5 ± 0.1 g) than individuals in mangrove ($\bar{x}$ = 0.1 ± 0.1). In our larger sample of individuals captured in late winter, we found that regardless of habitat type, males were in greater body condition than females (Figure 3, $F_{1,109}$ = 8.7, P = 0.004). The effects of habitat ($F_{1,109}$ = 0.4, P = 0.5) and the habitat × sex interaction ($F_{1,109}$ = 0.0, P = 1.0) were not significant (full model $F_{1,109}$ = 2.9, P = 0.04, r^2 = 0.05).

DISCUSSION

Our study represents one of the only detailed studies of the wintering ecology of Black-and-white Warblers. We
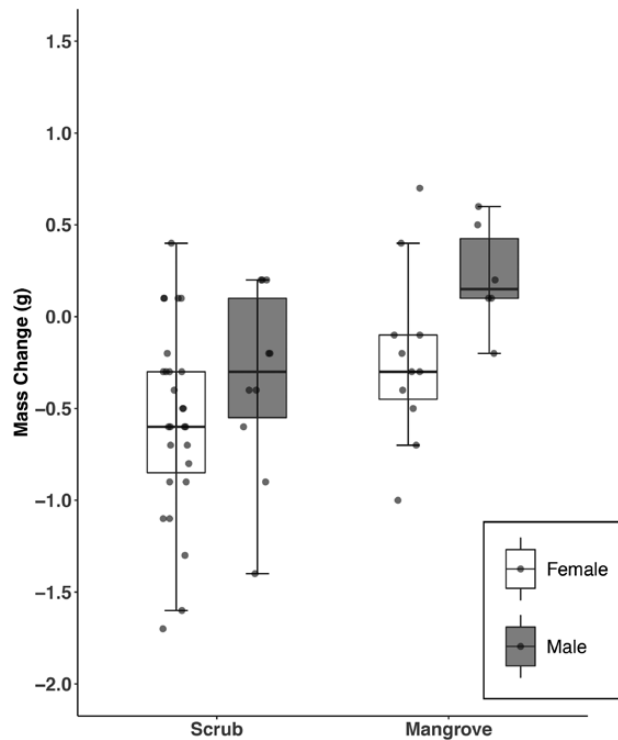
FIGURE 2. Mass change from mid- to late season of male and female Black-and-white Warblers wintering in Jamaica. Closed circles show data points for individuals. Boxes show median ± interquartile range (IQR), whiskers show 1.5 × IQR.

FIGURE 3. Late-winter body condition for female and male Black-and-white Warblers wintering in scrub and mangrove forests in Jamaica. Boxes show median ± interquartile range (IQR), whiskers show 1.5 × IQR.

found that Black-and-white Warblers were more abundant in scrub habitat, and that sex ratios appeared to be female biased in both habitats. Females showed no evidence of territorial behavior against either same- or opposite-sex conspecifics, but males often excluded other males from their home ranges and showed stronger responses to simulated territorial intrusions, suggesting that males are territorial. Although female and male home ranges overlapped horizontally, we found evidence of vertical habitat segregation within both habitats, with females occupying the understory and males occupying the mid-canopy and canopy. It is possible that differences in vertical space use reflect innate foraging preferences, but several lines of evidence suggest behavioral dominance is the cause of within-habitat sexual habitat segregation. Consistent with predictions of behavioral dominance, both sex- and habitat-based consequences on body condition were evident, with males and individuals in mangrove maintaining better body condition over the season.

Do Black-and-white Warblers Exhibit Sexual Habitat Segregation?

We captured approximately twice as many females as males in scrub and mangrove forests in Jamaica, which would typically indicate that sex ratios are female biased
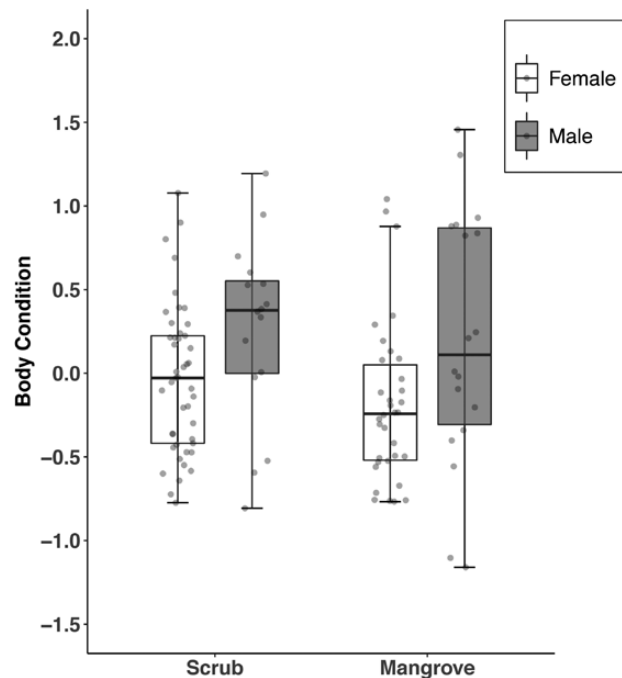
in both habitats. However, sex-based differences in vertical space use likely biased our capture rates because we operated mist nets close to the ground where females frequently foraged and males rarely foraged. We do not have any independent data with which to assess the sex ratios of these 2 habitats. Regardless, our prediction, based on previous work with American Redstarts at these same study sites, that males would largely exclude females from high-quality mangrove habitat was not definitively supported or refuted.

Although observed differences in vertical space use likely biased our capture rates, they also raise an intriguing possibility—that sexual habitat segregation is occurring, but within each habitat's vertical structure rather than between habitats. Our foraging observations revealed that females foraged primarily in the understory, to some degree in the mid-canopy and almost never in the canopy. In contrast, males foraged primarily in the mid-canopy and canopy. This striking difference in vertical space use suggests that Black-and-white Warblers segregate within each habitat by sex. Future research should confirm this finding by estimating 3-dimensional home range utilization distributions and overlaps to explicitly test for vertical differences in home range size, shape, and overlap (Cooper et al. 2014).

Sexual habitat segregation may exist across a broader range of habitats than we studied, especially when

considering the entire wintering range of this species. Black-and-white Warblers have one of the widest wintering habitat breadths of North-American wood warblers (Parulidae; Kricher 2020) and we know that the species uses a variety of other habitats in Jamaica, including dry and wet limestone forests, citrus farms, and coffee plantations (Johnson 2000, Kent and Sherry 2020). However, we do not have detailed information about abundances or sex ratios from these habitats and therefore conclusions are limited. It is also possible that males and females segregate at a regional scale (Bennett et al. 2019) or latitudinally within their wintering range, presumably with males wintering further to the north than females (reviewed by Komar et al. 2005), but no tracking data exist and almost nothing is known about their migratory connectivity (A. Scarpignato personal communication). In addition to its wide habitat breadth, Black-and-white Warblers also show variation in spacing behavior and have been regularly observed in mixed species flocks in other parts of their wintering range (Kricher 2020)—a behavior not observed at our sites in Jamaica. To determine how our findings apply more broadly in Jamaica and across the species' wintering range, future research should investigate a wider range of habitats and wintering locations.

Consequences of Habitat Use and Vertical Habitat Segregation

We found habitat- and sex-based differences in how body condition changed over the season. Irrespective of sex, individuals in mangrove were able to maintain their body mass better than scrub birds, suggesting mangrove is a higher-quality habitat for Black-and-white Warblers, similar to what has been found for American Redstarts at this same study site (Marra and Holmes 2001, Studds and Marra 2005). Differences in food availability between habitats likely drive the differences in mass change between habitats, because food availability has been shown both observationally and experimentally to be the main factor limiting American Redstarts in this system (Studds and Marra 2007, 2011, Cooper et al. 2015). The large habitat-based differences in ability to maintain mass over the season make it somewhat surprising that we did not find between-habitat sexual habitat segregation in scrub and mangrove forests. However, as mentioned above, our estimates of sex ratios in the 2 habitats may be inaccurate because of differences in vertical space use and the resulting biases in female and male capture probabilities. Moreover, we may have missed important age-based patterns of habitat occupation or use (Wunderle 1995, Marra 2000), which we could not examine due to incomplete aging data and small sample sizes in age and sex classes.

In addition to habitat-based differences in body condition, we also found important sex-based differences. Mass change within the same individuals from mid- to late winter indicated that males maintained greater body condition than females in both habitats. This finding was also supported by our larger data set, which included individuals only caught in late winter. Together, these data support the idea that by foraging in the mid-canopy and canopy, males have access to greater food availability or higher-quality prey and are better able to maintain body condition over the course of the season than females, but we do not understand the mechanism. In both scrub and mangrove habitats, branch density is visually greatest in the mid-canopy and canopy, which should provide a greater surface area of the woody substrate for Black-and-white Warblers to glean and probe for insects. Moreover, moisture levels may be higher in the canopy due to evapotranspiration of dew during the morning when birds are most actively foraging, and therefore insects may be more abundant higher in the canopy. Regardless of the mechanisms, both the consequences of habitat occupation and vertical segregation might have important carryover effects on the rest of the annual cycle.

Potential Carryover Effects

In other songbirds, including American Redstarts at this Jamaican study site, winter habitat use and its effects on body condition have been shown to have cascading effects on migration timing (Marra et al. 1998, Studds and Marra 2005, 2011, Rockwell et al. 2012, Cooper et al. 2015), reproductive success (Marra et al. 1998, Rockwell et al. 2012, Drake et al. 2013, López Calderón et al. 2019), and annual survival (Marra and Holmes 2001, Johnson et al. 2006, Rockwell et al. 2017), and similar effects may exist in Black-and-white Warblers. Paxton and Moore (2015) used stable isotopes to show that Black-and-white Warblers occupying drier winter habitats arrived later to a stopover site in Louisiana while en route to the breeding grounds, suggesting that habitat-based food availability, through its effect on body condition, affects migration timing. The reproductive consequences of spring migration timing for Black-and-white Warblers have not been studied. However, it seems likely that early arrivers benefit in terms of their reproductive success, as has been shown in many other songbirds (Reudink et al. 2009, Cooper et al. 2011, Tonra et al. 2011, Rockwell et al. 2012). Thus, Black-and-white Warblers wintering in mangrove may experience benefits in terms of earlier migration and greater reproductive success, and this should be confirmed through future studies.

Conditions on the wintering grounds are known to affect not only reproductive success but also survival. Seasonal variation in survival has not been investigated in Black-and-white Warblers, but in several other songbirds, mortality is greater during migration (Sillett and Holmes 2002, Paxton et al. 2017, Rockwell et al. 2017), and especially during spring migration (Rushing et al. 2017), compared to the breeding or wintering periods. Winter body condition

presumably plays some role in determining the probability of survival during spring migration given the extreme energetic demands of long-distance migration. Thus, individuals wintering in mangrove may survive at greater rates than individuals in scrub. Similarly, males may survive at greater rates than females because of their apparent ability to dominate access to the forest canopy and maintain overwinter body condition. Future work should focus on determining whether habitat use and within-habitat vertical segregation carry over to affect performance and survival in other periods of the annual cycle in this species.

Causes of Sexual Habitat Segregation

Few studies have explicitly tested whether winter sexual habitat segregation is driven by innate habitat specialization or behavioral dominance (Morton 1990, Marra 2000, Bennett 2018). Our foraging observations indicated that females and males foraged almost exclusively through gleaning and probing on woody branches and foraged at similar horizontal positions along tree branches. Although this suggests a similar overall foraging niche, we did find that females forage closer to the ground than males, and this within-habitat vertical segregation could result from either habitat specialization or behavioral dominance. Similar sex-based differences in foraging height have been shown in several woodpeckers (*Picidae*) and a number of songbirds but have been variously attributed to habitat specialization or social dominance (reviewed by Catry et al. 2006). We found that male Black-and-white Warblers were on average larger than females, but male and female body size overlapped strongly, so it is unclear how much body size might contribute to dominance hierarchies between the sexes. Nonetheless, males had much more aggressive responses to our simulated territorial intrusion than females, had lower same-sex home range overlap (see also Wunderle 1995), and were observed displacing females, whereas females were never observed displacing males. Furthermore, we also found strong sex-based differences in ability to maintain body condition over the season, consistent with the behavioral dominance hypothesis. Thus, multiple lines of evidence support behavioral dominance, and not habitat specialization, as the primary factor structuring patterns of vertical segregation in this species. In Black-and-white Warblers, additional observations of arrival patterns in the fall and removal experiments are needed to confirm our conclusions (Marra 2000).

Conclusion

Sexual habitat segregation on the wintering grounds appears to be common in the species with data available (Catry et al. 2006, Bennett et al. 2019). A growing body of literature suggests that differential habitat use on the wintering grounds, including sexual habitat segregation, can have important consequences for fitness (reviewed by Harrison et al. 2011) and also affect the success of conservation efforts. For example, Bennett et al. (2019) recently showed that failure to consider sexual habitat segregation can lead to ineffective wintering ground conservation because female-dominated habitats receive less conservation attention. If Black-and-white Warblers only segregate vertically within habitats, then this is less of a concern because conservation efforts are unlikely to target only specific vertical layers of a habitat. However, some anthropogenic activities like grazing by livestock could possibly reduce the quality of the female-dominated understory without affecting the male-dominated canopy. Furthermore, if sexual habitat segregation operates among a broader range of habitats than studied here, as we suspect that it does, then failure to protect some habitats could lead to different conservation outcomes for female and male Black-and-white Warblers.

Information on sexual habitat segregation on the wintering grounds is lacking altogether or inconclusive for many species (Bennett et al. 2019). Because sexual habitat segregation may have important fitness consequences, the patterns and consequences of sexual habitat segregation need to be better studied and explicitly tested for in other species. More generally, our knowledge of the wintering ecology of most bird species is severely lacking (Sherry and Holmes 1995, Marra et al. 2015, Albert et al. 2020), and much of what we do know comes from a single study system (i.e. American Redstarts in Jamaica) that cannot fully represent the behavioral, taxonomic, or geographic diversity of wintering birds. If we aim to understand and reverse the alarming population declines of so many of North America's birds (Rosenberg et al. 2019), we need research on more species including a better understanding of their wintering ecology and its consequences on events throughout the full annual cycle.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Cooper et al. (2020).

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