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Sexual habitat segregation in migrant warblers along a shade gradient of Jamaican coffee farms

Aaron B. Spidal[1,2] and Matthew D. Johnson[1,3]

Abstract Shade coffee has been shown to provide wintering habitat for migratory bird species. Canopy cover has been cited as a good indicator of habitat quality on coffee farms. Many species of sexually dimorphic migrant warblers show sexual habitat segregation on their wintering grounds, often related to habitat quality. To test if degree of habitat segregation followed a gradient of habitat quality, we sampled canopy cover and avian communities at nine different sites in coffee farms ranging from full sun to highly shaded. Proportion of all species of wintering warblers that were male was positively correlated with percent canopy cover. Species-specific male proportions of American Redstarts (*Setophaga ruticilla*), Black-throated Blue Warblers (*S. caerulescens*), and Prairie Warblers (*S. discolor*) showed positive correlations with canopy cover, though small sample sizes limited statistical power.

Keywords coffee, habitat quality, habitat segregation, migrants, Neotropics, Parulidae, shade coffee

Resumen Segregación sexual de hábitat en paseriformes migratorios a lo largo de un gradiente de sombra de granjas cafetaleras en Jamaica—Se ha demostrado que el café de sombra brinda un hábitat invernal para las especies de aves migratorias. La cobertura del dosel se ha citado como un buen indicador de la calidad del hábitat en las granjas cafetaleras. Muchas especies de paseriformes migratorios sexualmente dimórficos muestran, en las áreas de invernada, una segregación sexual en el hábitat usualmente relacionada con la calidad del mismo. Para examinar si el grado de segregación del hábitat sigue un gradiente relacionado con su calidad, muestreamos la cobertura del dosel y las comunidades de aves en nuevos sitios diferentes en granjas cafetaleras con una variación de esa cobertura desde totalmente al sol a altamente sombreada. La proporción de individuos de todas las especies de paseriformes migrantes que fueron machos estuvo correlacionada positivamente con el porcentaje de cobertura del dosel. Las proporciones especie-específica de machos de *Setophaga ruticilla*, *S. caerulescens* y *S. discolor* mostraron correlaciones positivas con la cobertura del dosel, a pesar de la potencia estadística limitada por los pequeños tamaños muestrales.

Palabras clave café, café de sombra, calidad de hábitat, migrantes, Neotrópico, Parulidae, segregación de hábitat

Résumé Ségrégation de l'habitat en fonction du sexe chez les parulines migratrices le long d'un gradient d'ombre dans des plantations de café en Jamaïque—Il a été montré que les plantations de café d'ombre fournissent un habitat d'hivernage à certaines espèces d'oiseaux migrateurs. La couverture de la canopée a été reconnue comme un bon indicateur de la qualité de l'habitat dans les plantations de café. De nombreuses espèces de parulines migratrices ayant un dimorphisme sexuel présentent une ségrégation de l'habitat en fonction du sexe dans leurs aires d'hivernage, souvent liée à la qualité de l'habitat. Pour vérifier si ce degré de ségrégation suit le gradient de qualité de l'habitat, nous avons échantillonné la couverture de la canopée et les communautés d'oiseaux des plantations de café sur neuf sites différents allant du plein soleil à des situations très ombragées. La proportion de mâles de l'ensemble des espèces de parulines hivernantes était positivement corrélée au pourcentage de couverture de la canopée. La proportion de mâle, au sein de chaque espèce, était positivement corrélée à la couverture de la canopée pour la Paruline flamboyante (*Setophaga ruticilla*), la Paruline bleue (*S. caerulescens*) et la Paruline des prés (*S. discolor*), bien que la taille réduite des échantillons ait limité la portée statistique de l'analyse.

Mots clés café, café d'ombre, migrateurs, Néotropiques, Parulidae, qualité de l'habitat, ségrégation de l'habitat

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Populations of many species of forest-associated Neotropical migratory birds have declined in the past several decades, prompting concern for human-caused habitat alteration on their breeding and wintering grounds, as well as on their migration routes (Robbins *et al.* 1989, Faaborg 2002, Newton 2004). How-

ever, numerous species appear amenable to habitat modification in tropical agricultural landscapes if farms contain adequate tree cover and are embedded in areas with patches of residual forests (Wunderle and Waide 1993, Petit *et al.* 1995). This is especially apparent in shade coffee farms in the Neotropics, which provide refugia for local biodiversity (Perfecto *et al.* 1996, Jha *et al.* 2014) and habitat for wintering warblers in the family Parulidae (Greenberg *et al.* 1997, Sherry 2000).

Warblers are largely insectivorous (Lack 1976) and can provide a valuable pest-control service for farmers (Greenberg *et al.* 2000, Kellermann *et al.* 2008, Karp *et al.* 2013, Railsback and Johnson 2014). On Jamaican coffee farms, birds have been shown to provide an economic benefit of up to US$310/ha (Johnson *et al.* 2010). Higher quality habitats have been shown to support more birds (Johnson *et al.* 2006), thus potentially providing a greater service to the farmer. Habitat quality in coffee plantations has typically been associated with the extent of canopy cover and other vegetation complexity (Greenberg *et al.* 1997, Tejeda-Cruz and Sutherland 2004), but avian-based characteristics of good habitat in coffee are not well defined (Johnson *et al.* 2006).

Many species of sexually dimorphic migratory parulid warblers display habitat segregation on wintering grounds, with males and older individuals typically occupying higher quality habitats (Lynch *et al.* 1985, Ornat and Greenberg 1990, Marra *et al.* 1993, Wunderle 1995, Marra and Holmes 2001). According to this theory of habitat-mediated behavioral dominance, the age and sex ratios of warblers should vary along a gradient of habitat quality. Coffee farms fall on a gradient from full sun to highly shaded (Moguel and Toledo 1999). Since highly shaded farms have been suggested to contain higher quality habitat, there should be an older or more male-biased population, or both, on these farms than on sun coffee farms. In this study, we tested for this pattern by examining age and sex ratios of migratory warblers along a gradient of canopy cover in Jamaican coffee farms.

Methods

Study Area

Nine study sites were selected from eight different coffee farms in Jamaica, West Indies (Appendix 1). Farms were located in major coffee growing regions across the island. Shade regimes varied from full sun to highly shaded. Two sites were selected on the Baronhall Estate, which is one of the largest plantations on the island and has markedly different shade regimes in different portions of the farm. The two sites on this farm were more than 1 km apart and differed strongly in shade cover. All sites were within 1 km of patches of disturbed second growth forest.

Study sites varied in the presence and abundance of shade trees. Common species of hardwood shade trees included *Inga vera*, *Cedrela odorata*, *Spathodea campanulata*, *Mangifera indica*, *Gliricidia sepium*, and *Leucaena leucocephala*. Most farms also had banana trees (*Musa* sp.) planted sporadically between rows. Coffee trees were generally pruned to stand between 1.8 and 3.0 m tall, with about 1.5 m between rows. Ground cover varied from bare soil to grass to a duff layer. All farms applied the insecticide Suldan (fenitrothion) locally to combat pests, especially the coffee berry borer (*Hypothenemus hampei*). Applications were made during the fruit ripening stages, and no insecticides were applied during our study. Several farms at higher elevations also used copper-based fungicides.

Vegetation and Bird Surveys

Data were collected in late December and January in 2010–2011 and 2011–2012. Canopy cover was quantified using a spherical densiometer (Lemmon 1956), which involves tallying cover from an image of the canopy projected onto a concave mirror. For the 2010–2011 field season, vegetation data were collected at five random locations within each site. For the 2011–2012 season, we sampled vegetation at each net (n = 12–15).

We sampled birds using mist nets (9 or 12 m, 30 mm or 36 mm mesh; n = 12–15) deployed to thoroughly sample 3–5 ha of each coffee farm. Nets were at least 10 m apart and precise locations were chosen to optimize bird capture success. Nets were oriented either parallel or perpendicular to coffee rows. We opened nets shortly after sunrise for at least 5 hr. Nets were operated for three consecutive days at each site, except at Forres Park (two days) and Abbey Greene (three non-consecutive days due to rain). Each bird was batch-marked by clipping about 0.5 cm off of a tail feather. A different tail feather was used for each day, allowing identification of within- and between-day recaptures. We determined age class and sex of migrant warblers based on plumage characteristics (Pyle 1997). We used the term "adult" to describe individuals with plumages indicative of being in Jamaica for their second or later winter (designated as after-hatch-year, AHY, before 1 January or after-second-year, ASY, after 1 January), and we used the term "young" to describe individuals with plumages indicative of being in their first winter in Jamaica (designated as hatch-year, HY, before 1 January or second-year, SY, after 1 January; Pyle 1997).

Analyses

We quantified migrant population structure by calculating the proportion of captured individuals that were males and those that were adult birds. Young male American Redstarts (*Setophaga ruticilla*) exhibit delayed plumage maturation, and like females they are behaviorally subordinate to adult males, so they were grouped with females for analyses (Marra and Holmes 2001). The overall proportion of males for migrant species was obtained at the site level by dividing the total number of males by the total number of sexed birds. For three of the most common wintering migrants on Jamaica (American Redstart, Black-throated Blue Warbler [*S. caerulescens*], and Prairie Warbler [*S. discolor*]), species-specific male proportions were calculated in the same manner. Only farms that had at least three known-sex individuals (of the species in question) were included in the species-specific analysis. We calculated site-level age proportions by dividing the number of adult birds by the total number of birds assigned an age class. We then ran Spearman's rank-order correlations on each of these sex and age proportions with percent canopy cover. We set alpha at 0.10 due to a low sample size (nine sites), which increased chances of making a type 1 (false positive) error, but it decreased the likelihood of making a type 2 (false negative) error and is appropriate given the importance of understanding variation in habitat quality in human disturbed habitat for declining species (Askins *et al.* 1990). One farm, Wallenford, had very few shade trees and

Table 1. Number of migrants captured during 2010–2011 and 2011–2012 winter field seasons at nine coffee farm sites in Jamaica, West Indies. Canopy cover from spherical densiometer also presented.

	Number of Migrant Warblers (Family Parulidae) Captured[a]														
Site	OVEN	WEWA	LOWA	NOWA	BAWW	SWWA	COYE	AMRE	CMWA	NOPA	BTBW	PALW	PRAW	BTNW	% Canopy Cover[b]
Ramble Hill Arnold	2	2	2		2	1		2			9				89.0
Windsor	6	1		1	2		3	2		4	10		1		84.4
Baronhall Shade	2	2			5		9	6		7	11		3		67.8
Whitfield Hall	1	1			1			1			12	1	3		59.8
Abbey Greene	3	6			2	3	2	1	2	2	15		2	2	56.9
Forres Park	4	1			4		2	14		1	6		4		54.3
Ramble Hill Hutchinson	2				2			4			13		2		51.1
Baronhall Sun	1				4			9		2	7	1	7	1	47.1
Wallenford							5	12		5	5	12	13		0.0

[a]OVEN = Ovenbird (*Seiurus aurocapilla*); WEWA = Worm-eating Warbler (*Helmitheros vermivorum*); LOWA = Louisiana Waterthrush (*Parkesia motacilla*); NOWA = Northern Waterthrush (*P. noveboracensis*); BAWW = Black-and-white Warbler (*Mniotilta varia*); SWWA = Swainson's Warbler (*Limnothlypis swainsonii*); COYE = Common Yellowthroat (*Geothlypis trichas*); AMRE = American Redstart (*Setophaga ruticilla*); CMWA = Cape May Warbler (*S. tigrina*); NOPA = Northern Parula (*S. americana*); BTBW = Black-throated Blue Warbler (*S. caerulescens*); PALW = Palm Warbler (*S. palmarum*); PRAW = Prairie Warbler (*S. discolor*); BTNW = Black-throated Green Warbler (*S. virens*).
[b]Windsor, Baronhall Shade, Baronhall Sun, and Wallenford were studied in winter 2011–2012; the other sites were studied in 2010–2011.

scored 0.0% canopy cover with our methods (see Results). This outlier could have a large effect on statistical significance, so we ran the correlation tests with and without this farm included.

Results

Nets were run for 792 net-hours in the 2010–2011 field season and 586 net-hours in 2011–2012, with 298 total captures of 14 species of migratory warblers, of which 216 were assigned a sex. The most common migrant captures were Black-throated Blue Warbler, American Redstart, and Prairie Warbler (Table 1). There were 82 between-day recaptures in 2010–2011 and 33 in 2011–2012; these were excluded from analyses.

Canopy cover varied from 0.0% to 89.0% with a mean of 56.7% (Table 1). Site-level overall proportions of males and adults varied from 0.21 to 0.67 and 0.27 to 0.79, with means of 0.52 and 0.50, respectively (Table 2). The average proportions of Black-throated Blue and Prairie Warblers that were male were 0.54 and 0.86, respectively. Average proportion of adult male American Redstarts was 0.39 (Table 2).

There were no significant correlations between proportion adult migrants and percent canopy cover for any species, nor all species combined (all $r_s < 0.5$, all $p > 0.28$). Across all species, there was a significant correlation between proportion male and percent canopy cover ($r_s = 0.61$, $p = 0.08$, $n = 9$; Fig. 1a). Similarly, the proportion male increased significantly with canopy cover for Black-throated Blue Warbler ($r_s = 0.60$, $p = 0.08$, $n = 9$; Fig. 1b). Correlations between the proportion male and canopy cover were also positive for American Redstart ($r_s = 0.80$, $p = 0.20$, $n = 4$; Fig. 1c) and Prairie Warbler ($r_s = 0.67$, $p = 0.22$, $n = 5$; Fig. 1d), but these relationships were not statistically significant. When

Table 2. Population structure of wintering warblers at nine coffee farm sites in Jamaica, West Indies.

	Proportion Males				
Site	All Species	American Redstart[a]	Black-throated Blue Warbler	Prairie Warbler	Proportion Adult
Ramble Hill Arnold	0.64	1.00[b]	0.75	N/A[b]	0.45
Windsor	0.57	0.00[b]	0.70	1.00[b]	0.42
Baronhall Shade	0.63	0.50	0.55	1.00	0.79
Whitfield Hall	0.67	1.00[b]	0.50	1.00	0.27
Abbey Greene	0.41	N/A[b]	0.36	1.00[b]	0.47
Forres Park	0.64	0.75	0.67	0.67	0.55
Ramble Hill Hutchinson	0.21	0.00[b]	0.73	N/A[b]	0.71
Baronhall Sun	0.53	0.22	0.43	1.00	0.38
Wallenford	0.39	0.08	0.20	0.62	0.43

[a]Proportion of adult males.
[b]Excluded from further analyses due to insufficient sample size.

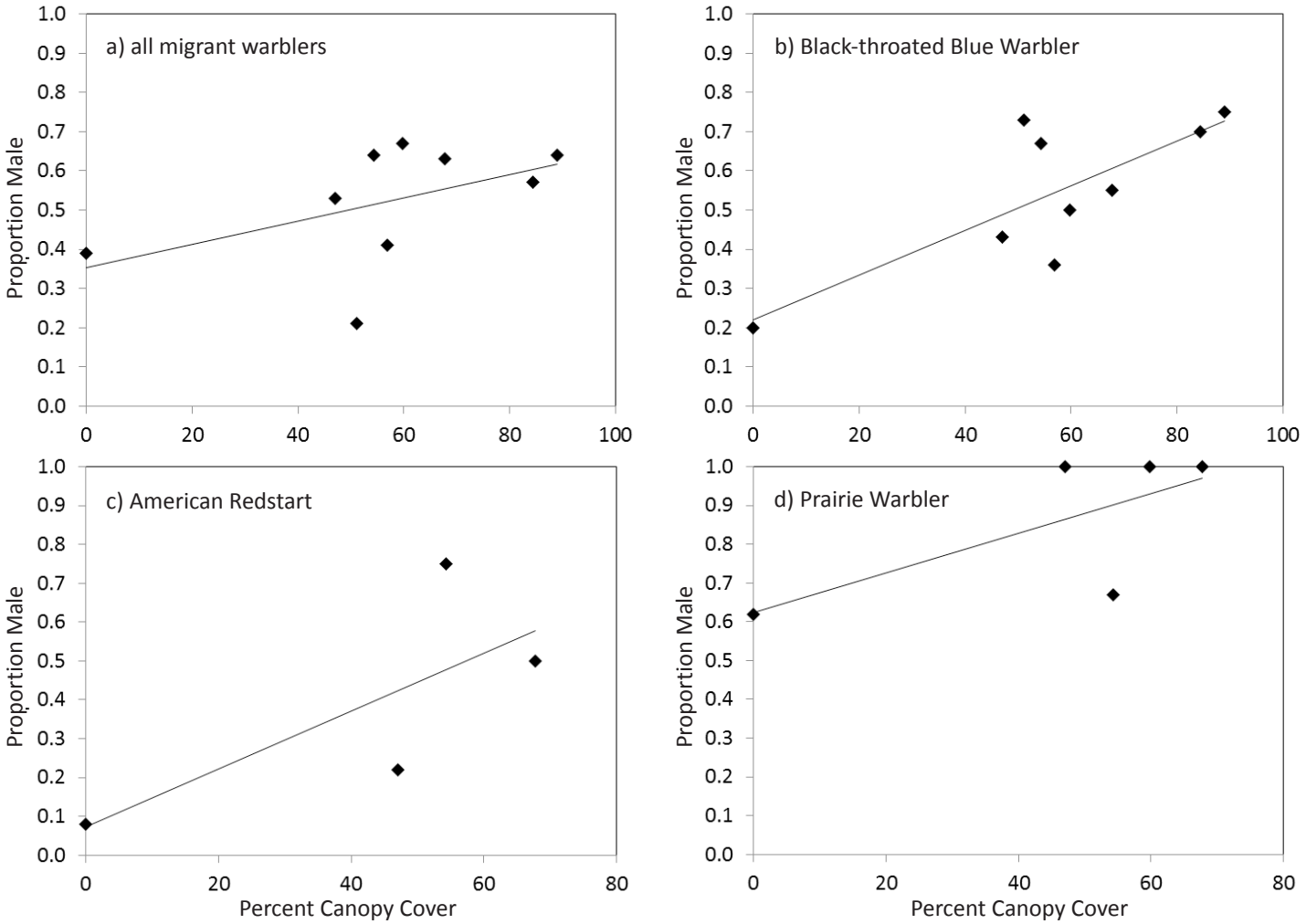

Fig. 1. Associations between shade and sex ratios of (a) all species of migrant warblers, (b) Black-throated Blue Warblers, (c) American Redstarts, (d) and Prairie Warblers on coffee farms in Jamaica, West Indies. Lines indicate linear correlations.

the Wallenford farm was removed from analyses, all regression coefficients remained positive but were lower in magnitude (r_s = 0.49, 0.50, 0.43, and 0.26 for all species, American Redstart, Black-throated Blue Warbler, and Prairie Warbler, respectively), and none of the relationships were statistically significant (all $p > 0.21$).

Discussion

Research on habitat segregation of wintering warblers has focused on highly contrasting habitats (Marra *et al.* 1993, Wunderle 1995, Marra and Holmes 2001, Studds and Marra 2005, Reudink *et al.* 2009). Results presented here are not strong; our small number of study sites limited statistical power, and the small number of individual birds of some species at some sites reduced precision in estimating the proportion male. Nonetheless, the proportions of males of all three species examined (American Redstart, Black-throated Blue Warbler, and Prairie Warbler) appeared to increase with increasing canopy cover, suggesting that segregation may also operate within a single habitat (coffee farms) along a gradient of habitat quality. This may merit further study. The trends we observed were driven especially by the low canopy cover and male proportions at the Wallenford farm, which was nearly a pure sun coffee farm. Future work will benefit from the inclusion of more intermediate canopy cover values, such as between 0 and 40% cover.

Low proportions of males in farms with little shade are consistent with the notion that shade coffee provides better habitat for wintering parulid warblers than does sun coffee (Greenberg *et al.* 1997, Sherry 2000, Tejeda-Cruz and Sutherland 2004). This trend was most conspicuous in American Redstarts and Black-throated Blue Warblers. Behaviorally-mediated sexual habitat segregation can be signaled by plumage variation among dominance classes (Marra and Holmes 2001), so it is interesting to note that the relationship between canopy cover and proportion male was weakest with Prairie Warblers, which are not as drastically dimorphic as either American Redstarts or Black-throated Blue Warblers.

Sexual segregation in wintering warblers has been explained as either an innate difference in habitat preference (Hooded Warblers [*Setophaga citrina*]; Morton 1990) or as the result of competitive exclusion by males for sites of higher quality, such as those with more food (American Redstarts; Marra *et al.* 1993). In coffee farms, food availability for insectivores is significantly higher in the canopy of shade trees than in the coffee shrub

understory (Greenberg *et al.* 1997, Smith *et al.* 2012). Therefore, the patterns of male-biased populations in farms with higher canopy cover is consistent with the hypothesis of behavioral dominance for food-rich sites. Additional behavioral research on whether warblers exhibit vertical stratification within a habitat (canopy versus understory) may further reveal the extent of intersexual aggression.

Regardless of the mechanism, our results suggest that the degree of sex class segregation of migrant warblers can be indicative of habitat quality on Jamaican coffee farms. However, there were myriad other environmental variables we did not include in our analyses that could also affect habitat quality and influence the proportion of males in a migrant population, such as distance to nearby forests, variation in insect abundance owing to differences in coffee shrub or ground cover layer, variation in shade tree species, and so on. Our results are generally consistent with the hypothesis that the proportion male could provide an index of habitat quality for Jamaican coffee farms, but confirmation awaits more controlled studies or experimentation.

Two migrant species (Palm Warbler [*Setophaga palmarum*] and Prairie Warbler) were most abundant at Wallenford, the site with the least shade. This is not surprising as both species are at least moderately specialized for disturbed or early succession scrub-type habitats (Wunderle and Waide 1993), which a sun coffee farm resembles. The second highest number of captures of American Redstart was also at Wallenford; these individuals were overwhelmingly female-type (Table 2). This magnitude of captures was slightly unexpected but other studies have also found large numbers of females in similar habitats (Ornat and Greenberg 1990, Marra and Holmes 2001), which may reflect an alternative strategy for obtaining food, especially for subordinate individuals.

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Appendix 1. Latitude and longitude of study sites (decimal degrees).

Study Site	Latitude (°N)	Longitude (°W)
Ramble Hill Arnold	17.9815	76.6261
Windsor	18.3612	77.6513
Baronhall Shade	18.2014	77.3700
Whitfield Hall	18.0479	76.6185
Abbey Greene	18.0502	76.6155
Forres Park	18.0265	76.6602
Ramble Hill Hutchinson	17.9898	76.6111
Baronhall Sun	18.2173	77.3855
Wallenford	18.0947	76.6901

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