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Research Paper

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ABSTRACT. The Golden-winged Warbler (*Vermivora chyrsoptera*) and Blue-winged Warbler (*Vermivora cyanoptera*) are both Neotropical migratory species of elevated conservation concern that overlap in distribution on their Central American wintering grounds, yet the extent to which they overlap in terms of habitat use is unknown, potentially hindering conservation efforts. We surveyed these two species along habitat and elevational gradients within a coffee-growing landscape during 2016 and 2017 in Yoro, Honduras. We used playback with a mobbing track known to enhance detections of female warblers, since examining sexual habitat segregation was another objective of our study. Habitat occupied by these two species differed, with male Golden-winged Warblers occurring in landscapes dominated by humid forest/coffee (forest with some dense shade coffee, which were indistinguishable with remote sensing at our sites) at higher elevations than male Blue-winged Warblers, which were positively associated with the amount of agriculture in the landscape. Six of seven female Golden-winged Warblers were encountered in shade coffee, however, this association was not significant, likely due to small sample size and low detectability. The association between male Golden-winged Warblers and humid forest/coffee and elevation, and contrasts in habitat use between male and female Golden-winged Warblers, are consistent with prior research in the region. Furthermore, the landscape associations of these non-breeding Vermivora species mirror their breeding landscape associations, with Golden-winged Warblers occupying more forested landscapes and Blue-winged Warblers occupying more agricultural landscapes. The use of shade coffee by female Golden-winged Warblers and Blue-winged Warblers suggests agroforestry could be a promising tool for conserving wintering populations of these species, although this result should be viewed with caution given that use of shade coffee is reported to elevate predation risk in other migratory species, and may not provide habitat for forest-dependent resident birds.

Associations avec l'habitat des Parulines à ailes dorées et des Parulines à ailes bleues en dehors de la saison de reproduction

RÉSUMÉ. La Paruline à ailes dorées (*Vermivora chyrsoptera*) et la Paruline à ailes bleues (*Vermivora cyanoptera*) sont deux espèces migratrices néotropicales dont la conservation est très préoccupante et dont la répartition se chevauche dans leur aire d'hivernage en Amérique centrale. On ne sait toutefois pas dans quelle mesure les habitats qu'elles utilisent se chevauchent, ce qui pourrait entraver les efforts de conservation. Nous avons suivi ces deux espèces le long des gradients d'habitat et d'altitude dans un paysage de culture du café en 2016 et 2017 à Yoro, au Honduras. Nous nous sommes servis de la repasse d'un enregistrement de houspillage connu pour améliorer les détections de parulines femelles, puisque l'examen de la ségrégation sexuelle dans l'habitat était un autre objectif de notre étude. L'habitat occupé par ces deux espèces était différent, les Parulines à ailes dorées mâles fréquentant des paysages dominés par la forêt humide/de caféiers (forêt avec un peu de caféiculture sous couvert forestier dense, qui était indiscernable au moyen de la télédétection sur nos sites) à des altitudes plus élevées que les Parulines à ailes bleues mâles, qui étaient associées positivement à la superficie de terres cultivées dans le paysage. Six des sept Parulines à ailes dorées femelles ont été détectées dans les plantations de caféiers sous couvert, mais cette association n'était pas significative, probablement en raison de la petite taille de l'échantillon et de la faible détectabilité. L'association entre les Parulines à ailes dorées mâles et la forêt humide/de caféiers et l'altitude, ainsi que le contraste d'utilisation de l'habitat entre les Parulines à ailes dorées mâles et femelles, sont cohérents avec les recherches antérieures dans la région. En outre, les associations paysagères de ces espèces de Vermivora non nicheuses reflètent leurs associations paysagères en nidification, la Paruline à ailes dorées occupant des paysages plus forestiers, et la Paruline à ailes bleues, des paysages plus agricoles. L'utilisation de plantations de caféiers sous couvert par les femelles de la Paruline à ailes dorées et de la Paruline à ailes bleues indique que l'agroforesterie pourrait être un outil prometteur pour la conservation des populations hivernantes de ces espèces; ce résultat doit toutefois être considéré avec prudence étant donné que l'utilisation de cet habitat a été signalée comme augmentant le risque de prédation chez d'autres espèces migratrices, et pourrait ne pas fournir d'habitat aux oiseaux résidents dépendant de la forêt.

Key Words: *agroforestry; coffee; landscape; Neotropical migrant; occupancy; winter*

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INTRODUCTION

Neotropical migrant birds are the subject of elevated conservation concern due their ubiquity, comprising the majority of species and individuals in eastern temperate forests (Terborgh 1989:73), as well as evidence of declines in many species (Rosenberg et al. 2019). Nevertheless, most migrants spend the majority of the annual cycle on their tropical non-breeding grounds (DeGraaf and Rappole 1995:11). For this reason, research on the habitat use of Neotropical migrants in the tropics is key to understanding their ecology and conservation needs (Albert et al. 2020), knowledge that is of increasing importance as natural habitats in the tropics are converted to agricultural or other uses.

Golden-winged Warblers (*Vermivora chrysoptera*) spend approximately two thirds of the annual cycle in the Neotropics, and thus their populations are likely affected by habitat conditions during the non-breeding season (Rosenberg et al. 2016, Kramer et al. 2018). Previous studies have reported that Golden-winged Warblers are associated with evergreen broadleaf forests with intermediate canopy heights in Costa Rica (Chandler and King 2011, Ritterson et al. 2021a). Research in Nicaragua and Honduras, however, has revealed that they use other forest types besides evergreen forest, including pine–oak and semi-deciduous forest (Chavarría and Duriaux 2009, Bennett 2012). Understanding these patterns of geographic variation in habitat associations are important to the comprehensive conservation of their populations, particularly since Honduras encompasses core non-breeding habitat for this species, including a number of focal areas (Bennett et al. 2016), yet is experiencing the highest rate of deforestation in Central America (-2.4%/yr; FAO 2015).

Sexual habitat segregation is another element that needs to be considered to generate a complete picture of the habitat needs of non-breeding migrants (Akresh et al. 2019, Bennett et al. 2019). Chandler and King (2011) reported that male and female Golden-winged Warblers occurred in similar habitats in Costa Rica, but noted fewer female Golden-winged Warblers than males within their study area. A subsequent study across Central America revealed that Golden-winged Warblers segregate by sex at both local and landscape scales, with females occupying semi-deciduous forest at lower elevations than males (Bennett et al. 2019). Part of the discrepancy between these studies could be due to segregation of habitats at geographic scales, or differences in the range of habitat types surveyed, however, it may also be due to the fact that Bennett et al. (2019) incorporated a mobbing call in the playback protocol, which increased responsiveness of females substantially over the male song and chips used by Chandler and King (2011). The same mobbing protocol was shown to increase the detection probability of the full community of migratory birds dramatically in a study in Guatemala, demonstrating its potential to increase the precision of occupancy and abundance models for non-breeding migrants (Bennett et al. 2018). This raises the possibility that our knowledge of the habitat needs of Golden-winged Warblers derived from surveys based on playback of male Golden-winged Warbler song and chips may be biased toward detections of male individuals and may not adequately represent habitats needed by females (Bennet et al. 2019).

Biotic interactions are potentially important in limiting the distribution of organisms and affecting habitat quality. Golden-winged Warblers could be affected by the congeneric Blue-winged Warblers (*V. cyanoptera*) in areas of sympatry. Declining populations of Golden-winged Warblers have been partially attributed to competition and hybridization with Blue-winged Warblers on the breeding grounds (Murray and Gill 1976, Confer and Larkin 1998, Gill 2004, Wood et al. 2016). It is not clear whether these species interact in the non-breeding grounds, however, segregation between Golden-winged Warblers and Blue-winged Warblers by elevation and habitat have been reported from Honduras (Bennett 2012). These species also differ in their migratory connectivity, with sympatric breeding populations in unique geographies during the non-breeding season (Bennett et al. 2017, Kramer et al. 2018). Regardless of their potential impacts on non-breeding Golden-winged Warblers, Blue-winged Warbler non-breeding habitat selection has been poorly studied compared to Golden-winged Warblers, even though Blue-winged Warblers are also a species of conservation concern (Rohrbaugh et al. 2016).

To address these deficiencies in our understanding of habitat segregation between male and female Golden-winged Warblers and between Golden-winged and Blue-winged Warblers, we undertook a study during the non-breeding period within a zone of inter-species overlap in Yoro, a coffee-producing region of Honduras. Specifically, our objectives were to assess (1) whether male and female Golden-winged Warblers occupy different habitats, and (2) whether habitat conditions differ between Golden-winged and Blue-winged Warblers. We used the same mobbing track as used by Bennet et al. (2018) for playback to increase detectability of female Golden-winged Warblers, and included male Blue-winged Warbler songs and chips in an attempt to increase detections of that species. These results will enable us to determine the extent to which prior habitat associations, based on surveys with male song, represent the needs of female Golden-winged Warblers and Blue-winged Warblers.

METHODS

Study area

This study was undertaken in 2016 and 2017 in a multi-use landscape in northwest Yoro, Honduras (15.20° N, 87.45° W; Fig. 1) that encompasses broad gradients of vegetation and land use. Lower portions of the study area consisted of pine or pine–oak forest, which transitioned to humid broad-leaved forest at approximately 800 m elevation as conditions become cooler and wetter with increased elevation. The mountainous landscape produces numerous rivers and streams that form riparian forest, especially at lower elevations. The annual average rainfall in the region is approximately 1500 mm, with a pronounced dry season from February through April. Coffee is a major source of income for the region, and coffee grown under shade trees ("shade coffee"), and increasingly with no shade cover ("sun coffee"), occupies approximately two thirds of the landscape, along with pasture and row crops (Bailey and King 2019).

Field methods

We conducted point count surveys at 57 points distributed along habitat and elevational gradients (793–1622 m) and spaced ≥ 500 m apart across an approximately 400 km² area. This elevational range encompasses the upper elevational range of both species in Honduras (13–1977 m and 0–1497 m, Golden-winged Warblers and Blue-winged Warblers, respectively; Bennett 2012). Survey locations were restricted to farms for which we could obtain

Fig. 1. Study area in western Honduras where Golden-winged (*Vermivora chrysoptera*) and Blue-winged Warblers (*Vermivora cyanoptera*) were surveyed in 2006 and 2007 indicated by the square on the map at left. On the right is an image of a typical landscape within our study area, consisting of pasture, scattered trees, and patches of forest and agroforestry systems.
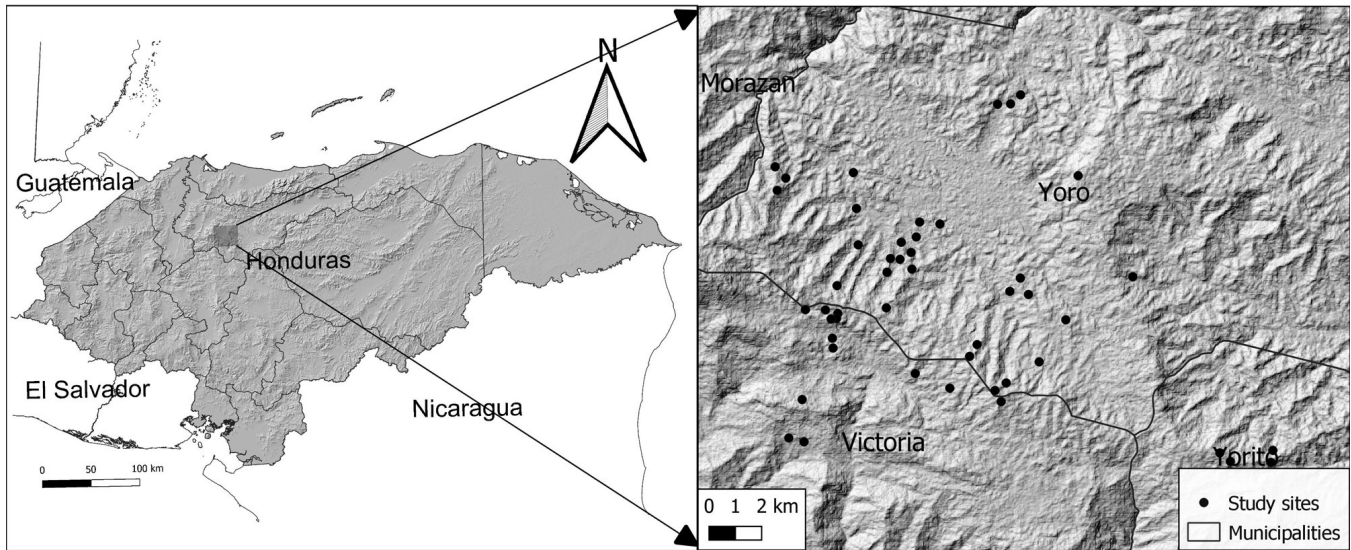
permission, and individual points located in a manner that maximized the number that could be located within the same farm using a GPS. We surveyed 48 points from January through March in both 2016 and 2017, eight additional points just in 2016, and 1 additional point in 2017. We placed 17 points (30%) in pine–oak forest, 13 points (23%) in humid forest, and 27 points in coffee (47%). All coffee points were in shade coffee ranging from commercial polyculture with planted shade tree to rustic coffee farms under natural tree canopy (Moguel and Toledo 1999). Points were visited once (31%), twice (39%), or three times (30%) per year. At each visit, three types of vocalizations were broadcast for 10 minutes each at a standardized volume (~100 dB at a distance of 1 m; Chandler and King 2011) for a total point count duration of 30 minutes. The three vocalization types consisted of male Golden-winged Warbler songs and chips, male Blue-winged Warbler songs and chips, and the standard mobbing track playback created by K. Rosenberg of the Cornell Laboratory of Ornithology used by the Golden-winged Warbler Working Group that included Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) and the Eastern Screech-Owl (*Megascops asio*), as well as the mobbing calls of various Neotropical resident and migratory birds (Bennett et al. 2018). Either the Golden-winged Warbler or Blue-winged Warbler playback was played first, the order chosen at random, while the mobbing track was always played last, with the rational that the mobbing call could alter the behavior of the full community of birds present, decreasing the probability that any individual would respond to a conspecific vocalization afterwards. The point count period was divided into twelve 2.5-minute intervals during which observers recorded the presence and sex of any Golden-winged or Blue-winged Warblers sighted within a 50 m radius. Finally, date, time of day, wind level classified from 0–5 (0 = smoke rises vertically, 1 = wind direction shown by smoke drift, 2 = wind felt on face, leaves rustle, 3 = leaves and

small twigs in constant motion, 4 = wind moves thin branches, raises loose paper, 5 = trees sway), noise from nearby rivers classified from 0–5, and survey conditions classified from 0–5 (0 = clear, 1 = partly cloudy, 2 = cloudy/overcast, 3 = fog/smoke, 4 = drizzle/light rain, 5 = showers) were recorded during each survey. Surveys were rarely conducted when wind, noise, or sky conditions exceeded the value "2," and in all cases the influence of these detection covariates were accounted for in our analyses.

We collected several habitat characteristics known to influence Golden-winged Warbler abundance at 48 of the survey points, including the presence of a stream or river within 100 m of the survey point and elevation (Chandler and King 2011, Bennett 2012). All trees with a dbh > 2.5 cm were counted within an 11.2 m radius plot centered on the survey point (James and Shugart 1970). We calculated basal area separately for three tree size classes: small (2.5–19 cm dbh), medium (> 19–58 cm) and large (> 58 cm). Vegetation structure in the understory (0–1 m) and shrub layer (> 1–3 m) was measured as the number of contacts of vegetation with a pole held vertically, with higher values indicate more understory structure or shrub structure, respectively. These were summed over 20 points established 2 m apart on orthogonal transects intersecting the survey point.

We also computed the proportion of major habitat types within a 1-km radius of the point using a land cover layer derived from high resolution satellite imagery, captured primarily in 2013 and interpreted by E. Duarte of the Instituto Nacional de Conservación y Desarrollo Forestal, Áreas Protegidas y Vida Silvestre (ICF). There was a 3–4 year time lag between the collection of the aerial imagery and our bird surveys, and Honduras is undergoing a net rate of forest loss of 2.4% per year (FAO 2015). Although we do not have specific information on the rate and spatial pattern of forest lost within our study area,

we assume of the sites assigned as forested in 2013, a few were cleared by the time the surveys were conducted, potentially slightly overestimating forest association in our analyses. Land cover was grouped into three main categories: "humid forest/ coffee" (forest with densely shaded coffee, which were indistinguishable with remote sensing at our sites), pine–oak forest, and agriculture (e.g., pasture and crops).

Statistical Analyses

We examined associations between bird presence and predictor variables using occupancy models with a logit link (MacKenzie 2002) and ran the models using the "occu" function with the "unmarked" package (Fiske and Chandler 2011) in the R Statistical Program version 4.2.1 (R Core Team 2022). Each 2.5-minute interval within the 30-minute point count was considered an interval for detection, which allowed us to estimate detection probability and account for playback type. Surveys conducted in each year were treated as separate occupancy samples ("stacking the years"; Wiest and Shriver 2016), because we were not interested in extinction/colonization rates at points over a period of just two years.

We examined each bird group (male Golden-winged Warblers, female Golden-winged Warblers, and male Blue-winged Warblers) in separate analyses. We used an information-theoretic framework (Burnham and Anderson 2002) and conducted a manual forward selection approach to obtain a model for each bird group that included important variables influencing the detection probability part of the model. We computed Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike's model weights for each model using the 'AICcmodavg' package (Mazerolle 2020). We first examined models with single detection predictor variables (date, time, wind level, river noise, playback type, and sky condition), and then combined the detection variables in further models if the variables were significant or if the variables reduced the AIC_c values (Roberts and King 2017).

Using a fixed set of detection covariates from the above model selection approach, conducted separately for each bird group, and an additional categorical variable of year, we tested relationships between occupancy probability and a number of predictor variables. These predictor variables of occupancy probability consisted of habitat type (coffee, pine–oak forest, or humid forest), river presence, elevation, basal area (by size class), percent humid forest/coffee within 1 km, percent pine–oak forest within 1 km, and percent agriculture within 1 km. We chose to only examine single main predictor variables in the occupancy part of the models (rather than combining occupancy variables) to avoid multicollinearity as well as to avoid overfitting models, given the small sample sizes of occupied sites for Blue-winged Warblers and female Golden-winged Warblers. Additionally, there were some missing data (16% of sites) for some of the occupancy covariates. All continuous variables were standardized to a mean of 0 and a SD of 1 to assist with model convergence. For seven surveys, we did not record when the individual bird was observed in the 2.5-minute intervals, and these surveys were removed from the occupancy models. We presented the 95% confidence interval (CI) of each predictor variable and deemed variables as significant if the 95% CI did not include or was very close to not including zero (Byers et al. 2016).

To visualize differences in habitat use among the three bird groups, we conducted a Discriminant Analysis (DA) using the point locations where Blue-winged Warblers or Golden-winged Warblers were detected. In the DA, we excluded certain variables to decrease multicollinearity (e.g., among the landscape variables and elevation), and we included variables that were found to be important in influencing Blue-winged Warbler or Golden-winged Warbler occupancy (results to follow). The reduced set of variables for the DA consisted of habitat type (coffee versus forest), river presence, percent agriculture within 1 km, and basal area of small trees. We also excluded five samples that had missing data for some variables. Prior probabilities for the DA were determined by group sizes. Due to some non-normality, we also conducted a Permutational Multivariate Analysis of Variance (PMANOVA) to statistically test for differences among all groups (Anderson 2001).

RESULTS

We encountered male Golden-winged Warblers at 31 (54%) of the 57 surveys points, female Golden-winged Warblers at 7 points (13%), and Blue-winged Warblers (all males) at 12 points (22%). Male Golden-winged Warblers were present at 57% of points where female Golden-winged Warblers were encountered and at 58% of points where Blue-winged Warblers were sighted (although not necessarily at the same time). Female Golden-winged Warblers were present at 33% of points where Blue-winged Warblers were encountered. Across all surveys, the probability of detection during a 2.5-minute survey interval was 0.22 (SE = 0.013) for male Golden-winged Warblers, 0.043 (SE = 0.016) for female Golden-winged Warblers, and 0.10 (SE = 0.02) for Blue-winged Warblers. Including significant detection variables in the models, the probability of occupancy across all points was 0.41 (SE = 0.05) for male Golden-winged Warblers, 0.13 (SE = 0.05) for female Golden-winged Warblers, and 0.19 (SE = 0.05) for Blue-winged Warblers.

Golden-winged Warbler males

Detectability of male Golden-winged Warblers was negatively affected by wind speed (ß = -0.21, SE = 0.084, 95% CI = -0.37 to -0.043), and time of day (ß = -0.22, SE = 0.082, 95% CI = -0.38 to -0.062; Appendix 1). Detectability was lower with Blue-winged Warbler playback compared to both Golden-winged Warbler playback (ß = 0.53, SE = 0.20, 95% CI = 0.14 to 0.91) and mobbing playback (ß = 0.64, SE = 0.19, 95% CI = 0.26 to 1.02), but did not differ between Golden-winged Warbler playback and mobbing playback (ß = -0.11, SE = 0.18, 95% CI = -0.46 to 0.24).

Accounting for the detection variables, occupancy of male Golden-winged Warblers did not differ among humid forest, pine–oak forest, and coffee (Table 1). Occupancy was marginally associated with higher elevation, positively associated with the percentage of humid forest/coffee within 1 km of the survey point, negatively associated with the amount of pine–oak forest within 1 km of the survey point, and positively associated with the basal area of small trees (Table 1, Fig. 2). Occupancy did not differ between years (ß = -0.048, SE = 0.41, 95% CI = -0.85 to 0.76).

Golden-winged Warbler females

Detectability of female Golden-winged Warblers was negatively affected by wind speed (ß = -1.24, SE = 0.48, 95% CI = -2.18 to -0.30), negatively affected by cloudy/overcast conditions (ß = -1.3,

Table 1. Parameter estimates, SEs, and 95% CIs for relationships between site variables and probability of occupancy. For male Golden-winged Warblers (*Vermivora chyrsoptera*), wind speed, time of day, and playback type were included as detection covariates. For female Golden-winged Warblers, wind speed, sky conditions, and playback type were included as detection covariates. For Blue-winged Warblers (*Vermivora cyanoptera*), wind speed, river noise, time, and ordinal date were included as detection covariates. A variable of year as an occupancy covariate was included in all models. All models were run separately. Most variables were tested with data from 57 sample points surveyed with point counts from 2016 to 2017 in Yoro, Honduras (103 observational units stacking years), but variables of "river presence," basal area, and understory/shrub structure had some missing data (90 observational units stacking years).

Bird Taxa	Parameter	Estimate	SE	95% CI
Golden-winged Warbler (male)	Coffee versus humid forest	-0.011	0.51	-1.02 to 0.99
	Coffee versus oak pine forest	-0.80	0.51	-1.80 to 0.21
	Humid versus oak pine forest	-0.79	0.59	-1.95 to 0.37
	River presence	0.70	0.46	-0.20 to 1.60
	Elevation	0.37	0.21	-0.05 to 0.78
	Humid forest/coffee within 1 km	**0.44**	**0.22**	**0.009 to 0.87**
	Pine oak forest within 1 km	**-0.48**	**0.24**	**-0.96 to -0.009**
	Agriculture within 1 km	-0.15	0.21	-0.57 to 0.27
	Basal area small trees	**0.46**	**0.23**	**0.001 to 0.92**
	Basal area medium trees	-0.37	0.23	-0.83 to 0.092
	Basal area large trees	-0.20	0.23	-0.65 to 0.26
	Understory structure	-0.13	0.22	-0.55 to 0.30
	Shrub structure	0.21	0.22	-0.23 to 0.64
Golden-winged Warbler (female)	Coffee versus humid forest	-1.40	1.17	-3.70 to 0.90
	Coffee versus oak pine forest	-13.2	313.3	-627.3 to 601.0
	Humid versus oak pine forest	-10.2	145.5	-295.4 to 275.0
	River presence	-0.50	0.92	-2.30 to 1.31
	Elevation	0.14	0.41	-0.66 to 0.94
	Humid forest/coffee within 1 km	0.21	0.43	-0.63 to 1.04
	Pine oak forest within 1 km	-0.62	0.63	-1.85 to 0.61
	Agriculture within 1 km	0.19	0.42	-0.64 to 1.02
	Basal area small trees	0.19	0.39	-0.57 to 0.95
	Basal area medium trees	-0.45	0.52	-1.47 to 0.58
	Basal area large trees	0.42	0.33	-0.23 to 1.07
	Understory structure	-0.79	0.49	-1.75 to 0.16
	Shrub structure	0.82	0.49	-0.13 to 1.77
Blue-winged Warbler	Coffee versus humid forest	-1.08	0.93	-2.91 to 0.75
	Coffee versus oak pine forest	**-2.30**	**1.15**	**-4.54 to -0.048**
	Humid versus oak pine forest	-1.22	1.32	-3.81 to 1.37
	River presence	**3.50**	**1.28**	**0.99 to 6.01**
	Elevation	-0.50	0.41	-1.31 to 0.31
	Humid forest/coffee within 1 km	-0.57	0.36	-1.28 to 0.14
	Pine oak forest within 1 km	0.21	0.32	-0.42 to 0.84
	Agriculture within 1 km	**0.75**	**0.39**	**-0.010 to 1.51**
	Basal area small trees	-0.41	0.45	-1.29 to 0.46
	Basal area medium trees	-1.63	1.01	-3.61 to 0.35
	Basal area large trees	-0.22	0.47	-1.15 to 0.70
	Understory structure	-0.66	0.50	-1.63 to 0.30
	Shrub structure	0.80	0.53	-0.23 to 1.83

SE = 0.62, 95% CI = -2.53 to -0.098), and higher when using the mobbing playback compared to the Blue-winged Warbler playback (ß = 2.09, SE = 1.09, 95% CI = -0.052 to 4.23; Appendix 1), and these covariates were included in occupancy models. Detectability did not differ significantly between using the mobbing playback versus the Golden-winged Warbler playback (ß = -0.39, SE = 0.63, 95% CI = -1.61 to 0.84) or between the Blue-winged Warbler versus the Golden-winged Warbler playback (ß = 1.71, SE = 1.12, 95% CI = -0.49 to 3.90).

Occupancy of female Golden-winged Warblers was marginally associated with more shrub structure and marginally associated with less understory/ground cover structure (Table 1, Fig. 3). Most female Golden-winged Warblers were encountered in coffee, with only one bird observed in humid forest and none in pine–oak forest, although the occupancy model with the habitat type predictor variable did not converge well and had very large SEs for some of the parameters (Table 1). Occupancy of female Golden-winged Warblers was not related to any other habitat characteristics (Table 1). Occupancy did not differ between years (ß = -0.59, SE = 0.91, 95% CI = -2.38 to 1.20).

Blue-winged Warbler males

Detectability of Blue-winged Warblers was negatively affected by wind speed (ß = -1.77, SE = 0.41, 95% CI = -2.57 to -0.97), positively affected by river noise (ß = 1.46, SE = 0.27, 95% CI = 0.94 to 1.98), lower later in the day (ß = -1.46, SE = 0.33, 95% CI = -2.11 to -0.81), and higher later in the season (ß = 0.69, SE =

Fig. 2. Male Golden-winged Warblers (*Vermivora chrysoptera*) occurred more frequently at survey points with more humid forest/ shade coffee (a); less pine–oak forest (b); higher elevation (c); and more small trees (d). Data are from 57 sample points surveyed with point counts in 2016 and 2017 in Yoro, Honduras. Dashed lines indicate 95% confidence intervals.
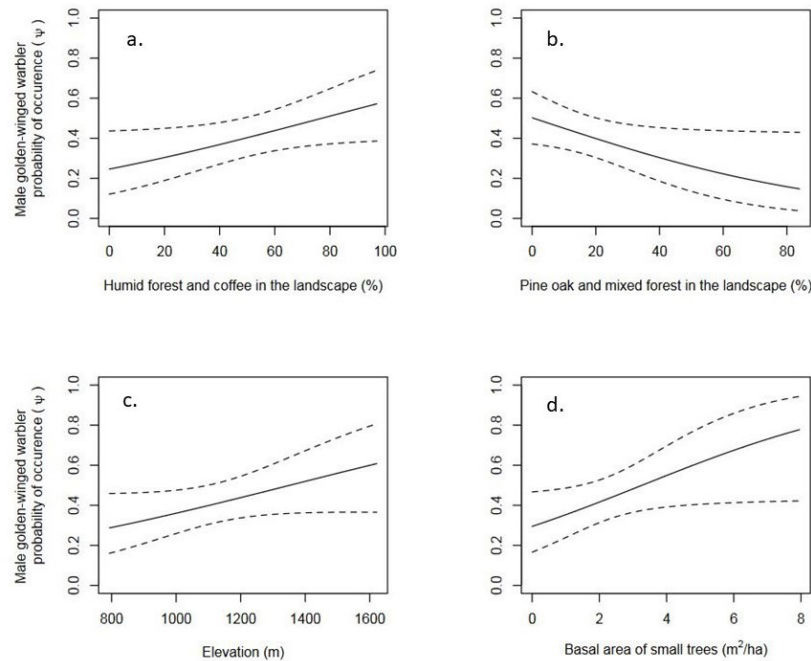
0.25, 95% CI = 0.20 to 1.17; Appendix 1). Detectability did not differ significantly for any of the playback types (mobbing, Golden-winged or Blue-winged Warbler; 95% CIs included 0).

Accounting for the above variables, the probability of encountering a Blue-winged Warbler in coffee was significantly higher than in pine–oak forest (Table 1, Fig. 4). There was no significant difference in the probability of Blue-winged Warbler occupancy between coffee and humid forest, or humid forest and pine–oak forest. The probability of Blue-winged Warbler occupancy was higher at points with a stream or river within 100 m of the point and higher with more agriculture within 1 km of the survey point (Fig. 4). Occupancy was also marginally higher in 2016 compared to 2017 (ß = -1.45, SE = 0.84, 95% CI = -3.09 to 0.19).

Linear discriminant analyses produced two components accounting for 72.8% and 27.2% of the variation in the data. The first component was positively associated with coffee, river/stream presence, and the percentage of agriculture within 1 km of the survey point, while the second component was positively associated with coffee and also negatively associated with river/ stream presence. Male Golden-winged Warblers, female Golden-winged Warblers, and Blue-winged Warblers all overlapped in linear multivariate space (Fig. 5), and the groups were not significantly different (PMANOVA: n = 45, F = 1.54, P = 0.21). However, female Golden-winged Warbler and Blue-winged Warbler points were located toward the positive regions of the coffee gradients, with more Blue-winged Warbler points along the positive gradient of agriculture, while male Golden-winged Warbler points occurred along the entire gradient from areas with little coffee to those with more coffee.

DISCUSSION

Habitat occupied by these two species differed, with male Golden-winged Warblers occurring in landscapes dominated by humid forest/coffee at higher elevations than male Blue-winged Warblers, which were positively associated with the amount of agriculture in the landscape. Female Golden-winged Warblers were marginally associated with more shrub structure and marginally associated with less understory/ground cover structure, however, our sample size was small and detectability low, likely hindering our ability to discern habitat associations. The association between male Golden-winged Warblers and humid forest/coffee and elevation, and contrasts in habitat use between male and female Golden-winged Warblers, are consistent with prior research in the region (Chandler and King 2011, Bennett et al. 2019). Furthermore, the landscape associations of these non-breeding *Vermivora* species mirror their breeding landscape associations, with Golden-winged Warblers occupying more forested landscapes and Blue-winged Warblers occupying more agricultural landscapes (Patton et al. 2010).

Few female Golden-winged Warblers were observed in this study, which affected our ability to detect statistically significant correlates of female occupancy. Additionally, the low occupancy probability of females at our sites limited our insights into sexual habitat segregation in this species. However, 6 out of 7 female Golden-winged Warblers were detected in coffee farms, a cover type not specifically associated with male Golden-winged Warbler occupancy (Chandler and King 2011), and female Golden-winged Warblers were negatively associated (albeit weakly) with habitat features that did not influence occupancy of male Golden-winged Warblers (understory and shrub structure). Small sample

Fig. 3. Female Golden-winged Warblers (*Vermivora chrysoptera*) were marginally negatively associated with understory structure (a) and positively associated with shrub structure (b). Data are from 57 sample points surveyed with point counts in 2016 and 2017 in Yoro, Honduras. Dashed lines indicate 95% confidence intervals.
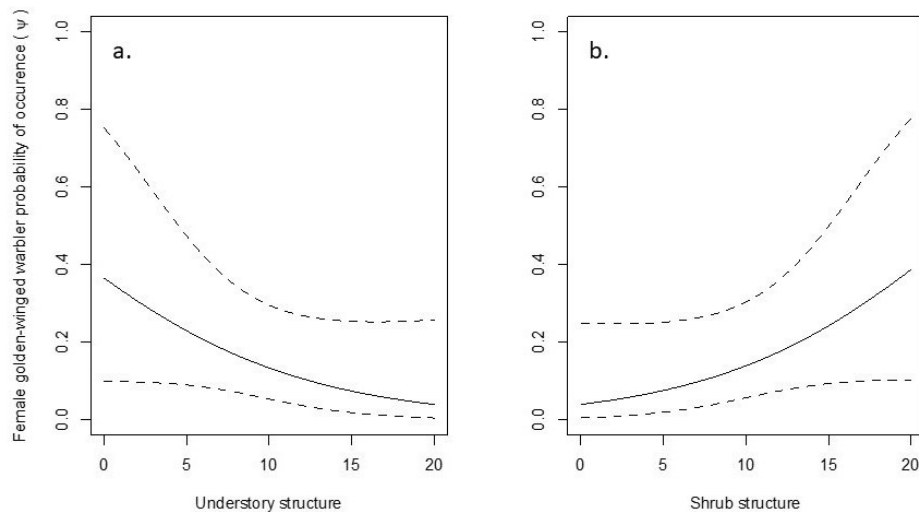

size likely also limited the statistical power of the PERMANOVA results, however, qualitatively, the ordination indicated female Golden-winged Warblers were more associated with shade coffee than male Golden-winged Warblers. This evidence of sexual habitat segregation supports the assertion that the distribution of males does not completely reflect the habitat associations of females (Bennett et al. 2019). Finally, the use of playback to enhance detection was necessary in our study due to the cryptic nature of the target species. In Costa Rica, Chandler and King (2011) encountered only 4 Golden-winged Warblers during the initial 10-minute survey period without playback, compared to 53 individuals detected during these same surveys in the subsequent 10 minutes during which playback was used. Nevertheless, we concede that birds could have been drawn from adjacent habitats to the survey location, potentially reducing our ability to detect differences in occupancy among habitat types, which would make our results conservative.

Bennett (2012) also reported contrasts between the distribution of male and female Golden-winged Warblers in Honduras, however, she found that males used evergreen forest more than semi-deciduous forest whereas females used semi-deciduous forest more than evergreen forest. Neither sex exhibited differences in occupancy between the two forest types in our study, and it was the use of coffee by females that suggested a contrast between the sexes. Bennett (2012) noted that semi-deciduous forest at her sites were more fragmented and disturbed than evergreen forest, and perhaps the amount of edge or forest disturbance drove this difference in habitat association between males and females. Indeed, shade coffee can be considered a type of highly disturbed forest, with lower canopy cover, lower tree density, and a modified understory replaced by coffee plants (Philpott et al. 2008) that creates a dense shrub layer, which was marginally associated with occupancy by female Golden-winged Warblers in our study.

The conservation significance of sexual habitat segregation depends to a large degree on the mechanism by which it arises. In some cases, non-breeding female migrants appear to have different habitat requirements from males, and in these cases, efforts should be directed at conserving those habitats to ensure the entire population is protected. This appears to be the case in non-breeding Hooded Warblers (Wil*sonia citrina*; Morton et al. 1987), Bicknell's Thrush (*Catharus bicknelli*; Townsend et al. 2012), and Wood Thrush (*Hylocichla mustelina*; McKinnon et al. 2015), in which females occupy different habitats or geographic locations than males yet do not exhibit evidence of intersexual aggression or exclusion or any difference in demographic parameters that would indicate decreased fitness in the habitat with which females are associated. In other cases, habitat segregation arises because dominant males appear to force females into marginal habitats (Marra and Holmes 2001, Cooper et al. 2021), habitats in which they are less able to maintain mass during dry seasons (Akresh et al. 2019). In our study, male Golden-winged Warblers were observed at 57% of the points where females were seen. Similarly, Chandler et al. (2016) reported extensive overlap in home-ranges of male and female Golden-winged Warblers in Costa Rica and Nicaragua despite evidence of strong territoriality between males. Although Bennett (personal communication) observed female Golden-winged Warblers moving into what had been a male-dominated site after males had vacated it later in the season, suggesting to some degree males do mediate access to male-dominated habitat, females maintained body condition equally well in male- and female-dominated habitats (Bennett et al. 2018). Regardless of whether females prefer different habitat than males or are being relegated to those habitats, the costs of these contrasting patterns of habitat association are unclear, with the exception that lowland areas are more susceptible to conversion to agriculture or other anthropogenic habitats (Townsend et al. 2012, Bennett et al. 2019).

Fig. 4. Blue-winged Warblers (*Vermivora cyanoptera*) occurred with higher frequency in shade coffee compared to pine–oak forest, but occupancy was not statistically different between shade coffee and humid forest (a). Occupancy was higher at points within 100 m of a river or stream (b) and also increased with increasing cover of agricultural land within 1 km radius of the sample point (c). Data are from 57 sample points surveyed with point counts in 2016 and 2017 in Yoro, Honduras. Dashed lines indicate 95% confidence intervals.
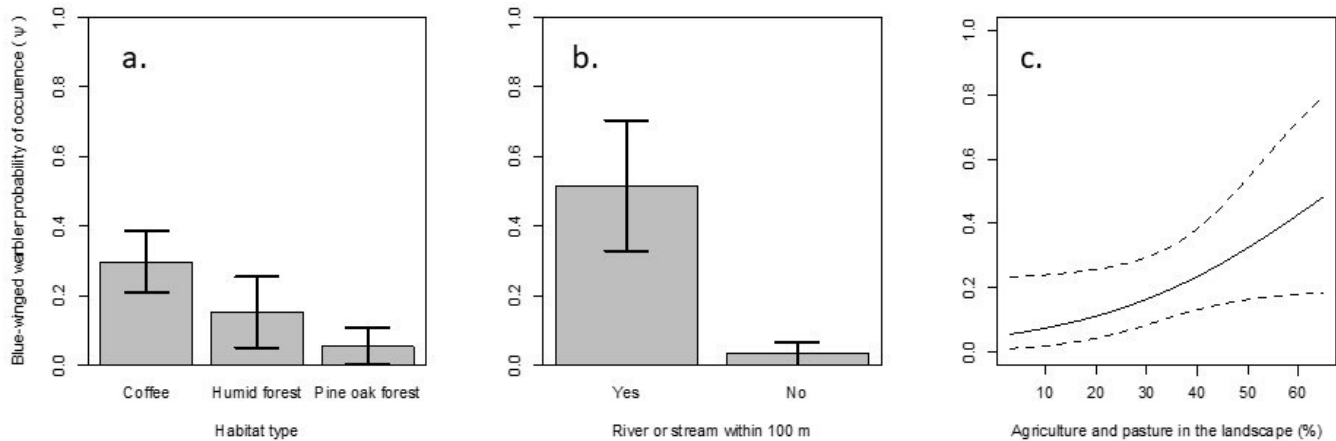

Habitat associations contrasted between male Golden-winged and Blue-winged Warblers, with male Golden-winged Warblers occupying landscapes with extensive humid forest canopy/coffee and Blue-winged Warblers occurring more frequently in landscapes with extensive agriculture. Similar species-specific differences in habitat associations have been reported in breeding site selection, where Golden-winged Warblers occupy sites at higher elevations (Patton et al. 2010) and in more forested landscapes farther from urban centers and roads than Blue-winged Warblers, despite nearly identical habitat selection at smaller spatial scales (Crawford et al. 2016, Wood et al. 2016). Our findings indicate this difference in habitat selection may occur throughout the full annual cycle. This has potential implications for the populations of both species, since being a forest-associated species makes Golden-winged Warblers susceptible in the face of ongoing pressure to convert native habitats, and occupying lowland areas makes Blue-winged Warblers susceptible because habitat conversion is more concentrated due to agricultural conversion (Bennett et al. 2019). Row crops and pasture are more extensive at lower elevations within our study area, raising the possibility that the association between Blue-winged Warblers and agriculture actually reflects a response to elevation, however, Blue-winged Warblers were not significantly associated with elevation (Table 1). Male Golden-winged Warblers were also positively associated with small trees, whereas occupancy of Blue-winged Warbler was higher in coffee than pine–oak forest and more abundant near rivers, conditions that did not appear to affect male Golden-winged Warbler occupancy. This suggests the two species exhibit habitat segregation at the site as well as landscape level.

In addition to habitat segregation within our sites, it appears there is also evidence of geographic segregation, with occupancy estimates of both female Golden-winged Warblers and Blue-winged Warblers lower at our sites in comparison to male Golden-winged Warblers. This is consistent with findings by Bennett et

al. (2019) who reported that female Golden-winged Warblers occurred at lower elevations and more eastern regions of Honduras in comparison to males, as well as observations by others who note that the non-breeding range distribution of Blue-winged Warblers are more northernly than Golden-winged Warblers (Rosenberg et al. 2016, Kramer et al. 2018). However, the mechanism for habitat segregation between these species is not clear. On the breeding grounds territories overlap extensively and aggressive interactions are rarely observed (Ficken and Ficken 1968, Confer and Larkin 1998), although there is distinct segregation between these two species by elevation in the Southern Appalachian portion of their breeding range (Rosenberg et al. 2016, Lin and Bulluck 2023). Male Golden-winged Warblers are strongly territorial on the non-breeding grounds, potentially because as dead-leaf foragers their prey-base is relatively limited (Chandler et al. 2016). Hence, it is possible they also exhibit territorial behavior against Blue-winged Warblers, which are also dead-leaf foragers on the non-breeding grounds (Gill et al. 2020), that we failed to observe. Alternatively, Wood et al. (2016) suggested a genetic driver of this difference in habitat selection during the breeding season as hybrids nested in intermediately forested landscapes, which could also affect their non-breeding habitat associations.

In contrast to males, occupancy by female Golden-winged Warblers was highest in the same habitats as Blue-winged Warblers (shade coffee and perhaps less-forested areas). The ecological significance of this is unclear, as unlike in the breeding season, encounters between these species would not lead to genetic introgression (Buehler et al. 2007). Furthermore, the implications of potential negative interactions between Golden-winged Warblers and Blue-winged Warblers, such as competition or competitive exclusion, is somewhat lessened because the area of sympatry during the non-breeding season is limited to the northern portion of the Golden-winged Warbler breeding range (Rosenberg et al. 2016, Kramer et al. 2018).

Fig. 5. LD1 is the first linear discriminant function and is positively associated with coffee, river/stream presence, and agriculture in the landscape, while the second function (LD2) is positively associated with coffee and also negatively associated with river/stream presence. BWWA = Blue-winged Warbler (*Vermivora cyanoptera*), GWWA M = Golden-winged Warbler male, GWWA F = Golden-winged Warbler female (*Vermivora chrysoptera*).
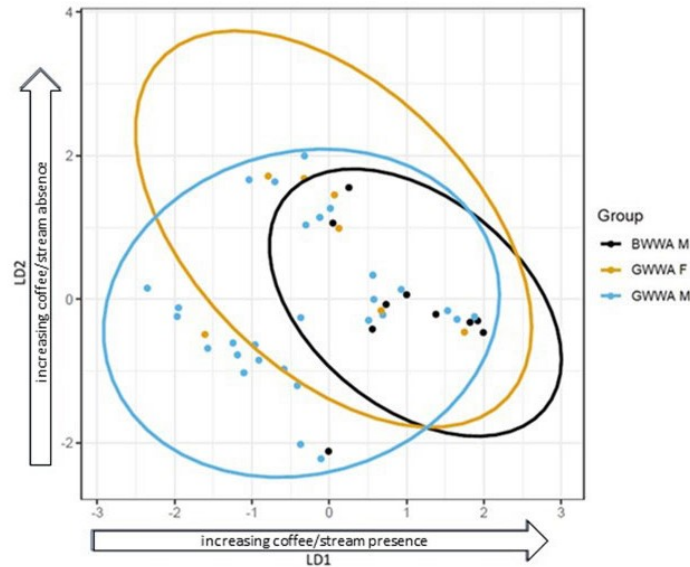
CONSERVATION IMPLICATIONS

Habitat segregation at our sites may be important from the perspective of designing and implementing conservation strategies (Catry et al. 2006, Mettke-Hofmann et al. 2015). The association of male Golden-winged Warblers with forest cover and dense shade coffee may be significant because forest habitat in the working landscapes in which we work enjoys no explicit conservation, and the expansion in the coffee sector in our study region consists of almost entirely sun coffee (King, personal observation). Forest conservation is a conservation priority in many regions where deforestation rates are high because the forest-dependent species are often imperiled, and protected areas directly conserve forest-dependent and threatened birds across the tropics (Cazalis et al. 2020). Nevertheless, in the case of our study system, protected areas and forest conservation alone may not sufficiently satisfy the habitat needs of female Golden-winged Warblers or Blue-winged Warblers that are also priority species from the standpoint of conservation, both of which appear to favor shade coffee to some extent. These findings reflect the potential of "land-sharing" and hybrid sharing–sparing conservation strategies (which encourage both forest conservation as well as agroforestry practices) to conserve bird communities in working landscapes. In land-sharing coffee systems, native shade trees are retained within coffee agriculture and where forest patches may be conserved along with shade coffee in the agricultural matrix (Chandler et al. 2013, Sánchez-Clavijo et al. 2020, Valente et al. 2022, Ritterson et al. 2021b). In the absence of habitat-specific survival, however, these habitat associations should be considered a first-order indication of habitat quality, since other migratory species (e.g., Wood Thrush) select shade coffee over native forest, yet their site persistence and survival are negatively associated with its use (Bailey and King 2019). Conservation opportunities for female Golden-winged Warblers may be limited within highland regions such as ours, and instead their fate, and likely those of Blue-winged Warblers as well, will depend on encouraging land use and conservation practices in regions where their numbers are greater (Bennett et al. 2019).

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Appendix 1. Model sets comparing different detection predictor variables for each bird group, with the full dataset and with just coffee points. Presented are the models, number of parameters (K), Akaike's Information Criterion value corrected for small sample sizes (AICc), difference in AICc from the top model (AICc), and model weight (MW).

GWWA M All Points

	K	AIC_c	ΔAIC_c	MW
WindPlaybackTime	6	1204	0	0.91
WindPlayback	5	1209.4	5.42	0.06
WindTime	4	1211.8	7.81	0.02
Playback	4	1215.4	11.35	0
Time	3	1216.1	12.12	0
Wind	3	1217.3	13.24	0
WindRiver	4	1217.6	13.59	0
WindDate	4	1219.4	15.36	0
WindSky	4	1219.4	15.38	0
River	3	1223.1	19.04	0
Null	2	1223.2	19.17	0
Sky	3	1224.8	20.74	0
Date	3	1225	20.93	0

GWWA M Just Coffee Points

	K	AIC_c	ΔAIC_c	MW
WindPlaybackTimeRiver	7	621.64	0	0.45
WindPlaybackRiver	6	622.24	0.6	0.33
WindRiver	4	624.29	2.65	0.12
River	3	625.35	3.71	0.07
Wind	8	627.7	6.05	0.02
WindPlaybackTime	6	632.62	10.97	0
WindPlayback	5	633.65	12.01	0
WindTime	4	634.57	12.93	0
Time	3	635.48	13.84	0
Playback	4	635.52	13.88	0
WindDate	4	636.67	15.03	0
WindSky	4	637.02	15.38	0
Null	2	637.82	16.18	0

	K	AIC$_c$	ΔAIC$_c$	MW
Date	3	638.21	16.57	0
Sky	3	638.69	17.05	0

GWWA F All Points

	K	AIC$_c$	ΔAIC$_c$	MW
WindPlaybackSky	6	137.18	0	0.58
WindSky	4	138.37	1.19	0.32
WindPlayback	5	143.35	6.17	0.03
Wind	3	144.48	7.3	0.02
WindDate	4	144.89	7.7	0.01
Sky	3	145.1	7.92	0.01
WindTime	4	145.27	8.09	0.01
WindRiver	4	145.58	8.4	0.01
Playback	4	146.96	9.77	0
Null	2	148.07	10.89	0
Time	3	149.28	12.1	0
River	3	149.68	12.5	0
Date	3	149.88	12.7	0

GWWA F Just Coffee Points

	K	AIC$_c$	ΔAIC$_c$	MW
WindPlaybackSky	6	116.81	0	0.5
WindSky	4	117.33	0.52	0.38
WindPlayback	5	122.79	5.98	0.03
Wind	3	123.29	6.48	0.02
WindDate	4	123.76	6.95	0.02
Sky	3	123.81	7	0.01
WindTime	4	124.18	7.37	0.01
WindRiver	4	124.73	7.92	0.01
Playback	4	125.02	8.21	0.01
Null	2	125.65	8.84	0.01
Time	3	127	10.19	0
Date	3	127.24	10.43	0
River	3	127.51	10.7	0

BWWA All Points

	K	AIC$_c$	ΔAIC$_c$	MW
WindRiverDateTime	6	287.94	0	0.73
WindRiverDateTimeSky	7	290.18	2.24	0.24
WindRiverTime	5	293.98	6.04	0.04
WindRiverDate	5	313.11	25.17	0
WindRiver	4	313.86	25.92	0
WindDate	4	327.08	39.14	0
WindSky	4	328.06	40.12	0
Wind	3	329.64	41.7	0
WindTime	4	330.45	42.51	0
WindPlayback	5	332.53	44.59	0
River	3	337.48	49.54	0
Time	3	343.81	55.87	0
Null	2	345.21	57.27	0
Sky	3	347.33	59.38	0
Date	3	347.33	59.39	0
Playback	4	348.07	60.13	0

BWWA Just Coffee Points

	K	AIC$_c$	ΔAIC$_c$	MW
Wind	3	170.17	0	0.35
WindTime	4	171.51	1.34	0.18
WindDate	4	172.21	2.05	0.13
WindSky	4	172.22	2.05	0.13
WindRiver	4	172.54	2.37	0.11
WindPlayback	5	172.64	2.48	0.1
Time	3	179.14	8.97	0
Null	2	179.15	8.99	0
Sky	3	180.77	10.61	0
Date	3	180.91	10.74	0
River	3	181.29	11.13	0
Playback	4	181.47	11.3	0