

VARIATION IN AGGRESSION OF BLACK-THROATED BLUE WARBLERS WINTERING IN JAMAICA

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Abstract. Variation in aggression among birds on different territories has been hypothesized to be influenced by intrinsic factors such as a bird's age, sex, or size and extrinsic factors such as density of neighbors, abundance of food, or territory size. However, little work has examined how and why aggression may vary within a bird's home range. We examined variation in aggressive behaviors of nonbreeding Black-throated Blue Warblers (*Setophaga caerulescens*) in Jamaican coffee farms by using experimentally simulated intrusions into home ranges. Our multivariate models confirmed that multiple variables associated with aggression included sex, home range size, proximity of intrusion to home range center, and the presence of another aggressive bird in the area. In addition, we found that birds responded more aggressively to intrusions in shade trees, where insects were more abundant, than in the understory of coffee or of small patches of remnant forest. These results suggest the birds responded to variation in habitat and/or food supply within their home ranges and varied aggressive responses accordingly, revealing a finer scale of behavioral resource matching than previously documented for bird territoriality.

Key words: aggression, behavior, coffee, defense, home range, territoriality, warbler.

Variación en la Agresión de Individuos de *Setophaga caerulescens* que Invernan en Jamaica

Resumen. Se ha hipotetizado que la variación en la agresión entre las aves en territorios diferentes está influenciada por factores intrínsecos como la edad del ave, el sexo y el tamaño, y por factores extrínsecos como la densidad de vecinos, la abundancia de alimentos o el tamaño del territorio. Sin embargo, poco se ha examinado cómo y por qué la agresión puede variar dentro del área de acción de un ave. Examinamos la variación en los comportamientos de agresión de individuos no reproductivos de *Setophaga caerulescens* en granjas de café de Jamaica mediante el empleo de simulaciones experimentales de intrusión en las áreas de acción. Nuestros modelos multivariados confirmaron que las variables asociadas con la agresión incluyeron sexo, tamaño del área de acción, proximidad de la intrusión al centro del área de acción y presencia de otra ave agresiva en el área. Adicionalmente, encontramos que las aves respondieron de forma más agresiva a las intrusiones en las plantaciones de café con árboles de sombra, donde los insectos fueron más abundantes, que en las plantaciones sin árboles de sombra o en pequeños parches remanentes de bosque. Estos resultados sugieren que las aves respondieron a variaciones en el hábitat o en la provisión de alimentos dentro de sus áreas de acción y que de acuerdo a esto cambiaron sus respuestas agresivas, revelando una escala de más detalle de ajuste del comportamiento a los recursos de lo que se había documentado previamente para la territorialidad de las aves.

INTRODUCTION

Territorial aggression is theorized to be the product of selective forces acting on the defense of a critical resource such as food (Brown 1964). In birds, aggressiveness during territorial behavior has been correlated with many individual and environmental factors including sex (Lynch et al. 1985, Marra 2000, Bard et al. 2002), position of encounter within a territory (Wunderle 1978a, Simpson 1985), size of territory (Watson and Miller 1971), body size and age (Marra 2000), time of day and season (Staicer 1989, Wiklund and Village 1992, Shy and Morton 2004), quality of habitat (Marra 2000), size of badge (and therefore rank) of opposing individual (Møller 1987), distance to singing neighbor (Simpson 1985),

whether singing individuals are strangers or neighbors (Wunderle 1978b, Brindley 1991), food availability (Davies 1980, Goldberg et al. 2001), prior occupancy (Lanyon and Thompson 1986), and more. Little is known, however, about how aggression is influenced by habitat variation within a territory, and very few studies have simultaneously examined which of multiple variables most strongly affect bird aggression (but see Shy and Morton 2004).

The nonbreeding territoriality of parulid warblers varies considerably. Some species defend clear territories from conspecifics whereas others defend no territories at all (Greenberg and Salewski 2005), and some species' territorial defense varies among individuals (Brown and Sherry 2008), by habitat (Tramer

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and Kemp 1980, Latta and Faaborg 2001), or within their geographic ranges (Chipley 1977, Lerner and Stauffer 1998).

The ecological drivers of nonbreeding territorial behaviors are diverse, but food supply and diet feature prominently (Tye 1986, Greenberg and Salewski 2005, Brown and Long 2007). The American Redstart (*Setophaga ruticilla*) is among the best-studied parulids in a tropical winter range, and it strongly defends space in association with the abundance of insects for food. By studying strong contrasts in insect abundance between adjacent mangrove and scrub habitats in Jamaica, Marra and his colleagues showed that birds in food-rich mangrove habitats were more aggressive toward simulated intrusions of their home range than were birds in comparatively food-poor scrub habitat (Marra 2000, Marra and Holmes 2001), and this habitat use had implications for body condition (Marra and Holberton 1998) and timing of spring departure (Studds and Marra 2005) that carried over and influenced breeding success (Norris et al. 2004).

Like the mangrove–scrub system, tropical shade-coffee farms also have strong contrasts in food supply, but over a much finer spatial grain, offering an opportunity for examination of fine-scale variation in aggressive behaviors within a home range. The understory of a shade-coffee farm is composed nearly entirely of *Coffea arabica*, which has chemically well-defended foliage and corresponding low biomass of insects (Perfecto et al. 1996, Johnson 2000b). In contrast, the shade-tree canopy, which can be composed of one to many tree species and range in cover from 10% to nearly 100% depending on the farm's management (Moguel and Toledo 1999), often supports much greater biomass of insects and provides sources of nectar and fruit (Johnson 2000b). In addition, because many coffee farms are small, irregularly shaped, and embedded within heterogeneous landscapes (Perfecto and Armbrrecht 2003), farm–forest ecotones are prominent, and many birds have home ranges that encompass areas of cultivated and uncultivated space. The Black-throated Blue Warbler (*Setophaga caerulescens*) is among the most abundant parulid warblers on Caribbean coffee farms (Wunderle and Waide 1993) and varies considerably in territoriality, making it a useful focal species for studies of aggressive behavior.

In this study, we examined variation in aggressive behaviors of the Black-throated Blue Warbler in Jamaican shade coffee farms by measuring birds' responses to a simulated intrusion of their home ranges by a conspecific. As noted above, previous work suggests that variation in aggression may be caused by a number of factors, including an individual bird's attributes (e.g., body size, age, sex), spatial factors (e.g., territory size, position of intruder relative to territory center), interactions with neighbors, and variation in food supply or other resources within a territory. Therefore, we incorporated these and habitat type as covariates into multivariate linear models to explain variation in aggression, with a special

emphasis on examining how birds' responses to intruders differed in the coffee-crop layer, shade-tree layer, and forest habitat within a home range.

METHODS

We conducted experiments at the Kew Park (18° 16' N, 77° 04' W) and Seven Rivers coffee farms (18° 20' N, 77° 55' W) in Westmoreland and St. James parishes, Jamaica, from 15 December 2009 to 25 January 2010. Kew Park farm consists of 18 ha of coffee, with an overstory of shade trees, bordered by dense second-growth tropical forest and pasturelands, interspersed with larger clumps of trees. Shade trees were primarily *Inga vera* but also included *Swietenia mahogoni*, *Cedrela odorata*, *Ceiba pentandra*, and fruit trees such as *Mangifera indica* and *Ficus* spp.). Seven Rivers farm (56 ha) is bordered by second-growth forests, with several rivers and adjacent riparian strips running through cultivated areas with widely spaced shade trees over the coffee. Most shade trees were *Inga vera*, though *Leucaena glauca*, *Blighia sapida*, and *Cocos nucifera* were also present; some areas also had high densities of banana plants (*Musa* spp.).

The Black-throated Blue Warbler is among the most abundant parulids in coffee farms in the Caribbean (Wunderle and Waide 1993) and has been reported to hold nonbreeding territories with some spatial overlap, especially between the sexes (Holmes et al. 1989, Wunderle 1995). Fidelity to winter sites is high (Holmes and Sherry 1992), but some birds "wander" and do not appear to defend strictly delineated territories (Wunderle and Latta 2000). Therefore, for purposes of this analysis, we use the term home range to describe an individual warbler's use of space on a coffee farm.

We presented simulated intrusions of the home range to 20 Black-throated Blue Warblers (10 on each farm). We selected these birds randomly by dividing each farm into five or six strata roughly equal in size, distributing 8–12 12-m mist nets within each stratum and opening nets for approximately 6 hr or until two Black-throated Blue Warblers per stratum were captured, banded, and fitted with radio transmitters. Random bird sampling yielded an uneven sex ratio, with 16 males and four females, reflecting the male-biased sex ratio in shade coffee (Wunderle and Latta 2000).

Using criteria from Pyle (1997) and molt limits in the alula, we aged warblers as either hatch year/second year (hatched in 2009) or after hatch year/after second year (hatched 2008 or earlier). For each bird we recorded wing chord (mean \pm 1 SE: 64.1 \pm 0.5 mm), weight (9.3 \pm 0.1 g), and length of white wing patch (9.4 \pm 0.9 mm) and scored visible subcutaneous fat as none (0; n = 9 birds), trace (1, fat not forming a solid layer at furcula; n = 10), or more (2; n = 1). We attached radio transmitters (0.36 g, model LB-2N, Holohil Systems, Ltd.) to birds \geq 8.4 g with eyelash adhesive (DUO, American International Industries, USA) to a small patch of skin on the bird's back we clipped free of feathers. Birds were

also fitted with a U.S. Geological Survey aluminum band and two colored bands to enable visual identification of individuals. We did not track warblers the day of capture to allow them time to adjust to the transmitter. For the next 6–8 days, we relocated each bird 3–7 times per day (≥ 45 min between successive locations) in daylight hours. We relocated the birds via radio telemetry by using either visual sightings of color bands or short-range biangulations (accurate to within 10 m²) to mark locations. At least 40 locations were taken per bird used in this analysis; home range sizes stabilized after 25 locations (Campos, unpubl. data). We estimated home-range size as the 95% volume contour fixed-kernel home range by using least-squares cross-validation to determine the bandwidths of kernel home ranges. We defined a home range's centroid as the 10% volume contour of kernel home ranges. We used Home Range Tools version 1.1 (Rodgers et al. 2007) in ArcGIS version 9.3 (ESRI, Redlands, CA) to generate all home ranges.

We simulated intrusions of home ranges by presenting a mounted male Black-throated Blue Warbler as a decoy and broadcasting 10 min of Black-throated Blue Warbler vocalizations (played from a 2-W speaker as loud as possible without distortion; 20 sec of chips and 15 sec of song, interspersed with 10-sec pauses between repetitions). Although chips are the most common vocalization made by warblers during the winter, using songs and chips can produce stronger and more consistent responses (Holmes et al. 1989, Marra 2000). We presented each individual bird this simulated intrusion once in three habitats—coffee, shade-tree, and forest—in a random order. We defined coffee habitat as an area within rows of cultivated coffee, >10 m from any patch of trees >25 m² and >8 m tall, shade-tree habitat as a tree >8 m overhanging coffee habitat and located >10 m from any patch of trees >25 m², forest habitat as a patch of trees or contiguous forest at least 100 m² and >8 m tall. We positioned the simulated intruder at least 5 m from the coffee's edge. Each decoy was positioned as close to the center of the target bird's home range (centroid) as possible. However, meeting criteria for habitat patches described above necessitated positioning the decoy at various distances from the centroid, so we included this variable (measured with ArcGIS) as a covariate in analyses. The mean distance from the decoy to the centroid was 19.3 m (± 2.2 SE; $n = 60$), and all but 10 playbacks were within the core of the target bird's home range (75% contour of kernel home range).

In the coffee and forest habitats, we affixed the decoy to a wooden perch wired to a conspicuous twig at 2–3 m; in the shade-tree habitat we raised it into the subcanopy on a 7-m bamboo pole. Time constraints prohibited an experiment in both the understory (3 m) and subcanopy (7 m) in the forest. We chose to use the understory height in the trials in the forest for three reasons. First, we were interested primarily in contrasting birds' aggressive behaviors in coffee versus the other habitats, so placing the decoy at the same height as in coffee facilitated that comparison (the shade-tree layer, by definition, must be located higher than the coffee layer). Second, in this study area, the forest's

vegetation structure from 3 to 7 m is relatively similar (Johnson 1999). Third, observations of foraging Black-throated Blue Warblers in these forests suggest they forage most frequently in the understory (Brian Robinson, unpubl. data).

We presented each bird with one simulated intrusion per day, between 06:45 and 10:30 under sunny or foggy conditions, usually completing all three presentations to that bird within 4 consecutive days. Some simulated intrusions were located within hearing distance of others conducted that day, creating the potential for habituation to the decoy. However, an ANOVA of aggression scores (see below for explanation of scores) showed there was no effect of treatment order on aggression scores over time ($F_{2,57} = 0.52$, $P = 0.59$), indicating individuals did not habituate or grow more aggressive with more exposure to playbacks.

Two observers monitored responses to the simulated intrusions from a distance of >13 m, using binoculars and telemetry to locate, identify, and monitor the movements of responding birds. To record a narration of events and their times we used a voice recorder (all narration by C. Smith to avoid observer variation), noting time spent within 5 m of the decoy, time spent within 20 m (used to calculate proportion of time spent within 5 m), time of first approach to within 5 m (no response yielded the maximum value of 10 min), and closest distance (m) of approach to the decoy. All times were measured in decimal minutes. In addition, we categorized each bird's response as "no response" (spent <20 sec within 20 m of decoy), "chipping response" (defined as chipping or giving "teak" contact calls for $\geq 50\%$ of its time within 20 m of decoy), or "silent response" (defined as no detectable vocalizations $>75\%$ of its time within 20 m of the decoy). On the basis of initial analyses, we coded these categories as 1, 2, or 3 from least to most aggressive, respectively (see first paragraph of Results for empirical justification).

During the trials, we also observed nontarget birds that responded, recording their number and sex, arrival time, time spent within 5 m of the decoy, and whether they occupied a position closer to the decoy than did the target bird. Nontarget birds were present during 45 of 60 trials, reflecting both the high density of Black-throated Blue Warblers and significant overlap of their home ranges in Jamaican shade-coffee habitat. If a nontarget bird occupied a position closer to the decoy while the target bird was present, spent more time within 5 m of decoy than did the target bird, or if only a nontarget bird responded to the playback (i.e., target bird stayed ≥ 20 m away), we categorized the trial as "dominated" by the nontarget bird. Fifteen of 60 trials were dominated by a nontarget bird, and we used this binary variable (dominated by nontarget bird or not) in the analyses.

Following Johnson (2000a), we estimated the biomass of arthropods at the site of each trial with five branch-clip samples. Branches were quickly enclosed in a cloth pillowcase fitted with a drawstring (on 7-m poles for shade-tree samples), clipped, shaken to dislodge all arthropods into the pillowcase, and weighed. We recorded the number and

length of individuals of each order of arthropod and checked branches for arthropods not dislodged. We estimated biomass from Johnson and Strong's (2000) length–weight regressions for foliage-dwelling arthropods in Jamaica, expressing it as milligrams per gram of clipped and sampled branch. We subtracted the biomass of ants from the total, as we never observed ants being eaten by Black-throated Blue Warblers and the literature suggests they do not eat ants (Holmes et al. 2005), though results were similar if ants were included in analyses (M. Johnson unpubl. data). Fruit can make up a small proportion of the Black-throated Blue Warbler's diet in winter (~16%, Wunderle 1995), but we observed very little foraging on fruit during our study (<5% of observations; B. Robinson, unpubl. data), so we report arthropod abundance as an index of food supply.

STATISTICAL ANALYSES

We used a principal components analysis (PCA) to obtain a single aggression score based on five variables (time to first approach, time within 5 m of decoy, proportional time within 5 m, distance of closest approach [ln-transformed to meet normality], and the coded response variable [1,2,3]). We used scores of each simulated intrusion for the first component of this PCA as aggression scores for further analyses; they were normally distributed (see Results for loadings and other details).

To obtain a measure of bird size potentially useful for explaining variation in aggression scores, we ran a second PCA on morphometric data: wing chord (mm), weight (g), white wing patch (mm), and fat score, then used the first component of this PCA as a composite measure of bird size (see Results for loadings and other details).

To examine variation in territorial aggression, we created generalized linear models to predict aggression score and used Akaike's information criterion scores, modified for small sample sizes (AIC_c), to select top models that balanced explanatory power and parsimony (Burnham and Anderson 2002). Following Anderson et al. (2000), we generated a priori hypothesized models that we expected could best explain the variation in aggression scores. We used each variable

individually and in biologically plausible additive combinations; the variables were sex (binary), age (binary), whether a nontarget bird dominated the trial (binary), habitat (three categories), bird size (continuous, from the PCA), territory size (in m^2), distance of playback to center of territory (in m, ln-transformed to meet normality), insect biomass (in mg per g clipped vegetation, ln-transformed to meet normality). We did not run models containing both habitat and arthropod biomass, since these variables proved to be strongly linked (see Results). Mixed models using bird identity as a random/blocked effect required additional parameters that rendered these models uncompetitive, so we restricted our candidate set of models to those without the individual bird's identity. To limit the number of candidate models, and because our sample size was relatively low, we emphasized models containing five or fewer predictor variables, although we did run two global models (one with habitat and the other six variables, the other with arthropod biomass and the other six variables). In total, there were 55 candidate models. We considered models within two points of the lowest AIC_c score competitive, and parameter coefficients and standard errors were model-averaged accordingly (Burnham and Anderson 2002). We used analysis of variance (ANOVA) to compare continuous behavioral response variables by the categorical responses of no response, chipping, and silent and to compare arthropod biomass by habitat (coffee, shade-tree, or forest).

RESULTS

PCA OF AGGRESSION AND BIRD SIZE

Before running a principal components analysis to yield a composite aggression score, we first tested for differences in the continuous response variables by categorical response types (no response, chipping, or silent). Mean values associated with a high level of aggression (e.g., high value for time within 5 m, low value for closest approach) were strongest for silent responses, intermediate for chipping responses, and weakest for no responses, and all variables were all statistically different among response categories (Table 1). Additionally, the four

TABLE 1. Behavioral responses (mean \pm 1 SE) of Black-throated Blue Warblers to simulated intrusions of their home ranges in Jamaican shade-coffee farms, December–January 2009–2010 ($n = 60$). Behavioral responses differed significantly among three responses categories; ranked in increasing order of aggression: no response, chipping response, and silent response. Means with superscripts of different capital letters were significantly different from each other on the basis of Tukey–Kramer post-hoc tests.

Variable	Response categories			<i>F</i>	df	<i>P</i>
	No response	Chipping response	Silent response			
Time to first approach (min)	9.77 \pm 0.53 ^A	2.43 \pm 0.74 ^B	2.49 \pm 0.46 ^B	45.22	2, 57	<0.001
Time within 5 m (min)	0.03 \pm 0.56 ^A	2.12 \pm 0.77 ^A	5.44 \pm 0.48 ^B	27.35	2, 57	<0.001
Proportion of time within 5 m	<0.01 \pm 0.01 ^A	0.27 \pm 0.08 ^B	0.70 \pm 0.05 ^C	34.94	2, 57	<0.001
Closest approach (m) ^a	31.81 \pm 3.18 ^A	5.35 \pm 4.40 ^B	2.15 \pm 2.76 ^B	64.17	2, 57	<0.001

^aData were ln-transformed to be normalized for ANOVA; untransformed mean and SE are shown.

TABLE 2. Factor loadings on the first principal component used as a score of aggression in behavioral responses of Black-throated Blue Warblers to simulated intrusions of their home ranges in Jamaican shade-coffee plantations, December–January 2009–2010 ($n = 60$).

Variable	Loading	Eigenvector
Ordinal response category	0.88	0.44
Time of first approach (min)	-0.82	-0.41
Time spent within 5 m (min)	0.92	0.46
Proportion of time within 5 m	0.92	0.46
(ln) Closest approach (m)	-0.95	-0.47
Variation explained (%)	80.76	

most aggressive birds, which landed on the decoy and pecked it, all approached the decoy silently and stayed silent the entire time before and after landing on it. We also observed that closest approaches to the decoy were nearly always made when birds were silent, and several times we observed birds chipping at a distance for several minutes, then falling silent and approaching suddenly much closer to the decoy. Holmes et al. (2005) also reported the Black-throated Blue Warbler’s most serious form of aggression (physical contact) as being silent. Therefore, we felt confident enough to use values of 1, 2, and 3 to indicate increasing aggression for no response, chipping, and silent responses, respectively, in subsequent analyses.

The first component of the PCA involving behavioral variables explained 81% of variation in aggressive behaviors. Each of the five variables contributed, with eigenvector values between 0.41 and 0.47, and the sign of loadings matched what would be expected with increasing aggression (Table 2). In further analyses we used the scores for this first component as a composite measure of territorial aggression.

The first component of the PCA involving morphometric variables explained 52.2% of variation. Each of the variables was positively loaded with the first component (Table 3). We used the scores for this first component as a composite measure of bird size included it as a predictor variable for variation in aggression scores.

Arthropod biomass in each of the three habitats differed significantly ($F = 17.5$, $df = 2$ and 57 , $P < 0.001$, Tukey post-hoc comparisons), with values highest in shade trees and lowest in coffee (Fig. 1). Because the variables arthropod biomass and habitat were strongly linked, we did not include both variables in the same candidate model for variation in aggression score.

MODELING AGGRESSION

Four top models emerged to explain variation in the aggression of Black-throated Blue Warblers toward a simulated intrusion of their home range, and they converged in five important variables (Table 4). All four top models included home-range size, sex, and whether or not the trial was dominated by a nontarget bird. The combined weights for all models containing these three variables were 0.98, 0.95, and 0.93,

TABLE 3. Factor loadings on the first principal component used to create a covariate of size for analysis of aggression in behavioral responses of Black-throated Blue Warblers to simulated intrusions of their home ranges in Jamaican shade-coffee plantations, December–January 2009–2010 ($n = 20$).

Variable	Loading	Eigenvector
Wing chord	0.86	0.60
Weight	0.77	0.53
White wing patch	0.70	0.49
Fat	0.50	0.35
Variation explained (%)	52.18	

respectively. The top model also included two additional variables: distance to centroid of the home range and habitat; models 2 and 4 each contained one of these additional variables. The combined weight for models containing distance to the home range’s centroid was 0.53; that for models containing habitat was 0.37. Models containing arthropod biomass (a variable similar to habitat) had a combined weight of 0.15, so the weight for models containing either habitat or arthropod biomass was over 50% (0.52). There was comparatively little support for bird size or age as predictors of variation in

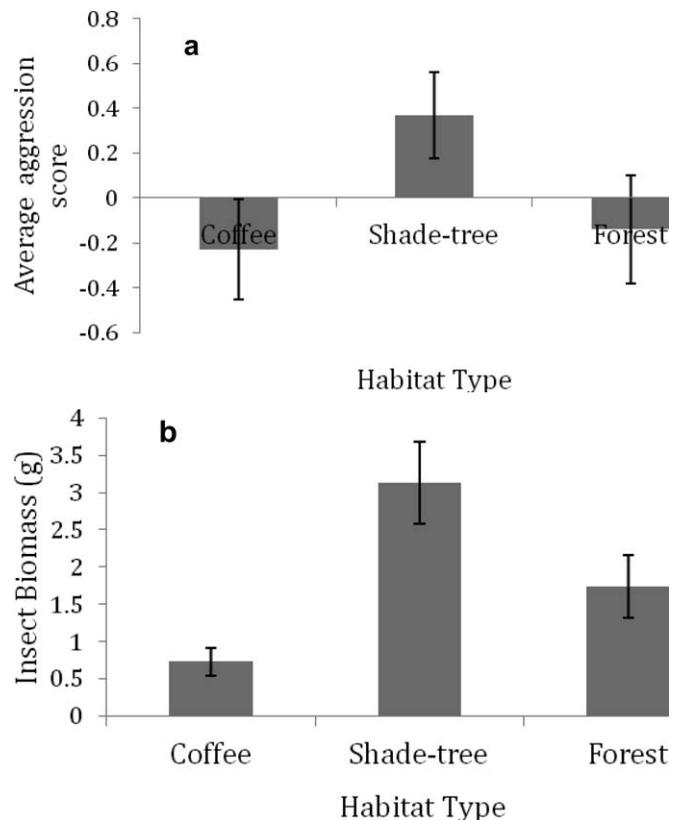


FIGURE 1. (a) Aggression scores and (b) insect biomass (mean \pm 1 SE) in three habitats within Black-throated Blue Warblers’ home ranges in Jamaica shade-coffee farms, 2009–2010.

TABLE 4. Statistics of top four and global models of aggressive responses of Black-throated Blue Warblers to simulated intrusions of their home ranges in Jamaican shade-coffee farms, December–January 2009–2010 ($n = 60$). The variables habitat and arthropod biomass were strongly linked, so global models containing one of these variables were run separately.

Model	K^a	Δ_i	% Deviance explained	w_i
Home-range size + sex + nontarget bird dominated + distance to centroid + habitat	7	0 ^b	47.9	0.17
Home-range size + sex + nontarget bird dominated + distance to centroid	5	0.15	43	0.15
Home-range size + sex + nontarget bird dominated	4	1.17	39.6	0.09
Home-range size + sex + nontarget bird dominated + habitat	6	1.21	44.4	0.09
Global model (all variables) with habitat	9	5.38	48.1	0.018
Global model (all variables) with biomass	8	7.57	43.6	0.006

^aNumber of parameters.

^bMinimum value of $AIC_c = 148.97$.

TABLE 5. Model-averaged parameter coefficients and standard errors for the top four models explaining aggression levels in Black-throated Blue Warblers in Jamaica, 2009–2010. Models within two AIC points of the top model were averaged.

Parameter	β	SE
Intercept	0.810	0.404
Home-range size	6.12×10^{-5}	1.30×10^{-5}
Sex ^a = female	-0.737	0.240
Nontarget bird dominate ^b = no	0.551	0.231
Distance to home range's centroid	-0.150	0.077
Habitat ^c = shade tree	0.205	0.120
Habitat ^c = coffee	-0.065	0.119

^aBinary variable; reference value was for males.

^bBinary variable; reference value was for trials that were dominated by a nontarget bird.

^cVariable with three categories; reference value was for habitat = forest patch.

aggression scores. The global model explained 48% of deviance in the data, while the four top models explained 40–48% of deviance and had a combined AIC_c weight of 0.50 (Table 4).

The signs of the parameter coefficients indicated aggression was negatively associated with home-range size and distance to home-range centroid, and it was positively associated with males and with cases in which a nontarget bird did not dominate the trial. Parameter coefficients indicate that, relative to forest habitat, aggression was greater in shade-tree habitat and less in coffee, and aggression was positively associated with arthropod biomass. None of the model-averaged standard errors for these coefficients overlapped zero except that for coffee habitat (Table 5).

DISCUSSION

Intrinsic factors, such as a bird's age, sex, or size, and extrinsic factors, such as the density of neighbors, abundance of food, or territory size, have been hypothesized to influence the differences in aggression of individual birds (Nowicki et al. 2002, Hyman et al. 2004). On the basis of multivariate

models, our results confirm that multiple variables were associated with aggression in wintering Black-throated Blue Warblers. Sex, home-range size, proximity to home-range center, habitat, food supply, and the presence of another aggressive bird in the area were all significant predictors of aggression. In other species of parulid warblers wintering in the tropics aggression varies within and between species (Greenberg and Salewski 2005), and these factors may also play a role in those systems.

We documented that differences in aggressive responses among habitats *within* an individual bird's home range were associated with local food supply. These findings suggest that Black-throated Blue Warblers recognize variation in food supply within their territories and defend areas of greater value more aggressively. We found the most aggressively defended areas corresponded to shade-tree habitat, which had biomass of arthropods significantly greater than in either the coffee-crop understory or the understory of nearby forest (Fig. 1). Previous research has shown that birds holding territories in different habitats may differ in levels of aggression (e.g., Ekman and Askenmo 1984, Lanyon and Thompson 1986, Silverin 1998, Marra 2000), but we could find no other study showing that individuals vary their aggression within their home range in response to habitat differences.

At our study sites, >50% of all shade trees were *Inga vera*. *Inga* has extrafloral nectaries that attract hosts of ants (Koptur 1984), and it was in fruit while we were sampling, which likely attracted additional insects and increased insect biomass. Johnson and Sherry (2001) found that *Inga*-shaded coffee supported the highest densities of warblers of all habitats surveyed across Jamaica because of its high insect biomass. More generally, the widely acknowledged abundance of warblers in shade-coffee farms may be largely due to the high biomass of insects in the shade trees (Johnson 2000b). Indeed, Wunderle and Latta (1998) found that Black-throated Blue Warblers in shade-grown coffee farms of the Dominican Republic foraged nearly three times more often in *Inga* than in coffee.

We found that sex was a very strong predictor of aggression, with females less aggressive, but all of our simulated

intrusions were with a male decoy, so we cannot determine with our data whether females would have responded more aggressively to a female intruder. Holmes et al. (1989) reported that male and female Black-throated Blue Warblers did not appear to differ in aggression levels but tended to direct their aggression especially to birds of the same sex. We optimized our study design to address variation in habitat, which required three trials per target bird, but this prevented us from testing how a male would respond to a female intruder. Repeating all trials with both a male and a female decoy would have doubled the field effort (six trials per bird) and risked habituation. Additionally, using same-sex decoys (e.g., male decoy only for males) would have confounded the influence of intrinsic (target bird's sex) and extrinsic (intruder's sex) factors. A future study not aimed at habitat variation should address sexual variation in aggression by presenting decoys of both sexes. Our results indicate such work must control or account for other factors that also affect aggression, such as habitat, home-range size, and neighboring birds' behaviors.

Marra (2000) found that aggression of wintering American Redstarts increased with body size and found the largest, most aggressive birds disproportionately in food-rich mangrove habitats. In contrast, we did not find a statistically significant relationship between a bird's size and aggressiveness. This may be partly explained by the relatively modest variation in bird size we observed. In addition, some of the variation correlated with size may have already been explained by the more influential variable sex (since females tend to be smaller than males; Pyle 1997). Nonetheless, large males were among the most aggressive individuals in our study, and aggression scores were statistically the highest in the food-rich canopy layer. Our observations of foraging birds indicated that males foraged disproportionately more in the shade-tree layer whereas females foraged disproportionately more in the coffee understory (B. Robinson, unpubl. data). Together, these results prompt the hypothesis of behavioral dominance manifested between vertical layers of the same overall habitat (shade-coffee farm). This could be an interesting area for further research, especially since the Black-throated Blue Warbler is probably the most important species for delivering ecosystem services of removing insect pests from the coffee understory in Jamaica (Kellermann et al. 2008, Johnson et al. 2010; Sherry et al., unpubl. data). Thus understanding bird behaviors may help reveal farm-management practices that may favor bird foraging within the coffee understory (Railsback and Johnson 2011).

We found a negative relationship between aggression and home range size. Territory size is hypothesized to be most affected by predation pressure (Gill and Wolf 1975), food availability (Gill and Wolfe 1975, Hixon 1980), intruder pressure (i.e., number and effort of competitors attempting to intrude into a territory; Krebs 1971, Ewald et al. 1980, Hixon 1980), or other special habitat requirements such as roosting or loafing sites. Predation of Black-throated Blue Warblers on their winter grounds is likely rare (Holmes et al. 1989). Special

habitat requirements are also unlikely to have a large influence on territory size in our study system; Jirinec et al. (2011) showed that our marked birds often roosted at night outside of their diurnal home ranges, and birds probably have few other special requirements in the nonbreeding season. In our case it is difficult to separate the cause and effect of a high intrusion rate or high food availability on home-range size because these two may be interrelated, and we did not measure food supply on a territory scale. It may be that the most aggressive birds are able to secure and at least partially defend the smallest home ranges richest in food. Alternatively, small food-rich home ranges may suffer from the greatest pressure from intruders and require more aggression to defend. Regardless, in theory the cost of territorial defense rises linearly with perimeter, while the benefits rise as a function of volume (Davies 1980), making the most profitable strategy the defense of the smallest defensible territory that contains sufficient resources (Marshall and Cooper 2004). In our study, this strategy was complicated by incomplete territorial defense (overlapping home ranges) and thus may have been achievable only for the dominant, most aggressive birds who usually excluded others from their home ranges.

Some of our findings suggest important areas for additional research. Our study was aimed at examining, especially, differences in aggression between habitats within birds' home ranges in shade-coffee farms. Therefore, we sampled birds randomly to represent the population on a farm, which resulted in a male-biased sex ratio and limited our ability to examine interactions among aggression, size, and sex. Given the important implications of sexual habitat segregation in other warblers (Marra and Holmes 2001), future work should further examine the behaviors, space use, and body condition of male and female Black-throated Blue Warblers in coffee. In Jamaica, shade coffee is typically a "commercial polyculture" (Moguel and Toledo 1999), which is ecologically noteworthy because it is so conspicuously layered vertically and results in such a strong contrast in food supply between the layers of coffee understory and shade-tree canopy. Field techniques to measure home-range boundaries typically assume a two-dimensional space, but it is certainly possible that birds defend areas of different sizes in the shade and coffee layers (e.g., a home range shaped like a mushroom) and that different habitats may serve different functions (e.g., coffee for shelter and shade trees for foraging). Indeed, given the strong differences in food supply, the economics of profitable territory defense may prescribe different optimal sizes of home ranges in different vertical layers of a shade-coffee farm. Future work should focus on insectivorous birds' three-dimensional space use in coffee.

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