Original Research Article

Habitat selection and habitat quality for wintering wood thrushes in a coffee growing region in Honduras

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ABSTRACT

Most Neotropical migrant birds spend the majority of the annual cycle in the tropics, and the continued population declines of some species is attributed at least in part to habitat degradation and destruction on the tropical wintering grounds. Many Neotropical migrants have been observed to use a range of disturbed, agricultural, and primary forest habitats on the wintering grounds, and this habitat-use information helps us better understand the potential effects of land use in the tropics on their populations as well as to develop programs and strategies to conserve these species. Although indices and estimates of habitat-specific abundance can be informative, some wintering migrants are reported to occur in similar or even greater numbers in marginal habitats due to despotic interactions with conspecifics. Thus, investigations of habitat-specific survival and other metrics potentially related to survival are a valuable supplement, and provide a more refined indicator of habitat quality. The wood thrush is a Neotropical migrant bird that has been undergoing range-wide population declines for the past half century or more, and although their numbers appear to be greater in disturbed habitats on the wintering grounds, they are reported to experience higher survival in primary forest. We captured and tracked wintering wood thrushes with radio-telemetry in a coffee growing region in Honduras, Central America, to evaluate habitat selection in this species, as well as to determine the habitat types and microhabitat characteristics associated with survival, movement metrics, and body condition. We found that wood thrushes preferred heavily-shaded coffee over forest and open agricultural habitats, although the probability of survival and of exhibiting stationary behavior was lower in heavily-shaded coffee compared to forest, especially at higher elevations. Our findings illustrate the hazards in assuming the presence of a species in a given habitat actually reflects habitat quality, as well as the importance of conserving forest within coffee producing landscapes.

1. Introduction

Neotropical migratory bird populations may be disproportionately vulnerable to habitat modification on their wintering grounds, where bird densities are as much as eight times higher than on the breeding grounds (Terborgh, 1980, La Sorte et al., 2017). The wood thrush (*Hylocichla mustelina*) is a Neotropical migratory bird species of high conservation concern which is

listed as "Near Threatened" by the IUCN as a result of severe population declines over the past several decades (BirdLife International, 2017). Wood thrushes spend over half of the annual cycle in the wintering grounds (Stutchbury et al., 2009), and recent analyses by Rushing et al. (2016) confirm earlier reports (FAO, 2010) of extensive conversion of forest to agricultural or other uses throughout Central America. Although the relative impact of winter habitat loss on wood thrush populations is debated, it appears it has at least contributed to recent declines in some breeding populations (Rushing et al., 2016, Taylor and Stutchbury, 2015).

Human-dominated landscapes converted from native forest encompass a range of vegetation conditions differing in structure and composition as well as area and juxtaposition, and these habitats are occupied by a variety of bird species (Petit et al., 1999; Daily et al., 2001; Mendenhall et al., 2016). Understanding the habitat associations of species is important to understanding their vulnerability and developing conservation strategies (Petit and Petit, 2003; Chandler and King, 2011). Some wintering migrants, like the Golden-cheeked warbler (*Setophaga chrysoparia*) are habitat specialists occupying only a narrow range of ecological conditions (Rappole et al., 1999) making it relatively straightforward to generate specific guidelines for conserving and managing habitats (King et al., 2012). In contrast, wood thrushes are reported to use a range of habitats in the wintering grounds, including closed canopy primary forest as well as second growth and agroforestry habitats (Blake and Loiselle, 1992a; Greenberg, 1992; Lynch, 1992; Petit et al., 1992; Powell et al., 1992; Rappole et al., 1992), making the generation of conservation guidelines based on habitat associations more challenging.

In the case of breeding birds, researchers have long expressed concerns about whether habitat-specific abundance reflects habitat quality based on reports that birds still may occupy or may even be more abundant in marginal habitats in which breeding success is depressed, such as forest fragments (Gibbs and Faaborg, 1990; Robinson, 1992, Pidgeon et al., 2003). The use of abundance estimates as an indicator of winter habitat quality for wood thrushes is similarly suspect, in that abundance of this species is reported to be higher in disturbed sites compared to intact forest (Winker et al., 1995), yet survival and persistence of this species is lower in disturbed forest relative to primary forest (Rappole et al., 1989; Winker et al., 1990). For this reason, the inclusion of habitat-specific survival is a valuable supplement to abundance estimates in studies directed at understanding habitat quality. Furthermore, observations by other researchers that wood thrushes wintering in Mexico typically exhibit sedentary behavior in primary forests, habitats in which they also experience higher survival compared to secondary habitats (Rappole et al., 1989), has lead others to suggest movement metrics such as sedentariness and home range size could be potential correlates of habitat quality (Winker et al., 1995; Peele et al., 2015). We captured and tracked wintering wood thrushes with radio-telemetry in order to evaluate whether winter habitat selection by this species corresponded to habitat quality, since wood thrush abundance appears to be decoupled from overwinter survival in at least some situations. We incorporated a suite of habitat quality metrics, including habitat selection and habitat-specific survival, site persistence, home-range size, and condition (Winker et al., 1995; Johnson, 2007). Information on wood thrush habitat quality will facilitate conservation by guiding the development of habitat conservation plans, and will also inform broader population modeling efforts by characterizing the response of wood thrushes to winter habitat destruction and degradation (Taylor and Stutchbury, 2015).

2. Methods

2.1. Study area

Our study area was located in the northern interior of Honduras, Central America, entirely within the Department of Yoro and to the southwest of the city of Subirana (15.20^0 N, →87.45^0 W). The area is sparsely populated and mountainous, with elevations ranging from 850 m to 1300 m and lower elevations characterized by pine oak forest and higher elevations giving way to humid broadleaf forest. Coffee is a major source of income for the region, especially for land holders at mid- and upper elevations, with small-scale commercial and subsistence agriculture at lower elevations. Remotely-sensed data for our region (Duarte n.d.) indicates that less than a third of the study area consists of native primary and secondary forest, with the remainder consisting primarily of coffee farms.

We captured wood thrushes at 12 sites across an approximately 45 km^2 study area. Nine sites were coffee farms ranging from "rustic coffee" with coffee planted under native forest to "traditional polyculture" with coffee planted under native and introduced trees, citrus and bananas (Moguel and Toledo, 1999). The remainder of the sites were humid forest, including a lowland riparian forest regenerated from coffee, a highland broadleaf forest relatively free of disturbance, and a selectively logged highland broadleaf forest. All sites were embedded within a landscape of pasture, other coffee farms, broadleaf and mixed forest, and at lower elevations, pine and pine-oak forest.

2.2. Capture and tracking

We captured wood thrushes using fixed arrays of 10−15 12-m mist nets during two winter seasons, 6 January − 4 March 2012 and 10 January to 22 February 2013. Nets were operated at least 2 consecutive days per site each season. All captured wood thrushes were banded with a numbered aluminum band and a unique color combination of three plastic bands. When possible, birds were aged as ASY and SY using the shape of rectrices and primaries and the color of wing coverts (Pyle, 1997). Subcutaneous fat scores (0−5), tail length, wing chord, and mass were also measured for each individual (Salewski et al., 2009). The residuals of mass regressed against tail length was selected as an index of condition (Conway et al., 1994). A

single retrix was collected for genetic determination of sex (Chin et al., 2014), however feather specimens were accidently destroyed during processing. A 0.5-g radio transmitter (<2% of body mass; Blackburn Transmitters, Nacogdoches, TX) with a 16-cm antenna of thin, flexible wire was attached to the lower back of each wood thrush secured with leg loops made of a thin elastic string (Rappole and Tipton, 1991). Radios had a battery life of c. 60 days, and we found these units had a range of 500−2000 m by an observer standing on the ground, depending on vegetation and topography. After banding and radio transmitter attachment, birds were released and observed for an additional 15 min to verify that the harness did not restrict movement.

We tracked wood thrushes on foot using handheld VHF receivers and three-element Yagi antennas. Each individual was typically located once or twice each week for the life of the transmitter. Locations were determined using a combination of homing and triangulation (White and Garrott, 2012). Since bird movements are often influenced by the approach of observers and visual confirmation of individuals is not always possible in dense vegetation, GPS points and bearings were collected during pursuit to triangulate locations. At least three points and bearings were recorded on approach towards a target wood thrush. Special effort was made to record GPS points and signal bearings from a variety of angles to minimize error in the resulting triangulation location. One or more GPS points collected for triangulation calculations were typically within a maximum of 20 m of the target individual. For individuals that could not be located, searches were conducted periodically from surrounding promontories for the rest of the duration of the field season. Program Location of a Signal (LOAS, 2010) was used to triangulate GPS waypoints and associated bearings to the target wood thrush. Within the LOAS software, Andrews maximum likelihood estimation was used to calculate triangulated locations since it automatically removes aberrant combinations of bearings (White and Garrott, 2012). If triangulated locations and visually verified homing locations were both available for a single tracking attempt, the triangulated location was dropped. Standard maximum likelihood or biangulation were occasionally used to triangulate locations if the Andrews method failed to converge. Triangulated points were screened for outliers and locations were removed if field notes and GPS tracks did not provide support for the estimated location.

2.3. Habitat measurements

Vegetation structure and composition were quantified on 5 m radius circular plots located at three randomly-selected telemetry locations per individual. Diameter of breast height (dbh) was measured for all trees >8 cm dbh on each plot, and the number of shrubs, (woody stems ≤2.5 cm dbh) and saplings (woody stems >2.5−8 cm dbh) were counted. Vertical structure of the understory (0−1 m) and subcanopy (1−3 m) was measured as the sum of the number of contacts with a pole held vertically at 20 points placed along four 5-m transects radiating in the cardinal directions from the center of each plot. We also identified the type of understory and subcanopy vegetation at each of the 20 points per plot as coffee, woody vegetation (non-coffee), ferns, forbs, grass, vines, and heliconia-like vegetation. Leaf litter depth was measured with a ruler at four points, 1 m in each cardinal direction from the center of each survey site. Since tree size is reported to influence wintering wood thrush habitat selection (Winker et al., 1990) we merged tree diameter measurements into three groups, small (>2.5−8 cm dbh), medium (>8−27 cm dbh), and large (27−50 + cm dbh), in order to reflect the contribution of trees of different sizes to the overall basal area at a site. Basal area was estimated for each size class category using the median dbh value for each class.

Landcover classes were obtained from an existing GIS layer for Honduras derived from high resolution satellite imagery captured primarily in 2013 and interpreted and ground-validated by Duarte (n.d.). The following habitat classes were present within our study area: secondary vegetation, which appears to encompass both young secondary forest and brushy regrowth, open habitats consisting of pasture and crops, humid broadleaf forest consisting of advanced second growth forest and selectively logged and pristine primary forest, heavily shaded coffee, lightly-shaded coffee, and open coffee. Ground truthing by our team revealed that shade coffee is not reliably distinguished from forest and other cover types at our sites, so we manually digitized cover types within home ranges of radio tagged wood thrushes using ArcMap 10.3 (ESRI, 2011), which resulted in the re-classification of several forest cover types as coffee. We refer to areas that were planted with coffee but originally misclassified as "humid broadleaf forest" as "heavily shaded coffee". These sites were characterized by a relatively closed, dense canopy and tall trees, and in our judgement encompassed "rustic" and "traditional polyculture" coffee (Moguel and Toledo, 1999). We refer to coffee that was originally classified as "humid secondary vegetation" as "lightly-shaded coffee", which was characterized by relatively low stature and less dense canopy and likely included "commercial polyculture" and "shaded monoculture" (Moguel and Toledo, 1999). Finally, we referred to coffee originally classified as pasture, crops, and dispersed trees as "open coffee", which encompasses "unshaded monoculture" (Moguel and Toledo, 1999), but also coffee with sparse and scattered shade trees. In addition to classifying these cover types within wood thrush home ranges, we defined "edge habitat" as the area within 20 m of habitat class boundaries.

2.4. Survival, home range, and movement

Survival rates were calculated using the R package SURVIVAL (version 2.39-2, Therneau, 2013). Kaplan-Meier survival curves for the entire study population were calculated using the survfit function. Kaplan-Meier estimates allow for integration of right-censored data, such as individuals that disappear from the study site (Kaplan and Meier, 1958; Krebs, 1989). Only individuals that were dead when located were assigned as mortalities, and these data were censored at the midpoint between the final and previous locations (White and Garrott, 2012). Wood thrushes that could not be re-located within the

minimum expected lifetime of the transmitters were believed to be transients that permanently emigrated from the study site.

Home-ranges were estimated to establish areas occupied by wood thrushes for the purposes of characterizing habitat use (above), as well as to provide a supplemental indicator of habitat quality. We assumed that home range size would be inversely related to habitat quality since presumably individuals in better habitat are able to acquire sufficient resources in a smaller area (Smith and Shugart, 1987). Both capture locations and telemetry locations were used to estimate home-range. The locations of depredated individuals were not included since they may have been relocated by the predator. All locations were separated by at least 2 h, and 95% of points were recorded at least one day apart (mean = 4 days). Birds with fewer than 5 locations were excluded from the analyses, which is below generally recommended sample sizes for home range estimation (Seaman et al., 1999).

Least-squares cross-validation (LSCV) was used to calculate home-ranges with the adehabitatHR package in R (version 0.4.13; Calenge, 2006). LSCV was selected as the most suitable kernel bandwidth estimator based on its ability to generate comparable results across all individuals, mainly by accommodating multiple centers of activity for many of the non-territorial individuals. The contours from the resulting LSCV utilization distributions (UDs) were used in analysis. To identify the core home-range contour, total area was graphed for each wood thrush across contour values of 5%−95% to identify a common inflection point (Harris et al., 1990). A 70% contour captured the core home-range for all individuals and a visual review of the home-ranges showed that this value also maintained separation between disjoint centers of activity. Disjoint centers of activity are common for non-sedentary individuals, underscoring the need for an estimator and contour capable of identifying them (Harris et al., 1990).

In addition to survival and home-range size, we considered a number of movement metrics as supplemental indicators of habitat quality. Previous studies have shown that wood thrushes wintering in Mexico typically exhibit sedentary behavior in primary forests, habitats in which they also experience higher survival compared to secondary habitats, where they more often adopt a "wandering" movement pattern and are subject to higher mortality (Rappole et al., 1989). Thus, we also considered stationary behavior as an indicator of higher habitat quality and wandering behavior as an indicator of lower habitat quality, as suggested by Winker et al. (1995). Previous studies have used movement distance and patterns of movement relative to a capture location or center of activity to distinguish between sedentary and non-sedentary individuals (Rappole et al., 1989; Winker et al., 1990; Roberts, 2007). We used the R package rhr (version 1.2.906, Signer et al., 2015) to calculate mean squared distance (MSD) from the center of activity based on the 70% kernels, and a linearity index (LI) as a metric to quantify the degree to which each individual tended to return towards the center of activity (Spencer et al., 1990). The metrics were then compared to 1000 MSD and LI values generated from random, bootstrapped samples of movement distances and angles for each individual. If the actual MSD and LI values appeared within the lower 10% of bootstrapped values, we considered that an indicator of restricted movement around a center of activity, and the individual was considered sedentary. Observed values above the 10% threshold were assigned a wanderer pattern, consistent with more linear movements away from a single center of activity.

Upon examination of the data it became evident that in addition to sedentary and wandering birds, there were a substantial number of individuals that did not remain in the study area but instead exhibited rapid, direct, long-range movements away from the point of capture and out of range of our telemetry equipment, and we considered them separately as "transients" since their distinctive movement patterns may reflect habitat quality (Winker et al., 1995). Movements of transients were clearly straight-line movements, or nearly so, and were not restricted around a center of activity, so we could not meaningfully calculate the same movement metrics used to discriminate between sedentary individuals and wandering individuals that were not transients.

Compositional analysis (Aebischer et al., 1993) was used to evaluate habitat selection among land classes using R package adehabitat HS (version 0.3.12; Calenge, 2011). Habitat availability was calculated for each wood thrush using the 95% contour of the LSCV home-range and use was determined from all point locations. Compositional analysis generates a ranked list of selected habitat and identifies significant levels of selectivity between any two habitat classes using the individual wood thrush as the sampling unit. This analysis generates both positive associations, which are interpreted as selection, and negative associations, which are interpreted as avoidance.

The relationships between survival and these habitat variables were conducted using the R package COXME (version 2.2−5, Therneau, 2012). The COXME function was selected to identify factors important to wood thrush survival using hazard ratios, exp(B) (Murray, 2006). Since the data for transients posed the same challenges as right-censored survival data, transience rates were calculated using the same process as survival, and COXME was used to model the relationship between transience and explanatory variables. In both survival and transient models, a positive parameter estimate indicates an increase in survival or likelihood of leaving the study site.

The relationships between wanderer status and home-range area with habitat class and microhabitat variables were modeled using generalized linear mixed models (GLMMs) in R package 'lme4' (Bates et al., 2015). A gamma distributed GLMM with logit link was selected to model 100% MCP home-range area, based on diagnostic quantile-quantile plots. Wanderer status was modeled using a binomial GLMM. Sedentary individuals were assigned a response variable value of zero while individuals displaying a wanderer pattern were assigned a one. Positive parameter estimates for the wanderer model indicate a positive correlation with a wanderer movement pattern.

Survival, movement metrics and home range size were analyzed relative to habitat class and microhabitat variables using mixed-effects models with site as a random-effect to account for non-independence of multiple birds within sites. Candidate

habitat class variables included the percent of locations within each major habitat class, percent of wood thrush locations within the coffee-vegetation edge zone, the percent of wood thrush locations within the forest-open edge zone, elevation, and all interactions between habitat class and elevation. Candidate microhabitat variables included leaf litter depth, vertical structure counts within the ground cover and subcanopy strata, percent cover coffee, and basal area for small, medium, and large size classes. Predictor variables were tested for collinearity, and a forward, stepwise model selection process using Akaike's Information Criterion (AIC) was conducted to identify models that best explained variation in each of the four habitat quality metrics; survival, wandering, transience and home range size). Models with $\Delta AIC \leq 2$ were considered to have a substantial level of support (Burnham and Anderson, 2002: 170), and individual variables within models evaluated based on AIC compatible 85% confidence intervals (Arnold, 2010).

3. Results

Forty-six wood thrushes were captured during the study period, of which 44% were ASYs, 50% were SYs, and 6% were not clearly classifiable by age. A total of 432 locations were recorded for tagged wood thrushes, which were tracked for 33 days, on average (range = 1−70 days). One-hundred-seventy locations were visual, 199 were obtained through triangulation, and the remainder were capture locations. An average of 10.6 points were recorded per individual (SE = 0.56). There was no correlation between number of locations and home range size (r = 0.17, P = 0.21).

Compared to bootstrapped permutations of movement distances and angles for each individual, 21 wood thrushes (45.7%) had Mean Squared Distance (MSD) and/or Linear Index (LI) values within the lower 10% of bootstrapped values, indicating sedentary movement patterns. In contrast, 15 individuals (32.6%) had MSD and/or LI values greater than 10% of bootstrapped values, indicating they were wanderers. The remaining 10 individuals (21.7%) were classified as transients. LSCV (95%) for all birds combined averaged 2.92 (SE = 0.59), 1.44 ha for sedentary individuals (SE = 0.22), and 3.95 ha for wanderers (SE = 0.47). Mean squared distance (MSD) values for tagged wood thrushes averaged 4764 m (SE = 10.4). The maximum distance moved from the site of capture by each of 46 individuals averaged 181.7 m (SD = 4.85).

Heavily-shaded coffee, lightly-shaded coffee and open coffee comprised 32.8%, 12.1% and 2.19% of area within wood thrush home ranges in our study area, respectively. The remainder consisted of humid secondary vegetation (26.4%), humid broadleaf forest (13.9%), pasture and crops (10.9%) and other habitats (1.71%). Most wood thrush relocations were in heavily-shaded coffee (41.2%), followed by lightly-shaded coffee (22.0%), secondary vegetation (21.3%), humid forest (9.49%), open coffee (2.31%), pasture/open (1.62%) and other habitats (2.08%). Compositional analysis indicated a significant level of habitat selection among habitat classes located within the 95% contour of all wood thrush home-ranges ($\lambda = 0.5$, P = 0.01). Wood thrushes showed a significant level of preference for all coffee classes compared to humid and secondary vegetation, and all coffee and forest habitats were preferred over pasture and open habitats (Table 1; $P < 0.05$).

A total of 6 individuals died during the tracking period, 1 in 2012 and 5 in 2013. Predation was the likely cause of death for all individuals, feathers were the only remains found at the sites of recovered transmitters, with the addition of cleanly severed legs at one location. The overall daily survival rate for all wood thrushes for all years was 0.995 (SE = 0.001), which corresponds to a 0.471 probability of a wood thrush surviving the 150 day winter season. Use of secondary vegetation, heavily-shaded coffee and coffee edge were negatively associated with wood thrush survival (Table 2). Survival increased with elevation, except perhaps for heavily-shaded coffee in which mortality increased with elevation, as indicated by a weakly supported negative interaction term. Ground cover structure and basal area of medium trees were negatively associated with survival (Table 3). Survival did not differ between sedentary and non-sedentary individuals (wanderers and transients combined; $P > 0.05$).

No land cover or habitat variables were associated with the probability of an individual exhibiting a wandering movement pattern (Table 2). Use of secondary vegetation, heavily shaded coffee, pasture and cropland, and coffee-forest edge were positively associated with transience (Table 2). Increased litter depth and basal area of small and medium trees decreased the likelihood of transience (Table 3). In many cases transients began making pronounced directional movements prior to loss of signal, and in no case did an individual maintain a stable home-range and then suddenly disappear.

Although the top model for home range included humid forest, open coffee, lightly-shaded coffee, and interactions between elevation and lightly-shaded and open coffee and elevation and humid forest, a competitive model ($\Delta AIC = 0.3$)

Table 1

Ranking matrix comparing proportional habitat use within home ranges with available habitat types of 46 radio-tagged wood thrush tracked in Honduras during 2012 and 2013. Plus signs indicate a positive deviation from random use, minus signs a negative one. A triple sign indicates a significant deviation from random use at $P < 0.05$, and "Rank" refers to the number of habitats of lower rank. Thus, higher ranks indicate habitats that are more preferred over others.

	Forest	Secondary vegetation	Heavily-shaded coffee	Lightly-shaded coffee	Open coffee	Pasture and crops	Rank
Forest	0	-	—	—	—	+++	1
Secondary Vegetation	+	0	—	—	—	+++	2
Heavily-shaded Coffee	+++	+++	0	+	+++	+++	5
Lightly-shaded Coffee	+++	+++	-	0	+	+++	4
Open Coffee	+++	+++	—	-	0	+++	3
Pasture/Open	—	—	—	—	—	0	0

Table 2

Output of top models of demographic parameters (SE in parentheses) as a function of habitat class and elevation for 46 radio-tagged wood thrush tracked in Honduras during 2012 and 2013. Only habitat classes associated with demographic parameters are presented. Coefficients for which 85% confidence intervals do not include zero are in bold type. "Wanderer" status was unrelated to any of the habitat classes. Only a single model was within 2 ΔAIC of the best model in all cases except for "home range".

Parameter	Secondary vegetation	Heavily-shaded coffee	Pasture and crops	Coffee edge	Elevation	Heavily-shaded coffee*elevation	AIC	ΔAIC	k
Survival	**−66.5 (39.1)**	**−18.7 (12.9)**		**−54.5 (35.4)**	15.4 (10.5)	−19.2 (15.4)	31.4	0	6
Wanderer									
Transience	**5.75 (3.42)**	**9.78 (2.20)**	**21.5 (8.49)**	**6.79 (2.33)**			53.4	0	5
Home-range		**−2.22 (1.24)**				**2.95 (1.21)**	54.9	0.3	3

Table 3

Output of top models of demographic parameters (SE in parentheses) as a function of micro-habitat measurements for 46 radio-tagged wood thrush tracked in Honduras during 2012 and 2013. Only habitat classes associated with demographic parameters are presented. Coefficients for which 85% confidence intervals do not include zero are in bold type. "Wanderer" status was unrelated to any of the micro-habitat measurements. Only a single model was within 2 ΔAIC of the best model in all cases.

Parameter	Leaf litter depth	Ground cover	Basal area small trees	Basal area medium trees	Basal area large trees	Percent cover coffee	AIC	ΔAIC	k
Survival		**−0.07 (0.04)**		**−1.23 (0.53)**			38.2	0	3
Wanderer									
Transience	**−1.07 (0.62)**		**−37.3 (13.7)**	**−6.86 (2.81)**			40.3	0	4
Home-range					**−0.06 (0.03)**	**−2.28 (0.73)**	65.1	0	3

indicated home ranges were smaller in heavily-shaded coffee, although an interaction term indicated this pattern reversed itself at lower elevations (Table 2). Home range size decreased with increased cover of coffee in the understory and increased basal area of large trees (Table 3).

Survival was unrelated to body condition or age ($P > 0.05$), however individuals in better condition were less likely to exhibit a wandering movement pattern ($Z = -2.65$, $P = 0.007$), and occupied smaller home-range areas ($Z = -2.87$, $P = 0.004$). Similarly, sedentary individuals were in better condition ($t_{(1,41)} = 2.18$, $P = 0.03$). In contrast, fat individuals were more likely to be transients ($Z = 1.96$, $P = 0.05$). Age was unrelated to survival, movement or home-range size ($P > 0.05$).

4. Discussion

Although our findings that wood thrushes selected heavily-shaded coffee and shade coffee over native forest are consistent with reports that shade coffee systems support high levels of biodiversity (Philpott et al., 2008) including wintering Neotropical migrants (Petit and Petit, 2003), we also observed that heavily-shaded coffee was associated with elevated wood thrush mortality, particularly at lower elevations. Cohen and Lindell (2004) attributed lower survival of fledgling white-throated robins (*Turdus assimilis*) in coffee and pasture relative to forest to the more open vegetation structure that characterized agricultural habitats. Consistent with this view, habitat structure 0–1 m above ground was greater on 24 forest sites compared to 24 shade coffee farms our study area (Bailey and King, unpublished), however habitat structure from 1 to 3 m was greater in coffee farms (probably because of structure provided by coffee plants). Furthermore, neither shrub nor sapling density was related to survival in the present study. Alternatively, lower survival of wood thrushes in heavily-shaded coffee might be due to the fact that coffee farms in our study area were bounded by high-contrast edges that are known to concentrate species that depredate nests (Vetter et al., 2013), some of which (e.g. snakes, raptors) also likely prey on adult birds. These high-contrast edges were negatively associated with wood thrush survival in the present study. Survival was unrelated to use of lightly-shaded or open coffee, which might be because wood thrushes used these other types sparingly (22.2% and 2.31% of locations, respectively), and thus they were less frequently exposed to potential hazards in those cover types.

Our observation that wood thrushes preferred habitats in which their survival was lower is consistent with the findings of from Mexico indicating that wood thrushes are more abundant in disturbed habitats (Winker et al., 1995) where they were subject to higher levels of predation (Rappole et al., 1989), however the mechanisms for the decoupling of habitat use and habitat quality between their work and our study may differ. Winker et al. (1990) speculated higher abundance in secondary habitats was the result of territory holders excluding conspecifics from forested sites, whereas at our sites wood thrushes appeared to select heavily shaded coffee, using it in greater proportion to its availability. Selection of coffee by wood thrushes in our study might be influenced by food abundance. Johnson and Sherry (2001) reported that food abundance was an important determinant of warbler distribution among habitats in Jamaica, and that shade coffee farms supported a high abundance of foliage-dwelling arthropods relative to natural habitats. In contrast, McKinnon et al. (2015) found that litter arthropods, which are preferred prey of wood thrushes, tended to be greater in forest habitats in Belize compared to disturbed habitats or scrub, however they also reported that arthropod abundance was strongly positively related to soil moisture, and arthropod abundance, soil moisture and wood thrush body condition all decreased with the progression of the dry season. Fifty-eight percent of 24 coffee farms visited by Bailey et al. (unpublished) were traversed by streams, while only 12.5% of

forested sites had streams, which is likely intentional on the part of farmers to provide water for irrigation. Increased soil moisture associated with streams combined with forest-like vegetation could enhance prey availability on coffee farms, and could explain why wood thrushes preferred coffee over forest. An alternative (or perhaps complimentary) explanation is that heavily-shaded coffee sites appeared to wood thrushes like humid forest, a habitat that has historically been more widespread in our study area and which did not elevate predation risk. Bock and Jones (2004) found that the relationship between habitat selection and reproductive success was more likely to be decoupled in human-altered habitats where they have not yet had the time to discriminate effectively between, what for this species may be an ecological trap, and suitable habitat.

The inverse relationship we observed between home range size and use of heavily-shaded coffee is consistent with the notion that food abundance was greater in heavily-shaded coffee. Smith and Shugart (1987) reported that territory size of breeding ovenbirds (*Seiurus aurocapilla*) decreased with prey abundance. Bakermans et al. (2009) and Colorado and Rodewald (2017) reported that several species of migrants netted in coffee farms in Colombia maintained or increased body mass during the winter season, suggesting food was sufficient at these sites. Similarly, Johnson et al. (2006) found that changes in body mass of wintering American redstarts (*Setophaga ruticilla*) in shade coffee in Jamaica was similar to the highest quality natural habitats (black mangroves).

Our findings that use of secondary vegetation was also associated with wood thrush mortality is consistent with the findings of Rappole et al. (1989) that wood thrush mortality was higher in secondary habitats compared to primary forest in Veracruz, Mexico. A key difference from a conservation perspective is unlike shade coffee, wood thrushes did not select secondary vegetation, and thus were not drawn into a habitat in which their risk of mortality was elevated. Wood thrushes are generally reported to be less abundant in secondary or degraded forest compared to primary forest (Lynch, 1989; Greenberg, 1992; Petit et al., 1992; Powell et al., 1992; Robbins et al., 1992; Rappole et al., 1992), and although these studies did not analyze habitat selection and thus a direct comparison was not possible, their findings appear to contradict our observation that there was no difference in habitat preference of wood thrush between forest and secondary habitats. The lack of difference in preference between forest and secondary vegetation in our findings could reflect the fact that "humid broadleaf" at our sites was mapped using remotely-sensed data, and it likely included the type of second growth and degraded forest these prior studies report support lower numbers of wood thrushes. In contrast to our findings, Conway et al. (1995) didn't detect a significant difference in wintering wood thrush survival rates between mature forest and secondary vegetation in Belize using a mark-recapture methodology, although they concede differences in monthly survival rates as great as 14% could have been overlooked given the modest precision of their estimates.

Mortality in our study was entirely attributable to predation, which is consistent with the findings of Rappole et al. (1989), who reported that all of the mortality events observed in their study of radio-tagged wood thrushes in Veracruz were killed by predators, including ferruginous pygmy owls (*Glaucidium brasilianum*), barred forest falcons (*Micrastur ruficollis*), and unidentified mammals. Estrada and Coates-Estrada (2005) witnessed attempted and successful predation attempts on songbirds in Veracruz by laughing falcons (*Herpetotheres cachinnans*) and roadside hawks (*Rupornis magnirostris*). Townsend et al. (2009) reported predation of wintering Bicknell's thrush in the Dominican Republic by introduced rats (*Rattus rattus* and *R. norvegicus*), and Chandler and King (2011) recorded a single predation event during a study of golden-winged warblers in Honduras by a palm pit-viper (*Bothriechis schlegelii*). Rappole et al. (1989) suggested that increased vulnerability of wood thrush in degraded habitats was due to their being forced to adopt a wandering movement pattern, because wanderers, by virtue of not occupying a stable home range, were less familiar with potential refugia from predators or areas of concentrated predator activity, information to which stationary birds were privy. Wood thrush mortality in our study area may also be exacerbated by increased abundance and/or concentration of predators of wood thrushes in heavily-shaded coffee, secondary vegetation and coffee/forest edge: All of the predator species cited above were present within our study area, and many of them (e.g. pygmy owl, laughing falcon, roadside hawk, eyelash viper) are reported to be more abundant in open or shrubby habitats and edge (Mehrtens, 1987, Vallely and Dyer, 2018).

Our observation that wood thrushes in habitats where survival is low (secondary vegetation, heavily-shaded coffee and coffee edge) were more likely to be transients is consistent with observations by Rappole et al. (1989) that wood thrushes in secondary habitats were more likely to disappear from their study sites than sedentary individuals in primary forest. Similarly, Roberts (2007) reported a higher incidence of disappearance of radio tagged wood thrushes from fragments compared to continuous forest in Costa Rica. Overwinter persistence (sustained occupancy of a site) is thought to reflect habitat quality because individuals that survive should be more inclined to abandon a low quality site (Holmes and Sherry, 1992; Winker et al., 1995; Johnson et al., 2006). Alternatively, it is possible that some individuals that left the study site were in fact depredated, and that the distinctive, nearly straight-line movement of transient birds may have represented individuals being carried from the study site by predators. Although we are unable to assert with complete confidence that we weren't incorrectly assigning mortality and transience, there are a number of reasons we believe that we seldom did so. First, we sighted a number of transients and confirmed they were live birds and that wood thrushes do in fact exhibit this behavior at our sites. Furthermore, our discovery of depredated bird remains at our sites suggests consuming prey locally is typical of at least some predators. Finally, 10 of 46 of wood thrushes at our sites were transients, and if these were all mortalities, it would result in an improbably low survival rate, compared to other published estimates (Rappole et al., 1989; Roberts, 2007). It is unclear why some birds select heavily-shaded coffee and others flee from it, although it is possible transients are reacting to predator presence, as reported for breeding birds (Fontaine and Martin, 2006), whereas birds that remain may not perceive the elevated predation risk in this habitat.

The probability of wood thrushes at our sites exhibiting transient behavior was also positively associated with their use of open pasture and cropland, which, as opposed to heavily-shaded coffee and secondary vegetation, were habitats that were selected against. The alignment between the avoidance of open pasture and cropland and the performance metric of habitat quality "transience" may be due to the absence of structural characteristics within pasture and cropland that could have acted as cues and caused wood thrushes to occupy low-quality habitat, cues that may have been responsible for the mismatch between survival and habitat selection in the case of heavily-shaded coffee. Birds were less likely to be transient at sites with deeper litter, which likely supports more invertebrate prey for this ground foraging species (McKinnon et al., 2015), consistent with our finding that birds with higher condition scores were more likely to exhibit sedentary behavior. Petit et al. (1992) reported that wintering wood thrushes are were positively associated with leaf litter in Belize.

Our finding that birds in better condition were more likely to adopt a sedentary movement strategy, a strategy that may reflect better habitat conditions (Winker et al., 1995; Johnson et al., 2006; although see Brown and Sherry, 2008), is consistent with previous studies showing that food abundance influences the habitat use, persistence and survival of wintering Neotropical migrants (Strong and Sherry, 2000; Johnson and Sherry, 2001; Sherry et al., 2005). Conversely, transience was positively related to subcutaneous fat stores in our study, which is consistent with the findings of Winker et al. (1990), who documented significantly higher fat levels in wandering wood thrushes in Veracruz compared to sedentary ones. Winker et al. (1990) reasoned that high fat scores reflect the need to maintain energy reserves under condition of uncertain food availability. Additional fat storage is potentially maladaptive in tropical habitats due to increased exposure to predators while foraging for extra calories and reduced capacity to escape predators (Kullberg et al., 1996; Katti and Price, 1999). The use of size-adjusted mass as reliable indicator of habitat quality is supported by our observation that our condition index was negatively correlated with transience, home-range area, and wanderer status, metrics which we considered as reflecting habitat quality (Johnson et al., 2006; Winker et al., 1995).

Despite the fact that this study took place in a highly disturbed agricultural region of Honduras, the survival rates we observed (0.995) were similar to those reported for wood thrush telemetry studies within primary forest in Mexico and Costa Rica by Rappole et al. (1989) and Roberts (2007) (0.996 and 0.994, respectively). Our survival rates are far higher than those derived by Conway et al. (1995) based on capture-recapture data from standardized mist-netting in Veracruz. This may be because movement patterns and home range in our study were also related to habitat, which may have confounded their survival estimates (Ruiz-Gutierrez et al., 2016). The fact that survival rates in the mixed habitat of our study are similar to survival rates reported elsewhere in forest is puzzling given that such a large proportion of the landscape (50%) consisted of habitats in which wood thrush survival was diminished (heavily-shaded coffee and secondary vegetation).

Survival did not differ between age classes, which is consistent with other findings for wintering wood thrush (Rushing et al. 2017), as well as black-throated blue warblers (Sillett and Holmes, 2002) and American redstarts (Marra and Holmes, 2001). We were unable to examine sexual segregation at our sites due to the destruction of tissue specimens we collected for that purpose, however other studies have reported higher proportions of wintering female wood thrushes in Costa Rican forest fragments (Roberts, 2007) and scrub vegetation in Belize (McKinnon et al., 2015). Similarly, Townsend et al. (2012) found that Bicknell thrush (*Catharus bicknelli*) females wintered in lower elevation forests compared to males in the Dominican Republic. Although these studies did not report differences in condition or survival associated with sexual habitat segregation, Marra and Holmes (2001) found sexual habitat segregation lead to lower condition, persistence and annual survival of female American redstarts. If female wood thrushes are similarly relegated to secondary vegetation at our sites, habitats where birds experienced higher mortality, it could have important impacts on the population dynamics of this species.

Clearly, there is evidence that agroforestry systems are not only occupied by wintering migrants (Robbins et al., 1992; Greenberg et al., 1997; Petit and Petit, 2003; Estrada and Coates-Estrada, 2005; Philpott et al., 2008), but that they are suitable habitats for many of these species in the sense that they promote the maintenance of over-winter condition (Bakermans et al., 2009; Colorado and Rodewald, 2017). Nevertheless, our analyses of a suite of performance metrics suggests that habitats that are widely used by wintering wood thrushes, heavily-shaded coffee and secondary vegetation, are in fact lower quality habitats in which individuals are subject to a greater risk of mortality and adopt a wandering or transient movement strategy. Thus, the conservation of forest seems to be key element to the conservation of this species on its wintering grounds. The establishment of park and preserves is one means of conserving forest, however parks in many regions are poorly protected, and may deny local human populations resources they need to survive (King et al., 2016). Payment for ecosystem services is a strategy that has been practiced in some regions, however sustaining payments through changes in administrations presents a challenge, and opportunity costs of not conserving forest may exceed the value of payment schemes (King et al., 2016).

Integrated Open Canopy (IOC) coffee cultivation is a land-sparing practice that conserves patches of forest on coffee farms in exchange for sales of carbon credits and ecosystem services provided by forest-associated pollinators and insectivorous birds (Arce et al., 2009; Chandler et al., 2013; King et al., 2016). Findings by Roberts (2007) suggest that wood thrush predation rates are not elevated in forest fragments such as the patches on IOC coffee farms, and we found no evidence of edge effects within forest patches not adjacent to shade coffee. However, our findings suggest that prioritizing older IOC forests and minimizing coffee-forest edge will be necessary to conserve wood thrush using this strategy. Additional research to identify thresholds for the effects of forest age and forest area on wintering wood thrush will contribute to the conservation of this vulnerable species in the face of accelerating expansion of coffee cultivation in Central America.

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