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Habitat selection by an avian predator of insect pests on Jamaican coffee farms

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ABSTRACT

Ecosystem services provided by mobile organisms can be influenced by the availability and vegetative complexity of the habitats those organisms select. On Jamaica's coffee farms, birds assist farmers by consuming the coffee berry borer (*Hypothenemus hampei*), and the Black-throated Blue Warbler (*Setophaga caerulescens*) is a foremost avian predator. Using radio telemetry, we investigated habitat selection of 47 Black-throated Blue Warblers on two coffee farms in Jamaica differing in vegetative complexity during two winter seasons (2008–2009 and 2009–2010). We modeled habitat selection using four variables describing coffee habitat: canopy cover, coffee cover, distance to non-cultivated habitat, and distance to nearest shade tree. Within their home ranges, birds used coffee farm and other habitats similarly at the complex farm but used the farm significantly less at the lower complexity farm. Within coffee farms, birds selected for home ranges with high coffee cover and high canopy cover, with stronger selection at the more complex farm. Within the portions of their home ranges on coffee farms, birds also selected for areas with high canopy cover. In contrast, bird use of the coffee layer itself decreased with increasing canopy cover, dropping from 100% to 30% use of the coffee layer from zero to full canopy cover. Our results suggest that while birds were more likely to use coffee farm habitat with increasing canopy cover, at very high canopy cover birds were less likely to use the coffee crop layer itself, where they could consume the coffee berry borer. In this system, farmers can likely maximize conservation biological control by maintaining high coffee shrub cover and moderate canopy cover. These results suggest an underappreciated reason why mobile organisms may fail to deliver conservation biological control: natural habitat becomes so attractive to pest predators that "spillover" use of crops is reduced.

1. Lay summary

- The coffee berry borer is a major pest in coffee farms, but it can be partially controlled by warblers, including the Black-throated Blue Warbler.
- To provide guidance to coffee farmers on how to reduce this pest naturally, in 2008–2010 we put radio transmitters on 47 Black-throated Blue Warblers to track them and study how they select habitat within coffee farms.

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- We found that warblers used coffee habitat more when farms were more vegetatively complex. Warblers generally used areas within coffee farms with high tree canopy cover shading the coffee and high cover of coffee shrubs; however, their use of the coffee shrub understory decreased in areas with higher shade cover.
- Our results suggest that consumption of the pest by warblers would be maximized in areas of intermediate canopy cover (20–50%), which encourages warblers to use the coffee farm habitat and also to feed within the coffee shrub layer.

2. Introduction

Balancing the production of crops required by a growing human population while minimizing the environmental and social impacts of agricultural intensification, including the use of chemical pesticides, is an enormous conservation challenge (Tilman et al., 2011; Heath and Long, 2019). As an alternative to dependence on chemical pesticides associated with environmental damage and risks to human health (Shields et al., 2019), conservation biological control encompasses a variety of management practices that promote natural pest predators as part of an integrated pest management strategy (Begg et al., 2017; Rayl et al., 2018). Conservation biological control is a complex strategy drawing on a number of ecological and behavioral processes, operating at multiple scales, and mediated by management actions targeting pest organisms and their natural enemies (Ehler, 1998; Heath and Long, 2019). Much of conservation biological control is provisioned by mobile organisms that "spillover" from natural habitats at local and landscape scales (Woodcock et al., 2016). The extent of spillover is governed by the distribution and selection of the habitats used by mobile pest predators (Kremen et al., 2002; Luck et al., 2009; Railsback and Johnson, 2014a; Schellhorn et al., 2014; Tscharntke et al., 2016). For this reason, conservation biological control strategies have relied heavily on the conservation and establishment of beneficial habitats to reverse the negative effects of agricultural intensification on natural pest predators by increasing the quality and diversity of habitat in agricultural landscapes (Shields et al., 2019).

Many bird species are highly mobile predators of insects that readily use coffee farms (Greenberg et al., 1997, Perfecto et al., 2004, Borkhataria et al., 2006, Milligan et al., 2016). In Jamaica, Costa Rica, and Tanzania, researchers have shown that birds boost coffee crop yields by consuming coffee berry borer (*Hypothenemus hampei*; Kellermann et al., 2008, Johnson et al., 2010, Karp et al., 2013, Classen et al., 2014), the most devastating pest of coffee worldwide (Jaramillo et al., 2006; Fotso et al., 2021). If the promotion of natural enemies improves yields and decreases recurring input costs with only modest expenses and small or negligible tradeoffs (Patrick et al., 2009; Buckley et al., 2012; Landis, 2017), farmers may be motivated to conserve the habitats and wildlife on which the pest management services depend (Gatzweiler, 2006; Isaacs et al., 2009; Power, 2010). Wunderle and Latta (2000) documented birds' use of the crop layer (coffee shrubs) vs. the canopy, showing that no species foraged exclusively in coffee, and that food-rich shade trees are likely vital to attract birds that will occasionally feed in coffee, where they might consume pests. Other studies have investigated habitat selection by birds in and around coffee farms (e.g. Bailey and King, 2019; Sánchez-Clavijo et al., 2019), but little of that work has focused on understanding how on-farm vegetation and habitat selection interact to affect foraging by known natural predators within the coffee shrub layer.

In Jamaica, evidence suggests the Black-throated Blue Warbler (*Setophaga caerulescens*) is a primary avian predator of coffee berry borer (Sherry et al., 2016a). The Black-throated Blue Warbler is a Nearctic-Neotropical migrant that overwinters throughout the Greater Antilles (Holmes et al., 2005) and is abundant in the elevation range of coffee cultivation. Throughout their winter range, the diet of Black-throated Blue Warblers is composed predominantly (75–95%) of small arthropods (Lack and Lack, 1972; Wunderle, 1995). A diet analysis of the five most common migrant warblers in a mid-elevation Jamaican coffee farm revealed that coffee berry borer was frequently found in Black-throated Blue Warbler stomach samples (Sherry et al., 2016b). Black-throated Blue Warblers primarily use a leaf gleaning foraging strategy and forage in low vegetation (Lack and Lack, 1972), making them the Jamaican bird most likely to utilize the coffee crop and find coffee berry borer. Additionally, the timing of coffee berry borer infestation and damage to the coffee crop coincides with the time period when warblers overwinter in Jamaica (Johnson et al., 2010), and coffee berry borers exist exclusively in coffee farms (they have no native alternate host plant, Damon, 2000), making this system ideal for examining the habitat selection of a premier natural enemy of an important coffee pest. The coffee berry borer is found only in the coffee layer of coffee farms (Damon, 2000), but birds attracted to shade trees on farms forage in both the canopy and the coffee layer, prompting the need to understand how farm canopy and habitat complexity affect birds' foraging in the coffee crop.

We evaluated habitat selection of Black-throated Blue Warblers on two Jamaican coffee farms to better understand relationships between farm vegetation, habitat selection, spillover from natural habitat, and the birds' use of the coffee crop layer. Specifically, we investigated three questions: (1) Do Black-throated Blue Warblers on coffee farms select areas of coffee cultivation over other habitats in and around the farms? (2) Within coffee farms, what habitat attributes do Black-throated Blue Warblers select? (3) How does use of the coffee crop layer by Black-throated Blue Warblers relate to habitat attributes of coffee farms?

3. Methods

We conducted field work at Kew Park (18 ha; 300 m; 18.260 N, 77.950 'W) and Seven Rivers coffee farms (56 ha; 140 m; 18.335 N, 77.910 W) in Westmoreland and St. James Parishes, Jamaica, over two winter field seasons from Dec–Jan, 2008–2009 and 2009–2010. Kew Park was varied in topography with coffee (*Coffea arabica*) interspersed on gentle slopes. Approximately 70% of the farm was shaded with *Cedrela odorata*, *Swietenia mahagoni*, *Ceiba pentandra*, *Terminalia latifolia*, *Inga vera*, *Mangifera indica*, *Ficus spp.*, and other cultivated fruit trees, typically 8–15 m in height. The farm provided a gradient of full-sun to full-shade coffee. Native forest adjoined most of the farm, with dominant tree species *Bumelia sp.*, *Brosimum alicastrum* and *Calophylum jacquinii*. Pasture and rural housing were present to the north and northwest of the farm. The Seven Rivers farm was situated in a flat alluvial valley with several river channels

intersecting the length of the farm. Forested riparian areas along the channels ranged from 0 to 50 m wide and were composed of various trees and shrubs, especially *Hibiscus elatus*, *Spathodea campanulata*, *Cedrela odorata*, and *Gliricidia sepium*. Over most of the farm area, coffee was grown with banana (*Musa sp.*) and coconut (*Cocos nucifera*) and was shaded by various tree species including *Inga vera*, *Leucaena glauca*, and *Ceiba pentandra*. Canopy cover varied from full-sun to full-shade coffee within the farm. Other habitats adjacent to the farm included pasture, two small citrus and ackee (*Blighia sapida*) orchards, and sparse rural housing. Importantly, both farms were mostly surrounded by forests of similar structure and composition, being characterized by a karst landscape of young-to-moderate-aged second-growth forest and an upper canopy thick with vines. Thus, most differences between the two farms arose from the vegetation composition and complexity within each farm, including the other cultivated crops.

3.1. Capture and tracking

We obtained a random sample of birds by distributing mist nets (12 m × 2.6 m, 30-mm mesh size) in a stratified randomized sampling design on each farm. At Kew Park the netting area was composed of the entire farm in coffee production, both field seasons. At the larger Seven Rivers farm, we captured birds in a northern netting area the first field season and a southern netting area the second field season, covering ~40% of the farm in coffee production. We deployed 10–14 nets for one morning in each of six areas of the farm per season per farm. Each morning we operated nets for six hours or until we radio-marked two birds from each netting area. Netting yielded an uneven sex ratio of captures and radio-marked birds (40 males, 10 females) reflecting the male-biased sex ratio in shade coffee on our study farms, which is consistent with patterns across the Caribbean (Wunderle, 1995, Wunderle and Latta, 2000, Spidal and Johnson, 2016).

We glued radio transmitters (0.36 g, model LB-2 N, Holohil Systems Ltd., Carp, Ontario, Canada) to 50 birds (Kew Park, n = 25; Seven Rivers, n = 25) with eyelash adhesive (DUO, American International Industries, Los Angeles, CA) to a patch of skin on the upper back clipped bare of feathers with scissors. We also equipped radio-marked birds with a standard USGS aluminum band and a unique color-band combination. We determined the age and sex of captured birds using plumage, alula molt limits, and morphometric measurements (Pyle, 1997). All telemetered birds weighed ≥ 8.4 g, such that the transmitter was ≤ 5% of body weight.

We began tracking telemetered birds the day following their capture with three-element Yagi antennas and TRX-2000S (Wildlife Materials, Murphysboro, IL) and R-1000 (Communications Specialists, Orange, CA) receivers. We tracked each bird from sunrise to sunset for 4–10 days between Dec 23 and Jan 25. Locations for an individual bird were taken ≥ 1 h apart to provide biologically independent locations (Lair, 1987). Birds could traverse an entire farm in much less than 1 h and never stayed in the same location for longer than 1 h. We tried to obtain visual confirmation of leg bands on radio-marked birds for all locations, but when this was impossible (21% of all locations) we used the strength of the telemetry signal and homing techniques to approximate the bird's location within a 5 × 5 m area, and used the central point of that area as the location. We recorded bird locations with a hand-held Global Positioning System receiver (Map60Cx or Legend Hcx, Garmin International, Olathe, KS). At all telemetry locations we also noted whether the bird was in the coffee layer or in the canopy layer, using the vertical variation in strength of the radio transmitter signal to determine the vegetative stratum when a visual of the bird could not be obtained.

Each day we cycled through a list of birds, locating each bird multiple times per day. If a bird could not be located, we searched the area off the farm via car and on foot, using all available high-points to locate a bird. We skipped less than 1% of scheduled telemetry locations because a bird could not be found and a bird was never missing for two consecutive scheduled locations. On a few occasions when birds could not be followed off the coffee farm, we bi- or tri-angulated locations, depending on accessibility and terrain. The maximum range of a deployed transmitter's signal was about 500 m.

We estimated bird home ranges using 100% minimum convex polygons (MCP). 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 deployed 50 transmitters in total, 10 on female and 40 on male Black-throated Blue Warblers (Supplementary Material table S1 and S2). We obtained 1–8 locations per bird per day (mean = 4.8) over 4–10 days (mean = 8.4) of tracking, yielding 13–44 locations per bird (mean = 35.7), totaling 1713 locations over the two seasons. We removed two birds from all analyses because they exhibited reduced movement and weak flight following transmitter attachment. In these cases we suspected stress or injury from handling, or faulty transmitter attachment. We removed an additional bird from the analysis because after capture it did not use coffee habitat. Final sample sizes from Kew Park and Seven Rivers were 10 and 13 birds in 2009, respectively, and 12 and 12 in 2010, respectively (n = 47). Nine of the radioed birds were observed shortly following the data-gathering period after the radios lost power; eight of them were confirmed to be without transmitters, suggesting most transmitters fell off prior to the start of the spring migration, about six weeks after data collection.

3.2. Definitions of habitat use and availability

Habitat selection is defined as the use of a habitat component disproportionate to its availability. We employed a used/available study design (Manly et al., 2002; Johnson et al., 2006) to evaluate Black-throated Blue Warbler habitat selection in winter on coffee farms at Johnson's 2nd and 3rd orders (Johnson, 1980): selection of areas for home range establishment and selection of habitat within a home range, respectively. We defined used points as telemetry locations. For second-order selection, we used the distribution of all radio-marked animals per farm-season to define the available area (McClean et al., 1998) with a collective 100% MCP of all telemetry locations. Because we were only interested in within-farm selection at the second order, we then clipped the resulting polygon by the boundary of the coffee farm (Kew Park: 2008–09, 12.89 ha, 2009–10, 10.38 ha; Seven Rivers: 2008–09, 14.90 ha, 2009–10, 8.70 ha). We created available points by distributing sample locations systematically across available areas at 40-m and 30-m spacing in the first and second seasons, respectively (Kew Park: 2008–09, n = 85, 2009–10, n = 104; Seven Rivers: 2008–09, n = 104, 2009–10, n = 83).

For third-order selection, we generated available location by randomly distributing 40 locations within each bird's 100% MCP home range.

3.3. Vegetation measurements

At each used and available location within coffee cultivation, we measured four physiognomic variables of coffee habitat potentially important to Black-throated Blue Warblers that can also be manipulated by coffee farmers (Table 1). We also hypothesized that the differences in vegetative complexity between the farms caused variation in warbler habitat selection. We first examined differences in vegetation variables between farms with a MANOVA, and after finding significance (see results), included farm as a fixed effect in models. No vegetation variables were strongly collinear (all $r^2 < 0.6$), so they were retained for analyses. We made no vegetation measurements outside of coffee cultivation.

3.4. Habitat selection analysis

We used generalized linear mixed models with binomial error and logit link function to compare used (telemetry) and available locations with Resource Selection Functions (RSF; Questions 1 and 2; McDonald et al., 2013), and use and non-use of the coffee layer at telemetry locations with Resource Selection Probability Functions (RSPF; Question 3; Manly et al., 2002). We fitted the regression models using the *glmer* function in the package lme4 version 1.1–26 (Bates et al., 2015) in program R (v. 4.0.2; R Core Team 2018). We included each bird's unique ID as a random intercept (Manly et al., 2002; Gillies et al., 2006; Johnson et al., 2006) to allow for individual variation in a population response and to compensate for unequal sample sizes and autocorrelation (Gillies et al., 2006). We *z*-scored (mean = 0, SD = 1) all covariates prior to modeling. For models of use/availability data (Questions 1 and 2) we used a log link function to back-transform top models for predictions, making the resulting RSF proportional to an RSPF along its entire length (Mcdonald, 2013; Northrup et al., 2022). For models of use/non-use data (Question 3), we used a logit link function to generate predictions (Manly et al., 2002).

For each study question, we crafted a small set of candidate models that reflected plausible hypotheses (Anderson et al., 2008). We considered a quadratic term for canopy cover to allow for selection of intermediate values. We also included an interaction with farm for some habitat covariates because we hypothesized the differences in vegetation complexity between the two farms may lead to different selection patterns; otherwise we emphasized additive models without interactions to keep the number of parameters within recommendations given our sample size. After comparing the candidate models with Akaike's Information Coefficient corrected for small sample size (AICc), we model-averaged coefficients and considered variables important if their model-averaged 95% confidence intervals did not overlap 0.

To investigate Question 1, whether birds selected for coffee relative to other habitats within their home range, we contrasted used and available locations classified as being either inside or outside coffee farm cultivation at Johnson's third order of selection. Sample sizes averaged 37 used (SD = 4.87) and 40 available points per bird.

To investigate Question 2, which habitat features birds selected within coffee farms, we contrasted vegetation measurements at used locations within the coffee farm perimeter (sample size mean = 21, sd = 8.7) to available locations across the entire coffee farm (second-order selection). Because we lacked coffee cover data at used locations for Kew Park in 2009, we first ran the analysis without Kew Park 2009 data. We found coffee cover to be important, so we proceeded without these data. For third-order selection, we contrasted vegetation measurements at used locations within the coffee farm perimeter to available points within each birds' home range. We did not measure coffee cover at third-order available locations, so we did not include it in this analysis. Sample sizes per bird averaged 101 ± 16.7 available and 17.8 ± 9.8 used (± SD) points for second-order selection, and 19.7 ± 9.9 available and 17.8 ± 9.8 used for third-order. Total sample sizes included 4779 and 926 available points for the two analyses respectively and 836 used points.

To investigate Question 3, whether habitat attributes influenced bird use of the coffee crop layer, we contrasted vegetation measurements at telemetry locations within the coffee farm perimeter where birds had been identified as either in the coffee layer or tree canopy above the coffee layer. For this question, we did not hypothesize that distance to non-cultivation or distance to shade tree would be relevant, so they were excluded from candidate models. Because we lacked coffee cover data at used locations for Kew Park in 2009, we first ran the analysis without Kew Park 2009 data. We found no evidence that coffee cover was important in explaining

Table 1
Habitat variables and features measured at each used and available location considered in habitat selection models for Black-throated Blue Warblers from two coffee farms in Jamaica.

Variable	Description
Coffee Cov	Percent coffee cover in 10 m × 10 m area. Estimated visually.
Can Cov	Percent canopy cover of shade trees. Averaged value from four directions using concave densiometer.
Dist Nearest Tree	Distance to the nearest shade tree taller than the coffee layer, measured using a laser rangefinder.
Dist Non-cult	Distance to nearest non-cultivated habitat, defined as a greater than 5 m × 5 m area with elements greater than 8 m tall (Kellermann et al., 2008).
Farm	Categorical for Kew Park or Seven Rivers Farm.
Coffee	Categorical for location in coffee habitat or other habitat (including other cultivation, non-cultivated patches within farms, or adjacent forests). Used in Question 1 only.

variation in use of the coffee layer, so we excluded this variable and fitted the full dataset to the remaining models. Sample sizes averaged 17.8 ± 9.8 locations per bird, totaling 836 observations (n = 47 birds).

All work in this study followed necessary guidelines and relevant laws in the United States and Jamaica, and was permitted by both the US Bird Banding Laboratory and Jamaica's National Environment and Planning Agency. The research was additionally approved by Cal Poly Humboldt's Institutional Animal Care and Use Committee (IACUC # 09/10.W.14. A).

4. Results

The two coffee farms were significantly different in vegetation complexity, with Kew Park (KP) being much more complex than the Seven Rivers farm (SR; MANOVA: Pillai's trace = 0.31, F=32.08, df=4 and 286, P < 0.001). Kew Park had higher mean canopy cover (mean ± s.d KP = 45 ± 30%, SR = 33 ± 24%; F=38.1, df=1 and 289, P < 0.001) and coffee cover (KP = 27 ± 13%, SR = 15 ± 13%; F=42.2, df=1 and 289, P < 0.001), a greater density of shade trees (mean of distance to nearest tree: KP = 4.7 ± 2.9 m, SR = 7.7 ± 5.5 m; F=36.9, df=1 and 289, P < 0.001), and higher density of non-cultivated habitat patches within the farm (mean distance to non-cultivation: KP = 17.1 ± 12.1 m, SR = 26.4 ± 12.1 m; F=34.0, df=1 and 289, P < 0.001).

Question 1. Selection of coffee vs. Other habitats.

At the vegetatively complex Kew Park Farm, Black-throated Blue Warblers selected coffee habitat within their territories with equal probability as other habitats (other cultivation, non-cultivated patches within farms, or adjacent forests). In contrast, birds at Seven Rivers selected other habitats over coffee (Fig. 1, Table 2). Model selection supported two models containing Farm and Coffee habitat, but the interaction between habitat and farm was the only covariate with much support (i.e., 95% confidence intervals did not overlap 0; Supplementary Material Table S3). R^2 values for the top model were 0.0058 marginal (fixed effects) and 0.0058 conditional (fixed and random effects), suggesting that little variation was explained by random effects.

Question 2. Selection of habitat within farms.

At Johnson's (1980) 2nd order of selection, birds selected for high coffee cover and high canopy cover, with stronger selection for these variables at Seven Rivers than at Kew Park (Fig. 2). The top model contained four terms that were important (95% confidence intervals not overlapping zero) including coffee cover, the quadratic term for canopy cover, and the interactions between canopy cover and farm, and between coffee cover and farm (Table 3, Supplementary Material Table S3). The top model had 98% of model weight, so we did not model-average. The scaled coefficients suggested that the interaction between farm and coffee cover had the largest effect size (0.468), followed by coffee cover (0.355), canopy cover and farm interaction (0.30), and the quadratic canopy cover term (0.24; Supplementary Material Table S3). R^2 values for the top model were 0.16 marginal and 0.25 conditional.

At Johnson's (1980) 3rd order of selection, birds selected for canopy cover with different strengths and patterns of selection between the two farms (Table 4). Birds at Kew Park selected for low and high canopy cover over moderate canopy cover, whereas at Seven Rivers, birds selected for high canopy cover, with stronger selection for high canopy cover than at Kew Park (Fig. 3). The only coefficients with 95% confidence intervals that did not overlap zero were for the quadratic term for canopy cover and the interaction between canopy cover and farm (Supplementary Material Table S3). R^2 values for the top model were 0.069 marginal, and 0.113 conditional.

Question 3. Use of the coffee layer.

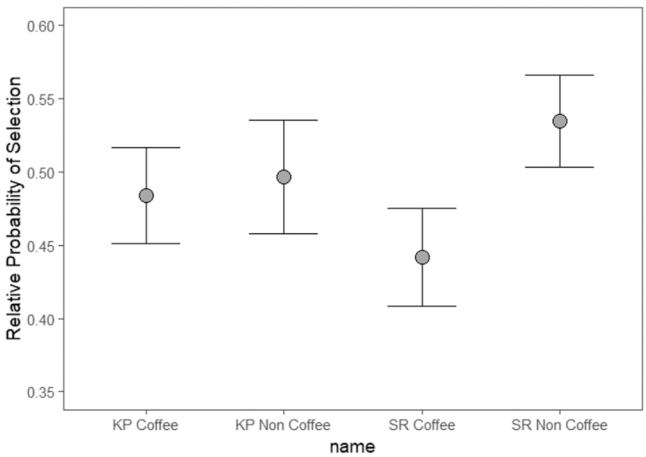

Fig. 1. Habitat selection by Black-throated Blue Warblers for using either cultivated coffee farm habitat or other non-coffee habitats (other cultivation, non-cultivated patches within farms, or adjacent forests) within their territories at the vegetatively complex Kew Park (KP) and the less complex Seven Rivers (SR) farms.

Table 2
Candidate model set and model selection results for Black-throated Blue Warbler habitat selection of coffee habitat relative to other habitats within their home ranges. Abbreviations for covariate names follow descriptions in Table 1.

Model	K	AICc	Δ AICc	AICc Wt	Cum Wt	LL
Farm*Coffee	5	4610.5	0.0	0.65	0.65	-2300.3
Coffee	3	4611.9	1.3	0.34	0.99	-2302.9
Null	2	4620.6	10.0	0	1	-2308.3
Farm	3	4622.5	12.0	0	1	-2308.3

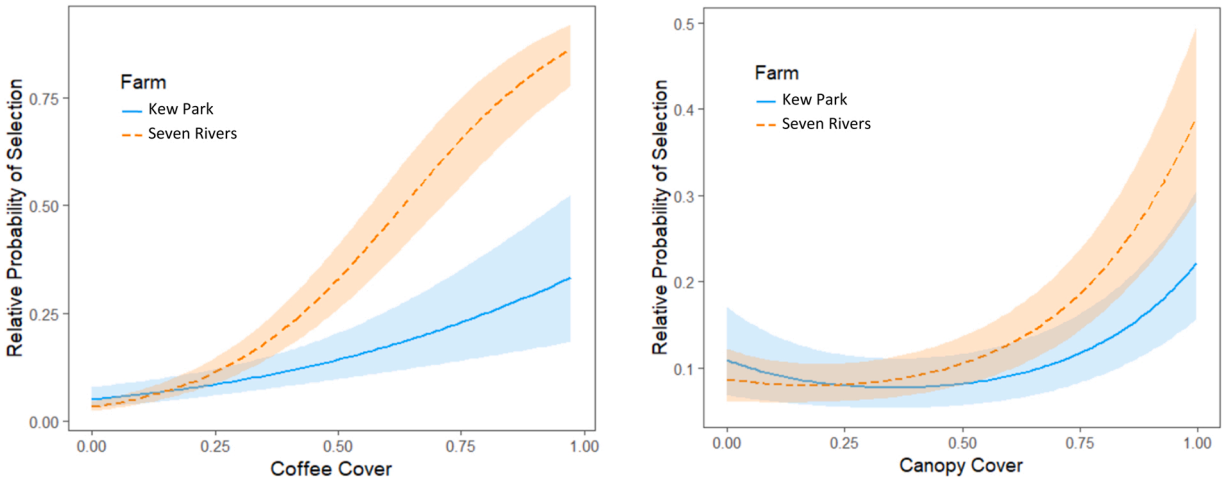

Fig. 2. Habitat selection by Black-throated Blue Warblers at Johnson's (1980) 2nd order of selection at Kew Park (blue lines) and Seven Rivers (orange lines) coffee farms predicted across gradients of coffee cover (left panel) and canopy cover (right panel). Shaded bands represent 95% confidence intervals that include variation from fixed effects.

Table 3
Candidate model set and model selection results for Black-throated Blue Warbler habitat selection of home ranges within coffee farms. Abbreviations for covariate names follow descriptions in Table 1.

Model	K	AICc	Δ AICc	AICc Wt	Cum Wt	LL
Coffee Cov * Farm + Can Cov^2 * Farm	8	3139.9	0	0.98	0.98	-1561.9
Coffee Cov * Farm + Can Cov^2	7	3148.2	8.3	0.02	1	-1567.1
Coffee Cov * Farm	5	3240.1	100.2	0	1	-1615.1
Coffee Cov	3	3260.5	120.6	0	1	-1627.2
Can Cov^2 * Farm	6	3389.6	249.7	0	1	-1688.8
Can Cov^2	4	3399.4	259.5	0	1	-1695.7
Can Cov * Farm	5	3412.2	272.3	0	1	-1701.1
Can Cov	3	3414.8	274.9	0	1	-1704.4
Dist Nearest Tree * Farm	5	3481.1	341.2	0	1	-1735.5
Dist Nearest Tree	3	3500.0	360.1	0	1	-1747.0
Null	2	3502.5	362.6	0	1	-1749.3
Dist Nearest Tree	3	3502.9	363.0	0	1	-1748.4
Dist Nearest Tree * Farm	5	3505.6	365.7	0	1	-1747.8

Warblers were less likely to use the coffee layer with increasing canopy cover when within coffee farm habitat (Fig. 4). Analysis of the first candidate model set did not support the inclusion of coffee cover in the models for the subset of birds including these data, so we dropped this variable and included data from all birds. The model with canopy cover had 61% of the model weight; no other model was competitive (Supplementary Material Table S3). R^2 values for the top model were 0.31 marginal and 0.52 conditional. Birds within coffee habitat at the two farms used the coffee layer in similar proportions (0.66 at Kew Park with 235 observations, 0.72 at Seven Rivers with 385 observations).

5. Discussion

Overall, results from this study confirm that coffee farm managers can generally provide habitats attractive to these pest-eating birds by maintaining a vegetatively complex farm, including increasing canopy cover and the density of the coffee crop layer. For

Table 4
Candidate model set and model selection results for Black-throated Blue Warbler habitat selection within their home range within a coffee farm. Abbreviations for covariate names follow descriptions in Table 1.

Model	K	AICc	Δ AICc	AICc Wt	Cum Wt	LL
Dist Tree + Can Covˆ2 * Farm	7	2356.7	0	0.66	0.66	-1171.3
Can Covˆ2 * Farm	6	2358.0	1.3	0.34	1	-1173.0
Can Covˆ2	4	2373.9	17.3	0	1	-1183.0
Can Cov * Farm	5	2392.7	36.0	0	1	-1191.3
Can Cov	3	2403.3	46.6	0	1	-1198.6
Dist Nearest Tree	3	2418.2	61.5	0	1	-1206.1
Dist Nearest Tree * Farm	5	2418.6	61.9	0	1	-1204.3
Null	2	2432.7	76.0	0	1	-1214.3
Dist Non-cult * Farm	5	2432.8	76.1	0	1	-1211.4
Dist Non-cult	3	2433.6	76.9	0	1	-1213.8

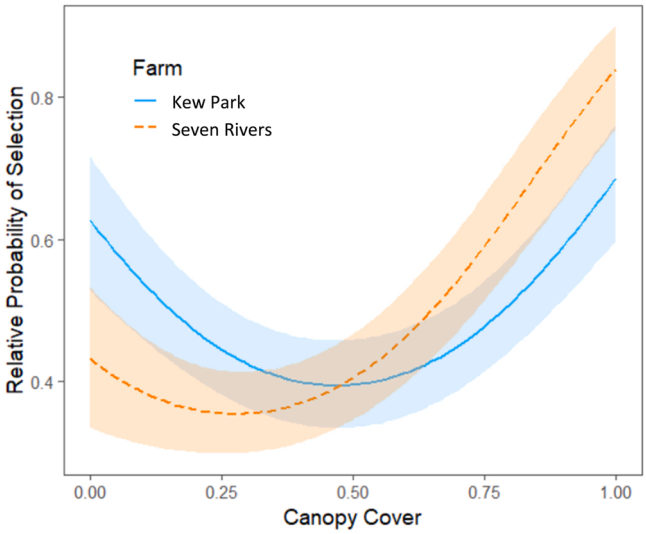

Fig. 3. Habitat selection within territories (Johnson's [1980] 3rd order) of Black-throated Blue Warbler when foraging within the coffee farms, predicted across a gradient of canopy cover. Blue lines represent a vegetatively complex farm (Kew Park) and orange lines a less complex farm (Seven Rivers), with shaded bands representing respective 95% confidence intervals that include variation from fixed effects.

example, we found that Black-throated Blue Warblers used coffee and forest habitats in proportion to their availability at the vegetatively complex Kew Park farm, whereas they disproportionately selected forested habitat (i.e., avoided coffee habitat) at the less complex Seven Rivers coffee farm (Fig. 1). This finding has the important conservation implication that trees and forest patches that contribute to farm complexity and biodiversity conservation also favor use of coffee habitat by insectivorous birds, where they may provide pest removal services (Johnson and Railsback 2014). Our study did not include full sun-coffee farms, but other work indicates Black-throated Blue Warblers can be common even in farms with almost no tree cover (Wunderle and Latta, 1996). In addition, birds within coffee farms chose to place their territories (2nd order selection) in areas with high coffee cover, especially at the less vegetatively complex farm (Fig. 2). Birds also selected areas with high canopy cover at both the complex and less complex farms (Fig. 2). Similarly, Black-throated Blue Warblers selected areas within their territories (3rd order selection) that had high canopy cover, especially at the less complex Seven Rivers Farm (Fig. 3). Although within-territory habitat selection at both farms appeared to rise at very low canopy cover values (<15%), these low values are not common on heavily shade coffee farms such as our vegetatively complex farm, Kew Park. These findings are consistent with general patterns of farm heterogeneity and complexity favoring biodiversity and biological control (Östman et al., 2001; Benton et al., 2003). Farmers in our study area are likely to maximize warbler's use of coffee farms by maintaining more complex vegetation and structure within their farms. Shade coffee farms exist on a gradient of vegetative complexity throughout Latin America and Africa (Komar, 2006; Hernández-Martínez et al., 2009; Buechley et al., 2015; Smith et al., 2015), and these results likely have implications for other regions.

Birds' selection for high canopy cover is likely attributable to the abundance of food resources provided by the overstory shade trees (Greenberg et al., 2000; Johnson, 2000; Smith et al., 2012). Black-throated Blue Warblers' selection for areas of high coffee cover may reflect habitat preferences from the breeding grounds, where the density of understory shrubs and deciduous leaves in the understory are strong predictors of territory quality for this species (Holmes et al., 1996; Rodenhouse et al., 2003). Thus, it is likely that the selection for coffee cover is not specifically for foraging opportunities on coffee shrubs, which harbor low insect abundances (Greenberg et al., 2000; Johnson, 2000), but rather for the density of woody understory vegetation 0–4 m from the ground.

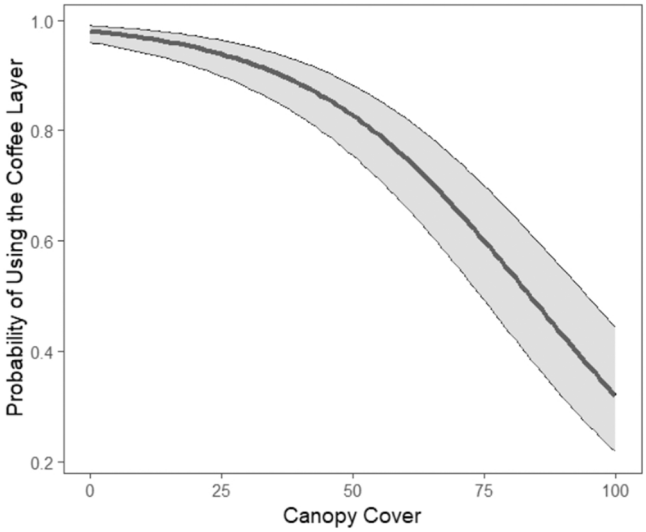

Fig. 4. The probability of a warbler foraging in the coffee layer rather than shade trees overhead as a function of the proportion of canopy cover over the coffee layer. The thick line represents the mean response and the shaded band represents the 95% confidence interval.

The probability a bird was found in the coffee layer was most attributable to canopy cover; rates did not vary strongly between farms or with varying coffee cover. Specifically, the probability of a Black-throated Blue Warbler occurring in the coffee layer, rather than in a shade tree or embedded patch of vegetation, declined sharply with increasing canopy cover (Fig. 4). This could be because the birds prefer to forage in the canopy due to its high insect availability. Smith et al. (2012) showed that insect abundance is higher in shade tree canopy than in coffee shrubs, and warblers' appear to be able to track insect abundance in the non-breeding season (Johnson and Sherry, 2001), so they may avoid the understory in places where canopy cover is high and they have the option of foraging in it. In coffee farms, the insect community is composed of relatively rare crop pests such as coffee berry borer and coffee leaf miner (*Leucoptera coffeella*), among more abundant non-pest insects (Johnson et al., 2009). This creates conditions whereby insect-rich natural habitats can hold natural enemies and potentially facilitate their spillover into crop areas (Railsback and Johnson, 2011). However, it should be noted that our sampling design yielded an uneven sex ratio of tagged warblers, and some work has suggested differences in foraging tactics of male and female Black-throated Blue Warblers (Holmes et al., 1989; Smith et al., 2012). Understanding if one sex contributed more to insect predation in the coffee layer, and possibly pest control, more than the other remains unresolved.

5.1. Tradeoffs in on-farm practices to encourage conservation biological control

Taken together, our results suggest an important trade-off for the management of conservation biological control in this system: shade trees and on-farm vegetation can favor Black-throated Blue Warblers on coffee farms, but where these attributes are abundant within a farm, these natural enemies of coffee pests foraged less in the comparatively insect-poor crop layer (Figs. 3 and 4). Tscharntke et al. (2016) identified five hypotheses for why natural habitat may fail to enhance biological pest control: (1) natural habitat can fail to enhance biocontrol and may even enhance pests; (2) pest populations may have no effective natural enemies in the region; (3) cropland may be more important for biocontrol than natural habitat; (4) intensive agricultural practices can override benefits from natural habitat; and (5) multiple mechanisms from local to landscape scales underlie high biocontrol variation. including. Our results suggest a sixth hypothesis: the relationship between natural enemies foraging in crop habitats may be mediated by natural habitat, such that an abundance of natural habitat may be so attractive to natural enemies that spillover use of crops is reduced. In other words, intermediate amounts of on-farm natural habitat may present a optimum scenario that amplifies the foraging of natural enemies within the crop. On one end, farms with too little natural habitat may fail to attract many natural enemies, whereas on the other end, birds on farms with too much insect-rich natural habitat may only rarely hunt within the crop. This hypothesis is analogous to the intermediate landscape-complexity hypothesis (Tscharntke et al., 2005a,2005b, 2012; Kleijn et al., 2011), which posits that local conservation efforts on farms, such as inclusion of hedgerows, will have less effect on biological pest control in very homogenous or very heterogeneous landscapes (Jonsson et al., 2015; Heath and Long, 2019). The interpretation of our results extends that hypothesis to a local scale operating vertically between the canopy and understory layer via individual birds' patterns of habitat selection within a farm boundary. Managing for natural enemies on-farm also requires consideration of the conservation of the habitats natural enemies use off-farm. In this system, farms are embedded in a matrix of other agriculture and second-growth native forest that Black-throated Blue Warblers used on average 43–50% of the time diurnally and 80–81% of the time nocturnally for roosting (Jirinec et al., 2011).

Multiple other tradeoffs and benefits related to shade trees on coffee farms exist that require evaluation by farmers when deciding on shade coverage (Beer, 1987; Beer et al., 1997). Conservation of natural habitat may preempt some space otherwise devoted to crops, and in the case of coffee, excessive shade (>50%) can curtail fruit yield, at least over the short term (Beer et al., 1998; Soto-Pinto et al., 2000). In some cases, certified shade coffee can fetch higher prices due to consumers' demand for environmental practices

(Hernandez-Aguilera et al., 2019) or improved coffee quality (Da Silva Neto et al., 2018). Thus, the amount of conserved natural habitat within a farm to optimize total saleable yield is a complex function of multiple factors including the coffee berry production, price, and number of natural enemies (Perfecto et al., 2004; Hernandez-Aguilera et al., 2019), as well as pollination services by bees favored by natural habitat and income from non-coffee farm products (Olschewski et al., 2007; Atallah et al., 2018; Davis et al., 2019). This study adds the habitat-dependent foraging behavior of individual birds to that list. Indeed, when Railsback and Johnson (2014b) used empirical data (including the habitat selection findings of this study) to parameterize an agent-based model for this Jamaican system (Railsback and Johnson, 2011), they found that coffee production showed a humped relationship peaking at intermediate values of percent cover of tree patches and shade in the system (59% of the parameter combinations predicted the highest production at 20% shade coffee). Similarly, work by Atallah et al. (2018) for Colombian coffee, Soto-Pinto et al. (2000) in Chiapas, and Hernandez-Aguilera et al. (2019) who modeled farms in Colombia, Mexico, and Peru, all suggest intermediate levels of shade are optimal (20–50%).

In contrast, biological control likely increases consistently with increasing coffee cover in this system. Thus, from a yield and bird-use perspective, increasing the density of the coffee crop layer is a win-win situation – both coffee yields and bird use are maximized by increasing the coverage of the coffee crop. However, creating a dense monoculture in the understory could have implications for other economically beneficial organisms and reduce biodiversity (Philpott et al., 2008), and it may promote fungal pests (Beer et al., 1998). It is likely that Black-throated Blue Warblers would respond to increasing cover of native understory shrubs, not just coffee, which was the only shrub present within coffee inside our study area.

5.2. Management considerations and future research

While increasing the availability of the habitat attributes favored by pest-eating birds should promote their use of a coffee farm, there are tradeoffs farm managers must consider in managing shade trees and coffee cover on their farms. As mentioned above, increased coffee shrub cover is predicted to benefit crop production and biological pest control, though excessive coffee density could encourage detrimental fungi (Johnson et al., 2009). In contrast, Soto-Pinto et al. (2000) found no relationship between shade cover and coffee leaf rust fungus (*Hemileia vastatrix*), suggesting tree cover favorable to avian predators of coffee berry borer may not increase fungal load. In this system, intermediate levels of shade tree cover are predicted to optimize fruit yield and pest control. The economics of this optimum however, could be strongly influenced by the species of shade trees selected. Some shade tree species harbor more insect prey than others, which would likely influence shade optima. For example *Inga vera* was present as a shade tree on both of our study farms and is known to have abundant (non-pest) insects at certain times (Johnson, 2000); in general native tree species are hypothesized to be beneficial to insect-eating birds and the delivery of pest control (Narango et al., 2019; Kammerichs-Berke et al., 2022). In addition, some shade trees offer supplementary income either as timber (e.g. *Grivelia* sp.) or the production of fruit (Davis et al., 2019), and the value gained by increased cover of these trees could offset impacts to coffee yield or reductions in bird foraging in the coffee layer. Likewise the potential for payments from carbon sequestration (Peeters et al., 2003) and benefits to soil fertility (Nesper et al., 2019) may vary among shade tree species. Recent work suggests shade trees may help maintain favorable temperatures in the face of global climate change (Rahn et al., 2018) and certain tree species may outperform others in this service (Kammerichs-Berke et al., 2022). Future research should continue to examine the relative benefits of using shade trees for coffee crop production and maintenance of ecosystem services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02479.

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