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Research Paper

Factors influencing home range size and overlap in nonbreeding Kirtland's Warblers on Eleuthera, The Bahamas

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ABSTRACT. Knowledge of space use provides insight into a species' habitat requirements needed for conservation. Little is known about space use of the near threatened Kirtland's Warbler (*Setophaga kirtlandii*) wintering in The Bahamas, and how the warbler's home range size and core area overlap among individuals and vary with sex and age, food availability, winter season, and habitat characteristics. To address these knowledge gaps, we used radio telemetry to determine sedentary home range size (95% adaptive kernel), core area (50% AK), and overlap for 27 radio-tagged warblers during two winters on Eleuthera, The Bahamas. Warblers monitored for ~3 weeks each had a median sedentary home range of 8.87 ha (range: 0.53–118.50 ha) and a median core area of 1.04 ha (range: 0.05–12.69 ha). Foliage of the warbler's principal fruit species (*Lantana involucrata*, *Erithalis fruticosa*, *Chiococca alba*) was present in more warbler core area plots than in outlier plots (telemetry fix points outside the 95% AK home range) or in random plots within the landscape. Both size of home range and core areas increased with site disturbance age – consistent with declines in fruit abundance associated with age of vegetation. Warbler core areas displayed little pairwise overlap in two sites, “RS” and “MR,” examined during October–December (RS, $\bar{x}$ = 1.49%; MR, $\bar{x}$ = 0.55%) and at a site in January–February (MR, $\bar{x}$ = 3.32%), indicating areas of exclusive use or territoriality. In contrast, a fruit-rich site (“OH”) in March–April had higher pairwise overlap in core areas (OH, $\bar{x}$ = 8.56%), which may have resulted in competition for fruit. Our findings re-emphasize the importance of conservation at a landscape scale if spatiotemporal variation in food resources increases or become more concentrated prior to migration with extreme weather due to global climate change.

Facteurs influant sur la taille et le chevauchement des domaines vitaux chez les Parulines de Kirtland hivernant à Eleuthera, aux Bahamas

RÉSUMÉ. La connaissance de l'utilisation de l'espace permet de comprendre les besoins d'une espèce en matière d'habitat en vue de sa conservation. On sait peu de choses sur l'utilisation de l'espace par la Paruline de Kirtland (*Setophaga kirtlandii*), espèce quasi-menacée qui hiverne aux Bahamas, et dans quelle mesure la taille du domaine vital et la zone centrale se chevauchent entre les individus et varient en fonction du sexe et de l'âge, de la disponibilité de nourriture, de la saison hivernale et des caractéristiques de l'habitat. Pour combler ces lacunes, nous avons utilisé la radiotélémétrie pour déterminer la taille du domaine vital sédentaire (noyau adaptatif [NA] de 95 %) et de la zone centrale (NA de 50 %), et le chevauchement de 27 parulines radiomarquées pendant deux hivers à Eleuthera, aux Bahamas. Les parulines suivies pendant ~3 semaines chacune avaient un domaine vital sédentaire médian de 8,87 ha (intervalle : 0,53-118,50 ha) et une zone centrale médiane de 1,04 ha (intervalle : 0,05-12,69 ha). Le couvert des principales espèces fruitières utilisées par cette paruline (*Lantana involucrata*, *Erithalis fruticosa*, *Chiococca alba*) était présent dans plus de parcelles de la zone centrale que dans les parcelles aberrantes (points de fixation télémétriques en dehors du domaine vital du NA de 95 %) ou les parcelles aléatoires dans le paysage. La taille des domaines vitaux et des zones centrales a augmenté avec l'âge de perturbation du site, en cohérence avec le déclin de l'abondance de fruits associé à l'âge des arbustes. Les zones centrales des parulines présentaient un peu de chevauchement par paire dans deux sites, « RS » et « MR », examinés en octobre-décembre (RS, $\bar{x}$ = 1,49 %; MR, $\bar{x}$ = 0,55 %) et dans un site en janvier-février (MR, $\bar{x}$ = 3,32 %), indiquant des zones d'utilisation exclusive ou de la territorialité. En revanche, un site riche en fruits (« OH ») en mars-avril présentait un chevauchement par paire plus important dans les zones centrales (OH, $\bar{x}$ = 8,56 %), ayant peut-être entraîné une compétition pour les fruits. Nos résultats soulignent à nouveau l'importance de la conservation à l'échelle du paysage si la variation spatio-temporelle des ressources alimentaires augmente ou devient plus concentrée avant la migration sous les conditions météorologiques extrêmes imputables aux changements climatiques mondiaux.

Key Words: *frugivory; habitat use; near threatened species; Nearctic-Neotropical migrant bird; radio telemetry; Setophaga kirtlandii; space use; wintering grounds*

INTRODUCTION

Because an animal's space use reflects access to resources required for survival and reproduction, it is expected to be sensitive to a variety of factors (McLoughlin and Ferguson 2000, Whitaker and Warkentin 2010). Space use is often measured as home range, which is the “area traversed by the individual in its normal

activities of food gathering and caring for young” (Burt 1943). The defended area of the home range (whole or part) is designated as a territory (Noble 1939). Territoriality arises when there is competition for a limited resource and the resource is economically defensible enabling exclusive use by the territorial individual (Brown 1964). An individual's space use can be influenced by a variety of factors (reviewed in McLoughlin and

Ferguson 2000, Whitaker and Warkentin 2010) including body mass, age and sex, population density, competitor density, resource abundance or dispersion, habitat age and characteristics, and landscape features. Assessment of the factors influencing space use is simplified in the nonbreeding period when interpretations are not confounded by immediate reproductive requirements (Hutto 1985).

Space use by Nearctic migrants on their Neotropical nonbreeding grounds is influenced primarily by food availability (Johnson and Sherry 2001, Sherry et al. 2005, Cooper et al. 2015), predation risk (Winker et al. 1990, Cuadrado 1997), and intraspecific dominance interactions (Marra 2000, Johnson and Sherry 2001). These factors contribute to a diversity of nonbreeding space use strategies ranging from fixed home ranges to flocks, solitary wandering or floating, the prevalence of which varies among or within species (reviewed in Greenberg and Salewski 2005). Birds reliant on ephemeral, patchy, or widely dispersed food resources (e.g., flowers and fruit) are less likely to have fixed home ranges than birds reliant on more predictable and evenly dispersed resources (Greenberg and Salewski 2005). Fixed home ranges that overlap those of conspecific neighbors are typical of nonterritorial behavior (Brown and Sherry 2008) in contrast to the absence of overlap, which indicates exclusive use or territorial behavior (Marra et al. 1993, Townsend et al. 2010). In some instances, overlap of a home range may be extensive, except for a core area, which is used intensively or exclusively by the occupant (e.g., Brown and Sherry 2008). Additionally, birds with fixed home ranges may be sedentary for the entire winter (Townsend et al. 2010) or for only a portion of the winter, especially when drought-induced food resource declines cause site abandonment (Latta and Faaborg 2001, 2002, Smith et al. 2011).

Flexible space use is associated with food availability in the nonbreeding Nearctic-Neotropical migrant Kirtland's Warbler (*Setophaga kirtlandii*, henceforth the warbler) on its wintering grounds in The Bahamas (Wunderle et al. 2014). The near-threatened (IUCN 2023) warbler overwinters here during the November to April dry season, when its food resources (fruit and arthropods) decline at some sites as the dry season progresses. The warbler has been captured in early successional sites with shrubby vegetation ranging in age from 3 to 28 years after human disturbance on the Bahamian island of Eleuthera (Wunderle et al. 2010), and elsewhere in the archipelago (Jones et al. 2013, Cooper et al. 2019). On Eleuthera, capture sites have higher frequencies of foliage presence of the warbler's favored fruit shrubs than random plots in the landscape. By surveying sites throughout a winter and resighting color-banded birds, Wunderle et al. (2014) observed the warblers abandon sites where food availability declined, but remain on food-rich sites, resulting in a positive association between warbler site fidelity and biomass of fruits and arthropods. As the warblers shift from food-poor to food-rich sites in late winter, warbler densities become positively correlated with fruit and arthropod biomass at a given site, which in drought years can result in high densities in small food-rich patches.

Little is known about the warbler's nonbreeding home range and core area size and various factors that influence the size and overlap of home ranges of sedentary individuals in The Bahamas.

Previous analyses examining capture locations and/or resighting locations of color-banded warblers were limited because these locations did not encompass the full extent and range of space use by individual birds. Resighting observations were restricted to accessible study sites, because the warblers were rarely followed beyond the study sites when they entered the dense vegetation surrounding sites. These site-restricted observations undoubtedly underestimated the warbler's space use because home ranges determined only by resighting marked individuals can be considerably smaller and differ from those calculated from radio-tracked birds (Anich et al. 2009, Can et al. 2019).

To facilitate tracking of the warblers in dense vegetation on Eleuthera, we used radio telemetry to quantify size and overlap of space use to identify some of the variables influencing nonbreeding space use by sedentary birds. As per Brown and Sherry (2008), we defined sedentary individuals as those with "relatively small fixed locations throughout the battery life span of the transmitter." We related home range and core area size to various factors (reviewed in Mcloughlin and Ferguson 2000) expected to influence size based on previous studies (sex, age class, year, winter period, age since disturbance, vegetation structure, fruit biomass and fruit shrub foliage cover). We compared abundance of favored fruiting species (fruit biomass and shrub foliage cover) in core areas with less intensively used areas of the home range (outlier sites) and with randomly selected reference sites in the landscape, with the expectation of finding greater fruit biomass and fruit shrub foliage in the core areas. Finally, we compared the average pairwise overlap of home range and core areas with neighboring co-occurring sedentary radio-tagged individuals to determine how overlap varies with sex, age, site, and winter period, to provide insights into the potential for food resource competition on the wintering grounds.

Understanding home range size and space use relationships with food resources on the wintering grounds is important for conservation. Climate change induced sea-level rise is predicted to reduce habitat availability throughout the low-lying islands of The Bahamas (Wolcott et al. 2018), yet we lack knowledge about how much winter habitat the warblers need and use. Additionally, drought-induced food resource declines affect the warbler's body condition during the winter dry season (Wunderle et al. 2014), as in other migrants wintering in the Caribbean (Marra and Holmes 2001, Brown and Sherry 2006, Akresh et al. 2019a). Carry-over effects have also been documented for the warbler, in which male reproductive success and annual survival are positively associated with March rainfall in The Bahamas (Rockwell et al. 2012, Rockwell et al. 2016). Thus, nonbreeding space use and interactions with food resources can have implications for population-level trends (Brown et al. 2017, 2019) in this near-threatened migratory bird.

METHODS

Study area

We conducted our study on Eleuthera (25°15' N, 76°20' W), a low elevation (51 m max) subtropical island with an area of 518 km² in the central Bahamas. Rainfall on Eleuthera is seasonal with most of its annual rainfall ($\bar{x}$ = 1090 mm/yr) occurring in the May through October wet season, in contrast to the November to April

dry season (Sealey 2006). Although monthly rainfall tends to decline over the course of the winter dry season (Sealey 2006) as occurred in the second winter (2005–2006) of our study, the monthly rainfall was low in October and November and increased through the end of the first winter (2004–2005) as shown in Wunderle et al. (2014). The dry season and limestone substrate contribute to a dry broadleaf evergreen plant community, locally designated as coppice, which is present throughout Eleuthera. Coppice includes both evergreen and deciduous broadleaf shrubs and trees (Correll 1979, Franklin et al. 2015). Eleuthera's current landscape is typical of most Bahamian islands (Byrne 1980) and consists of a mosaic of variably-aged vegetation primarily as a consequence of shifting agriculture, fire, or failed development (Helmer et al. 2010).

Our study occurred in southern Eleuthera (Tarpum Bay to 3 km south of Wemyss Bight and Greencastle) where sites had been previously established to study the warbler (Wunderle et al. 2010, 2014). To reduce travel time between radio-tagged birds and because we were interested in determining the overlap of space use by neighboring warblers simultaneously residing in an area during the same winter period, we concentrated radio-tagging and tracking at sites with neighboring warblers; however, in some instances radio-tagged birds shifted away from the initial capture site. Each study site contained a grid or system of trails, which allowed access through the dense vegetation. Intersections of trails and flagged markers along transects were uniquely labeled and georeferenced with a GPS unit (Garmin eTrex Vista; ± 5 m; with WAAS or Wide Area Augmentation System enabled: <https://www.garmin.com/en-US/aboutgps/waas/>) and served as bearing points.

Study sites were of different sizes due to variation in extent of usable habitat. The number of study sites used each winter varied as a result of availability of several neighboring warblers simultaneously occupying a site. We required multiple warblers in proximity because home range overlap was a key study objective. Five study sites (described in Wunderle et al. 2014) were used for capture, radio-tagging, and monitoring of warblers, including DD Road (DD), Rock Sound (RS), Wemyss Bight (WB), Ocean Hole (OH), and Madera Road (MR)

Field Methods and Analyses

Field work occurred in three nonbreeding periods, designated as early (1 October to 20 December), mid (6 January to 29 February), and late (1 March to 30 April) winter. Warblers were captured, radio-tagged, released, and followed in two winters including in early and late winter 2004–2005 and early and midwinter 2005–2006. Birds were captured in mist nets either with or without the use of tape-recorded playback of conspecific vocalizations (Wunderle et al. 2014). Standard morphometrics were obtained from all captured birds and sex (henceforth M for male and F for female) was determined by wing length and plumage, whereas age was determined by a combination of tail shape and other plumage traits (Pyle 1997). Warblers were classified as either adult (ASY; > 1 yr old) or juvenile (HY/SY; < 1 yr old) as per the U.S. Fish and Wildlife Service (1977). All birds were banded with an aluminum U.S. Geological Survey band and a unique combination of three plastic color bands under permit # 21669.

Warblers were monitored using 0.43 g transmitters (model LB-2N, Holohil Systems, Ltd., Ontario, Canada), which

represented 3.1% (range: 2.5–3.3%) of the warbler's 13.9 g average body mass. Transmitters were attached using a backpack harness of thin cotton thread (Rappole and Tipton 1991). We radio-tracked the warblers starting 24 h after the bird was released and continued daily tracking until transmitter battery failure. Transmitter battery life ranged between 6 to 27 days; individuals with less than ten days of data excluded from analyses. Birds were located using a handheld 3-element Yagi antenna. Six telemetry fixes (predicted warbler locations based on triangulation described below) for each radio-tagged bird were obtained per day, every hour between 0600 h - 1200 h or every hour between 1200 h - 1800 h on alternate days.

Because the radio-tagged warblers were rarely visible, we determined their location by triangulation from a series of georeferenced locations within the study sites (i.e., fixed bearing points) that were also plotted on study site maps. Pairs of compass bearings were gathered on a tagged individual from two fixed bearing points every hour. The predicted location of individuals from each set of bearings was determined using GIS software (ArcView 3.x; ESRI 2002), with the intersection of the two bearings providing the bird location (designated as a “telemetry fix point” or just “fix”). To minimize errors, we only used bearing pairs from fixed bearing points that were more than 40° apart, which we found reduced fix errors (Wunderle et al. unpublished data). Because time delays between triangulated bearings may reduce data accuracy (Schmutz and White 1990), we attempted to take bearing pairs within 5 min of each other; only 71 (2%) of 3082 bearings were more than five minutes apart. We re-took the bearings from other fixed bearing points if the angles to the tagged bird were less than 40° or if it was evident that the bird had moved between the two bearing readings (e.g., bird visually observed moving). To calculate bearing errors, radio tags were placed at fixed bearing points within the RS grid and seven observers took bearings from a total of 40 fixed points within the same grid (mean tag-observer distance = 162.73 m $\pm$ 22 SD, range = 27–382 m). Mean bearing error was 13.33° $\pm$ 0.02 SD (n = 138), which is equivalent to $\pm$ 12.01 m error at 50 m.

An average of 12.6% of paired bearings per bird (384/3701; range 1.6–19.7%) failed to intersect and were excluded from analyses. These errors were either a result of the radio-tagged bird moving between bearing readings, which went undetected, and/or human error. Only 125 consecutive bird locations (taken each hour) were less than 10 m apart and we, therefore, considered all individual bird locations to be distinct. We determined the average distance (m) per hour moved successively between locations (fixes) by each radio-tagged warbler within a day and report the average of the daily averages in m/hr per individual. We also report the maximum distance (m) between telemetry fix points, which refers to the maximum linear distance between two fixes obtained for an individual.

Home range was described by the minimum convex polygon (MCP; Southwood 1966, Jennrich and Turner 1969) and adaptive kernel (AK; Worton 1989) methods. We used the CALHOME program (Kie et al. 1996) to determine the shape and size of MCP and AK home ranges (95%) and core areas (50%). The CALHOME program automatically set the optimal band widths for the AK home range calculations. We use the term “home range” to indicate the 95% AK or 95% MCP and “core area” to designate the 50% AK or 50% MCP. We report MCP values for

95% home ranges and 50% core areas to enable comparisons with other studies because AK size can vary depending on the analytical software and bandwidth (Bauder et al. 2015), but we only use AKs in our analyses.

Habitat measurements

Vegetation structure, composition, and fruit biomass were measured in 10 m radius plots (0.03 ha) centered on a random subset of warbler telemetry fix points (hereafter, warbler plots). For each warbler, three plots were sampled at telemetry fix points in the 50% AK core area and three plots (with an exception for individual YY-YX with only two plots) sampled at telemetry fix points outside the 95% AK home range (designated as 95% AK outliers). We sampled vegetation at telemetry fix points that were at least > 20 m apart from each other to ensure that vegetation plots did not overlap. We sampled vegetation plots for each radio-tagged warbler within 3.5 weeks of termination of radio tracking. Within each 10-m radius plot, we determined foliage height profiles (percent cover and plant species) from 20 points at 2-m intervals along the north, east, south, and west radii of the circular plot (Wunderle et al. 2010). Percent foliage cover was determined within each specific vertical height class (>0–0.5 m, >0.5–1.0 m, >1.0–1.5 m, >1.5–2.0 m, >2.0–3.0 m, >3.0–4.0 m, >4.0–6.0 m, >6.0–8.0 m, and >8.0–10 m) and was calculated as the percent of the 20 points in each height interval in which foliage contacted the vertical pole. For height intervals > 3 m, we recorded the presence or absence of foliage along the vertical sight line of the pole and estimated height classes. We calculated the mean canopy height for each plot as the mean of the 20 midpoints of the highest height class with pole-contacting foliage. Age or time since last disturbance of each georeferenced plot was determined from a map of forest age and disturbance type developed from a chronosequence of Landsat satellite image composites that minimized cloud cover (Helmer et al. 2010).

We compared habitat characteristics of warbler plots with those of 51 reference plots in the vicinity of the study sites in southern Eleuthera. Each reference plot was located randomly within areas stratified by disturbance age and type as indicated in the satellite image-based map of Helmer et al. (2010). Reference plots were placed without knowledge of warbler presence. The reference plots were originally established to compare habitat characteristics of random plots with plots placed at warbler capture sites (Wunderle et al. 2010). Although none of the reference plots occurred in the study sites used in the current study, some reference plots were within 100 m of study sites. The reference plots were distinct from the plots at warbler fix points situated outside of each warbler's 95% AK home range. Reference plots were of the same size as warbler plots and were sampled similarly (Wunderle et al. 2010), though fruit biomass was not sampled in reference plots.

For each plot, the total number of height classes in which foliage of the warbler's principal fruit shrubs (*Erithalis fruticosa*, *Chiococca alba*, and *Lantana involucrata*) was present were tallied for each individual fruit shrub species, as well as the total number of height classes with the presence of foliage of one or more principal fruit shrubs. Also, both live (unripe and ripe fruit) and ripe fruit of the individual principal fruit shrubs were counted in 20 m x 1 m belt transects along the north-south and east-west transect in each core and 95% AK outlier plot in late winter 2004–

2005 and early and midwinter 2005–2006. Biomass of both live and ripe fruit of the principal fruit species was calculated by multiplying the dry pericarp or pulp mass for each species by the number of individual fruits.

We expected that the number of foliage height classes with the presence of a species' foliage in a plot could serve as a proxy for the species' fruit biomass in the same plot. Indeed, we found significant positive associations between the mean count of height categories with each principal fruit species' foliage (foliage abundance) and the biomass of its live and ripe fruit in all sample plots (125 core and 95% AK outlier plots). For example, significant associations occurred for *E. fruticosa* (live fruit, Spearman $r = 0.620$, $P = 0.01$; ripe fruit $r = 0.441$, $P = 0.01$), *L. involucrata* (live fruit $r = 0.761$, $P = 0.01$; ripe fruit $r = 0.659$, $P = 0.01$), and *C. alba* (live fruit $r = 0.661$, $P = 0.01$; ripe fruit $r = 0.591$, $P = 0.01$). We, therefore, examined foliage abundance and live and ripe fruit biomass as predictor variables below.

To determine the effects of various factors on the size of core and home range areas, we conducted separate analyses for each predictor variable and for each of the two response variables (95% and 50% AK). Predictor variables included winter (2004–2005 vs. 2005–2006), winter period (early, mid, late), sex/age class (ASY M, ASY F, SY M, SY F), age since disturbance, mean canopy height, principal fruit shrub foliage abundance, and biomass of live and ripe fruit. Use of separate models prevented overfitting the models with too many parameters given low sample sizes. It also averted issues with multicollinearity among correlated predictor variables. Generalized Linear Models (GLMs) were fit using Gamma distributions with a log link, because the home range data were positive, non-integers, and were often right-skewed (Bolker 2008). We removed 1-2 bird outliers from the analyses because these individuals (YX-RY, XY-RW for 95% AK; individual XY-RW for 50% AK) were highly influential in the respective models and were not representative of the relationships occurring in the rest of the data. For both sets of models (95% and 50% AKs), we examined vegetation predictor variables using data collected solely from the core plots (as the 95% AK outlier plots were outside of the 95% AKs). For categorical variables with >2 groups (i.e., winter period and sex/age class), we used the “multcomp” package (Hothorn et al. 2008) to conduct Tukey's tests to examine pairwise comparisons while controlling for the family-wise error rate. The R Statistical Program version 4.1.2 (R Core Team 2021) was used in all these analyses.

We expected that plots at fix sites in a warbler's 50% AK core would have more fruits than plots at fix sites outside of its 95% AK home range. Therefore, we used paired tests to compare fruit biomass and principal fruit shrub foliage between core plots and 95% AK outlier plots for each radio-tagged warbler. Differences between core and 95% AK outlier plots were compared for live fruit biomass and separately for ripe fruit biomass with Wilcoxon Signed-Ranks Tests. We also compared live and ripe fruit biomass separately within winter periods. Abundance of fruit shrub foliage was compared between core and 95% AK outlier plots per individual bird with paired t -tests. In addition, we used categorical analyses (row x column test of independence with a G -statistic) to compare presence versus absence of species of fruiting shrubs in foliage profiles of core versus reference plots and separately in foliage profiles of 95% AK outlier versus reference plots.

Categorical analyses were also used to examine if core plots differed by sex or age, in terms of the presence versus absence of species of fruit shrubs in foliage profiles.

Principal component analysis (PCA) in SPSS, version 20 (SPSS, Chicago, Illinois) was used to assess habitat variation among warbler core areas (50% AK) sampled in different sites (RS, DD, WB, OH, MR), winter periods (early, mid, late), and winters (2004–2005, 2005–2006). Seven habitat variables (Table 1), each averaged from the three core plots per warbler, were included in the PCA. The habitat variables were previously identified as important for characterizing warbler habitat at capture sites (Wunderle et al. 2010).

Table 1. Component scores or factor loadings for the first two principal components from a principal component analysis of seven habitat variables measured in 0.03 ha circular plots in 27 Kirtland's Warbler (*Setophaga kirtlandii*) core areas (50% adaptive kernel) on Eleuthera, The Bahamas. The PCA was based on the average of habitat measures from three plots per warbler, each plot centered on three randomly selected telemetry fix sites per warbler core area. Methods and variables are described in the text.

Variable	PC1	PC2
Age since disturbance	0.912	-0.098
Canopy height	0.862	0.340
Foliage at 0-0.5 m	-0.586	0.666
Foliage at 0.5-1.0 m	-0.225	0.893
<i>Lantana involucrata</i>	-0.904	0.202
<i>Chiococca alba</i>	0.758	0.357
<i>Erithalis fruticosa</i>	0.473	0.633
Eigenvalue	3.585	1.936

We also examined multivariate habitat traits of warbler core and 95% AK outlier plots versus reference plots with a Discriminant Analysis (DA) in R. We examined most of the same variables in the DA as in the PCA, but we used the foliage combined for the principal fruit plants (rather than individual species). Prior probabilities of the DA were determined by group sizes (McGarigal et al. 2000). There was some slight skew in the distributions of some of the included variables, and we conducted a Permutational Multivariate Analysis of Variance (PMANOVA) to statistically test for differences between the core, 95% AK outlier, and reference plots (Anderson 2001).

We determined overlap of 95% AK home ranges and overlap of 50% AK core areas using AK values of radio-tagged individuals simultaneously occupying the same study site during the same period and winter. Two individuals (WX-RR and YR-XY) had home ranges that included portions of RS and the edge of the DD site in early winter 2004–2005 and were included as RS individuals, because there were no neighboring DD birds available. Mean overlap was computed separately for home range and core area estimates, between all possible pairs of individuals within a given study site and winter period following Minta (1993). For instance, we calculated how much (%) of individual A's home range overlapped individual B's home range, and the percent individual B's home range overlapped individual A's home range. We then multiplied these two values and took the square root of

the product to obtain the mean pairwise overlap. This calculation was done between all possible pairwise combinations of radio-tagged warblers within a site and period, and the overlap pairwise values were then used as our response variable in our analyses. Overlap values could potentially range from 0 to 100, with 0 indicating absolutely no overlap in area and 100 indicating that the two areas were identical in size and location (Vega Rivera et al. 2003).

We examined mean overlap values separately for 95% AK home range and 50% AK core area estimates within four site-periods: RS-early winter 2004–2005 (4 birds, 6 pairwise overlap values), MR-early winter 2005–2006 (6 birds, 15 pairwise overlap values), MR-midwinter 2005–2006 (8 birds, 28 pairwise overlap values), and OH-late winter 2004–2005 (5 birds, 10 pairwise overlap values). We did not include other site-periods in our overlap analyses due to small sample sizes within other study sites (only one bird tracked in DD, three birds in WB). One individual (RX-) was tracked both in MR-early winter and MR-midwinter, but we deemed these overlap values as independent because the individual bird was mostly paired with different birds during the two periods and food resources varied between periods. We chose to examine site and periods combined in our analyses because two of the three study sites were not examined in multiple periods and it was not possible to partition out the effects of site versus period.

Comparisons of pairwise overlap between either 95% AK home ranges or 50% AK core areas were made with Kruskal-Wallis tests because overlap values were highly right-skewed and did not fit normal or Gamma error distributions. With pairwise overlap values as the response variable for either 95% or 50% AK, we tested the following predictor variables in separate models: site-period, sex (M-M pair, M-F pair, or F-F pair), and age (ASY-ASY, ASY-SY, or SY-SY). We also conducted post hoc Dunn's tests to examine comparisons between groups of the categorical predictors (Dunn 1961) and adjusted pairwise *P*-values using the Benjamini-Hochberg method (Benjamini and Hochberg 1995).

Associations between variables were assessed with Pearson's correlation coefficient (*r*) when normality assumptions were met and a Spearman's Rank Correlation (Spearman's *r*) when normality assumptions were not met. We defined significant results as *P* < 0.05, but show values that approach significance for descriptive purposes. Means were presented unless otherwise noted; standard deviation (SD) was used to gauge variation around means and standard error (SE) was used to compare means.

RESULTS

Movement and home range descriptive statistics

We radio-tagged 32 individual warblers, but censored results from five individuals due to insufficient sample size because two tags stopped transmitting; one bird departed from a study site; one was depredated (possibly by a cat); and one bird had a possible leg injury so the tag was removed. For this study we monitored 27 Kirtland's Warblers for ≥ 10 days, one of which (RX-) was radio-tagged twice in MR and followed in two separate periods

in the same winter (early and midwinter 2005–2006). These 28 movement samples (Appendix 1) were obtained during an average of 21.0 ± 2.24 SD days (range: 16–27 days) per bird and resulted in an average of 115.1 ± 15.1 SD fixes (range: 79–155 fixes) per bird. The warblers moved an average of 81.9 m (± 39.7 SD) per hour between successive fixes in a day, with a median daily average of 75.7 m/h (range 25.1–202.7 m/h), whereas the median maximum linear distance between fixes in a home range was 491 m (range: 120–3067 m) per tagged bird.

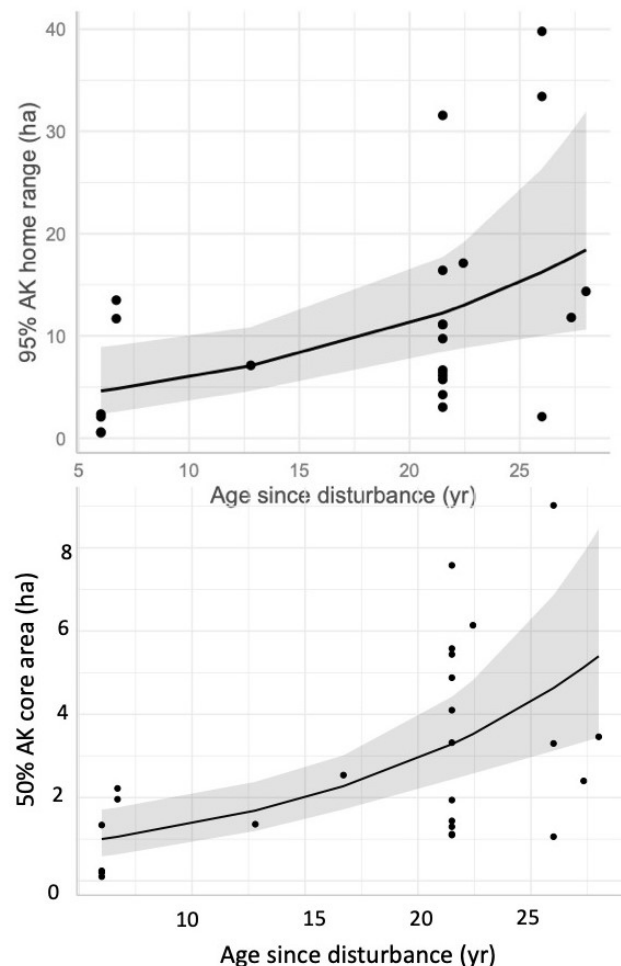
Measures of home range and core areas (Appendix 1) were highly variable and tended to be right-skewed, with a few individuals using very large areas. Overall, the median 95% AK home range was 8.87 ha (interquartile range or IQR = 10.92 ; range: 0.53 – 118.50 ha), slightly larger than the median 95% MCP home range of 6.13 ha (IQR = 0.04 ; range: 0.27 – 99.91 ha). Median 50% AK core area was 1.04 ha (IQR = 1.57 ; range: 0.05 – 12.69 ha) and slightly larger than the median 50% MCP core area of 0.69 ha (IQR = 0.76 ; range: 0.04 – 11.43 ha). An individual's 95% home range and its 50% core areas were more strongly correlated for the MCPs ($r = 0.64$) than the adaptive kernels ($r = 0.49$).

Effects on home range size

When the two influential outlier warbler 95% AK home ranges (individuals YX-RY, XY-RW) were removed from the analyses (median = 7.56 ha; IQR = 9.74 ; range 0.53 – 39.79 ha) the 95% AK home ranges ($n = 26$) were significantly smaller in late winter (1.39 ha ± 0.48 SE) than midwinter (22.30 ha ± 13.79 SE; $z = 4.01$, $P < 0.001$) and early winter (14.25 ha ± 3.04 SE; $z = -5.73$, $P < 0.001$), but the difference between midwinter and early winter was not significant ($z = -1.55$, $P = 0.27$). Home range size (95% AK) did not differ significantly between years ($t = -1.34$, $P = 0.19$) or among sex/age classes (all pairwise comparisons $P > 0.1$). The warblers had significantly larger home range sizes in older vegetation (longer time since disturbance) in core plots ($t = 2.73$, $P = 0.01$; Fig. 1). Home range size did not vary significantly ($P > 0.10$) with mean canopy height, measures of principal fruit plant foliage abundance, or biomass of live and ripe fruit in core plots.

Analyses of the 50% AK core areas (median = 0.97 ha, IQR = 1.32 ; range 0.05 – 4.53 ha) without the influential outlier (individual XY-RW) also indicated significantly smaller warbler core sizes in the late winter (0.24 ha ± 0.15 SE) compared to the mid winter (1.20 ha ± 0.25 SE; $z = 3.44$, $P = 0.002$) and early winter (1.79 ha ± 0.34 SE; $z = -4.64$, $P < 0.001$); the difference between midwinter and early was not significant ($z = -1.17$, $P = 0.47$). Core size was significantly smaller for adult females (0.54 ha ± 0.09 SE) compared to juvenile females (2.11 ha ± 0.85 SE; $z = 2.79$, $P = 0.03$) and adult males (1.69 ha ± 0.28 SE; $z = 2.97$, $P = 0.02$), but not significantly ($P > 0.10$) smaller than juvenile males (1.19 ha ± 0.59 SE). Other pairwise comparisons among age/sex classes were not significant ($P > 0.1$). Core size did not differ between years ($t = -0.35$, $P = 0.73$). The warblers had larger core sizes with older vegetation ($t = 4.07$, $P < 0.001$, Fig. 1) and taller mean canopy heights within core plots ($t = 2.54$, $P = 0.02$, Fig. 2). All other variables (principal fruit shrub foliage abundance in core plots, biomass of live and ripe fruit of principal fruit shrubs in core plots) were not significantly related to core size (all $P > 0.10$).

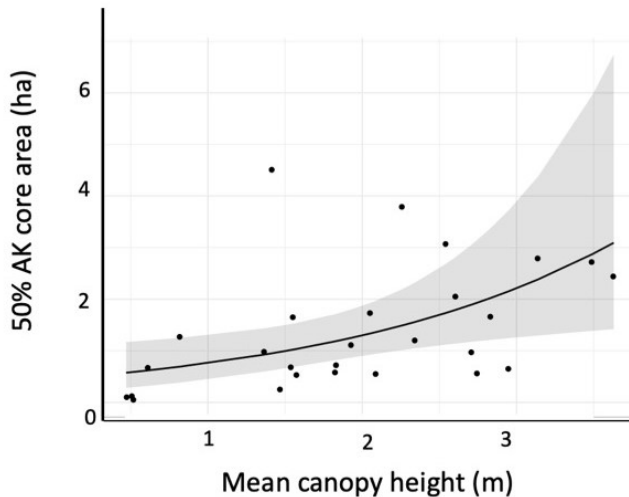
Fig. 1. Size of home range (95% adaptive kernel) in relation to age of disturbance (upper panel) and size of core area (50% adaptive kernel) in relation to age of disturbance (lower panel) for radio-tagged Kirtland's Warblers (*Setophaga kirtlandii*) followed for approximately 3 weeks each in winters 2004–2005 and 2005–2006 on Eleuthera, The Bahamas. Age of prior disturbance was determined for three randomly-selected telemetry fix points per warbler home range and three per warbler core area. Each warbler telemetry fix point was georeferenced and disturbance age based on a chronosequence of satellite imagery by Helmer et al. (2010) as described in the text. Lines and gray shading represent the regression curves and 95% CIs.



Spatial overlap

Across all radio-tracked individuals within study sites and periods, overlap between pairs of birds averaged 16.4% for the 95% AK home range area (median = 8.2% , SD = 18.4% , range = 0 – 71.3%) and averaged 3.3% for the 50% AK core area (median = 0% , SD = 11.8% , range = 0 – 83.2%). The amount of pairwise overlap in 95% AK home range areas differed significantly among site-periods (Kruskal-Wallis $\chi^2 = 9.52$, $P = 0.02$; Fig. 3), with the

Fig. 2. Size of core area (50% adaptive kernel) in relation to mean canopy height in the core areas for 27 radio-tagged Kirtland's Warblers (*Setophaga kirtlandii*; one individual radio-tagged in two separate site-periods) followed for approximately 3 weeks each in winters 2004–2005 and 2005–2006 on Eleuthera, The Bahamas. Canopy height was measured in 0.03 ha sample plots randomly-situated on three telemetry fix points in the core areas. For methods, refer to the text. Line and gray shading represent the regression curve and 95% CIs.



OH-late winter (Fig. 4) having more pairwise overlap in home range areas compared to MR-early winter ($P = 0.03$, Fig. 5) and MR-midwinter ($P = 0.04$). Other comparisons among sites were not significant ($P > 0.1$). Pairwise overlap in 50% AK core areas also differed significantly among site-periods ($\chi^2 = 20.02$, $P < 0.001$, Fig. 3), with more overlap in OH-late winter (Fig. 4) compared to the three other site-periods (MR-early winter, $P < 0.001$; MR-midwinter, $P < 0.001$; RS-early winter, $P = 0.02$). Other comparisons among site-periods were not significant ($P > 0.1$).

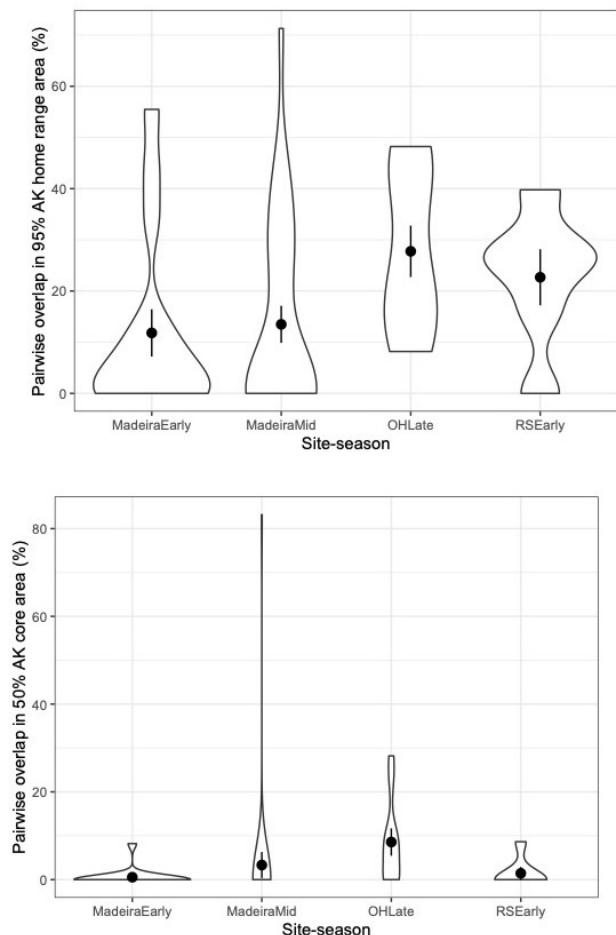
Examination of 22 M-M pairs, 31 F-M pairs, and 6 F-F pairs indicated that there were no significant differences among sex pair groupings in 95% AK home range area overlap ($\chi^2 = 1.26$, $P = 0.53$, all Dunn's tests $P > 0.1$), or in 50% AK core area overlap ($\chi^2 = 1.32$, $P = 0.52$, all Dunn's tests $P > 0.1$). Additionally, for 29 ASY-ASY pairs, 26 ASY-SY pairs, and 4 SY-SY pairs, there were no significant differences among age pair groupings in 95% AK home range area overlap ($\chi^2 = 2.68$, $P = 0.26$, all Dunn's tests $P > 0.1$), or in 50% AK core area overlap ($\chi^2 = 2.39$, $P = 0.30$, all Dunn's tests $P > 0.1$).

Habitat characteristics of warbler core and 95% AK outlier plots

Fruit biomass in warbler core vs. outlier plots

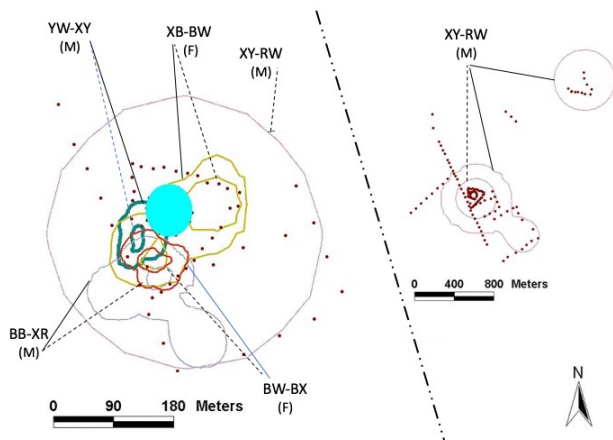
Significantly higher fruit biomass of *L. involucreata* occurred in core compared to 95% AK outlier plots for live fruit (core median = 0.01 gm/20 m², range 0.00–1.63 vs outlier median = 0.00, range 0.00–0.06; Wilcoxon signed-ranks test, $Z = -3.032$, $P = 0.002$) and ripe fruit (core median = 0.00 gm/20 m², range 0.00–0.21 vs.

Fig. 3. Violin plots with means and standard errors for pairwise overlap of home ranges (95% adaptive kernel; upper panel) and pairwise overlap of core areas (50% adaptive kernel; lower panel) of radio-tagged Kirtland's Warblers (*Setophaga kirtlandii*). The warblers were each followed for approximately 3 weeks in the same study sites and winter periods on Eleuthera, The Bahamas. Site-periods monitored include Rock Sound (RS) in early winter and Ocean Hole (OH) in late winter of 2004–2005 and Madera Rd (MR) in early and midwinter 2005–2006. Home ranges of two individuals (WX-RR and YR-XY) straddled both RS and DD sites and were included with the RS individuals in values shown here. Winter periods include early (October–December), mid (January–February), and late (March–April).



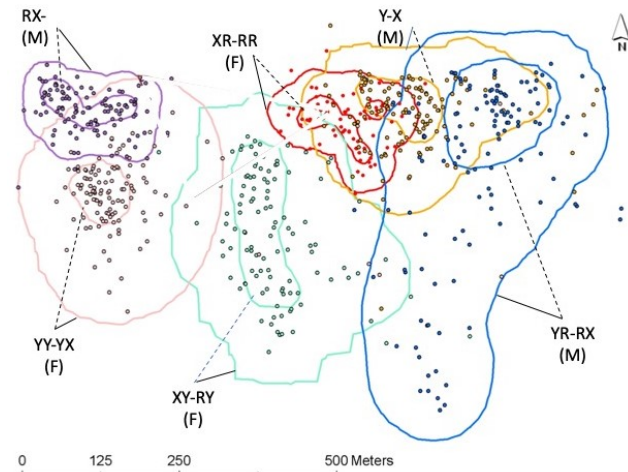
outlier median = 0.00, range 0.00–0.02; $Z = -2.727$, $P = 0.006$). Correspondingly, ripe principal fruit biomass per 20 m² (of all principal fruit shrubs) was significantly higher in core than 95% AK outlier plots (core median = 0.070; range 0.01–2.38 vs. outlier median = 0.02, range 0.00–0.82; $Z = -2.842$, $P = 0.004$), but live principal fruit biomass did not differ significantly between core and 95% AK outlier plots ($P > 0.20$). Fruit biomass did not differ significantly between core and 95% AK outlier plots for live fruit or ripe fruit of *E. fruticosus* and for *C. alba* ($P > 0.20$).

Fig. 4. Home ranges (95% adaptive kernel) and core areas (50% adaptive kernel) of five radio-tagged Kirtland's Warblers (*Setophaga kirtlandii*) simultaneously monitored for approximately three weeks in late winter (14 March to 4 April 2005) at Ocean Hole on Eleuthera, The Bahamas. Individual warblers are designated by abbreviations of color-band combinations and sex indicated by letters F (female) or M (male). Black lines originating from each banded warbler connect to its uniquely colored home range by a solid line and core area by a dashed line. Map on the left shows home ranges and core areas for four individuals and only a core area for individual XY-RW (home range is not depicted here because of scale limitations). The blue circle in left map indicates the ocean hole (i.e., pond). The black dots in both maps indicate georeferenced bearing sites used for triangulation of warbler fix sites during radio telemetry as described in the text. Because XY-RW had an exceptionally large home range and core area it is shown separately at a different scale to the right, which includes its core area and the complete home range (note the disjunct 95% AK home ranges).



Fruit biomass differences between core and 95% AK outlier plots displayed some seasonality as well. In late winter 2004–2005 OH, significant differences occurred in *L. involucrata* live fruit biomass (core median = 0.67 mg/20 m², range 0.13–1.63 vs. outlier median = 0.00 range 0.00–0.06; $z = -2.023$, $P = 0.043$) and *L. involucrata* ripe fruit biomass (core median = 0.07, range 0.06–0.21 vs. outlier median = 0.00, range 0.00–0.06; $z = -2.032$, $P = 0.042$). Similarly, in late winter 2004–2005 OH, ripe principal fruit was significantly more abundant in core than 95% AK outlier plots (core median = 0.07, range 0.06–0.21 vs. outlier median = 0.02, range 0.00–0.04; $z = -2.023$, $P = 0.043$), although the difference in live principal fruit was marginally significant (core median = 1.11, range 0.13–1.63 vs. outlier median = 0.60, range 0.00–0.34; $z = -1.753$, $P = 0.080$). In contrast, no significant biomass differences were found between core and 95% AK outlier plots for live or ripe fruit in early 2005–2006 or midwinter 2005–2006 for any principal fruit plant species individually or combined ($P > 0.09$). For midwinter 2005–2006, however, core vs. 95% AK

Fig. 5. Home ranges (95% adaptive kernel) and core areas (50% adaptive kernel) of six radio-tagged Kirtland's Warblers (*Setophaga kirtlandii*) simultaneously monitored for approximately three weeks in early winter (November–December 2005) at Madera Rd. on Eleuthera, The Bahamas. Individual warblers are designated by abbreviations of color-band combinations and sex indicated by letters F (female) or M (male). Black lines originating from each banded warbler connect to its uniquely colored home range border by a solid line and core area border by a dashed line.



outlier differences in biomass of ripe principal fruit were marginally significant (core median = 0.03, range 0.01–0.16 vs. outlier median = 0.02, range 0–0.07; $z = -1.673$, $P = 0.094$).

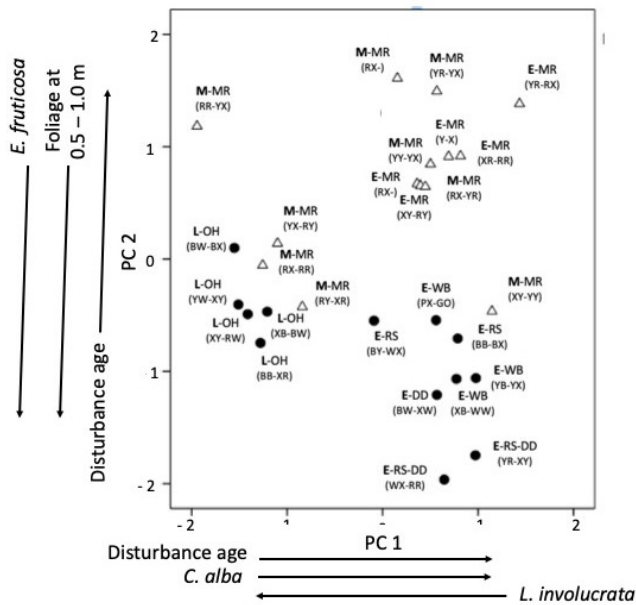
Fruit shrub foliage abundance in core vs. 95% AK outlier plots and among sex/age classes

The number of height classes with foliage of principal fruit species was higher in core than 95% AK outlier plots per individual bird (5.17 ± 0.53 SE vs. 3.76 ± 0.35 SE; paired $t = 3.21$, $df = 27$, $P = 0.003$). For individual shrub species, only *L. involucrata* had a significantly higher mean tally of foliage in core than 95% AK outlier plots (1.09 ± 0.16 SE vs. 0.33 ± 0.12 SE; paired $t = 4.47$, $df = 27$, $P < 0.001$), whereas the difference for *E. fruticosa* foliage was less (1.50 ± 0.36 SE vs. 0.85 ± 0.26 SE; paired $t = 1.819$, $df = 27$, $P = 0.08$), and *C. alba* (2.59 ± 0.35 SE vs. 2.59 ± 0.24 SE) did not differ between core and 95% AK outlier plots. The core plots did not differ significantly ($P > 0.05$) by sex or age of the warblers in the foliage presence of any of the principal fruit species.

Habitat variation among the 50% AK core area plots

Seven habitat variables measured in three 50% AK core plots were averaged for each radio-tagged warbler and the mean values per bird used to characterize variation with a PCA (Table 1), for both winters and all sites and periods (Fig. 6). The first three principal components accounted for 88.0% of variation in habitat characteristics, with 51.2% contributed by PC1, 27.7% contributed by PC2, and 9.2% by PC3. For PC1, the most influential negative loadings were *L. involucrata* foliage

Fig. 6. Graph of the first two principal components (PC1 against PC2) based on seven habitat variables (defined in Table 1) measured in 0.03 ha circular plots in 27 Kirtland's Warbler (*Setophaga kirtlandii*) core areas (50% adaptive kernel) in southern Eleuthera, The Bahamas. The PCA was based on the average of habitat measures from three core plots per warbler, each plot centered on three randomly-selected telemetry fix points per warbler core area. Black dots represent birds followed in winter 2004–2005 and open triangles represent birds followed in winter 2005–2006. Letter codes in bold besides each symbol represent the winter period (E for early; M for mid; L for late) followed by a dash for the study site code (MR for Madera Rd.; WB for Wemyss Bight; RS for Rock Sound; DD for DD Rd; OH for Ocean Hole). Letter sequences in parentheses represent unique color band combination for each warbler. Strong positive and negative factor loadings are shown each for PC1 and for PC2. Factor loadings for each of the seven habitat traits are shown in Table 1 and measurements are described in the text.



abundance, and foliage abundance of all shrub species at 0–0.5 m, whereas plot age, mean canopy height, and *C. alba* foliage had the highest positive loadings. Core plots were arrayed along PC1 axis with late winter 2004–2005 and some midwinter 2005–2006 plots at the negative extreme and early winter 2004–2005 and early 2005–2006 plots at the positive extreme. Therefore, PC1 indicates that the warbler core areas of late winter 2004–2005 and some midwinter 2005–2006 core areas had an abundance of *L. involucrata* foliage, high foliage densities at 0–0.5 m, were of young age with low canopy stature. At the other extreme, early winter 2004–2005 and some midwinter 2005–2006 core plots were of relatively old age with tall canopies with an abundance of *C. alba* foliage. For PC2, influential positive loadings were foliage abundance at 0–0.5 m and 0.5–1.0 m and *E. fruticosa* foliage

abundance. In contrast to PC1, core areas arrayed along PC2 indicated that early and late winter 2004–2005 core plots had less foliage abundance at 0.5–1.0 m and *E. fruticosa* foliage compared to early and midwinter 2005–2006 core plots. Although warblers in 2005–2006 were tracked during both early and midwinter in the MR site, the early winter birds (E-MR) had relatively less variation in their habitat use among core sites (spread along both PC1 and PC2 axes) than the midwinter birds (M-MR).

Comparisons of core, 95% AK outlier, and reference plots

Within the foliage height profiles, the foliage of each individual principal fruit shrub species had higher proportions of presence in the 87 warbler core plots than in the 51 reference plots. For *E. fruticosa* the difference was 38.1% vs. 13.7% ($G = 10.70$, $df = 1$, $P = 0.001$), for *C. alba* 69.0% vs. 35.3% ($G = 14.96$, $df = 1$, $P < 0.001$), and for *L. involucrata* 57.5% vs. 25.5% ($G = 13.71$, $df = 1$, $P < 0.001$). Presence of the foliage of the principal fruit species combined was also more frequent in the foliage height profiles of the warbler core plots than in those of the reference plots (98.9% vs. 61.0%; $G = 38.47$, $df = 1$, $P < 0.001$). There were fewer significant differences in the presence of the fruit shrub foliage in the 86 warbler 95% AK outlier plots relative to the presence of the corresponding species in the 51 reference plots. Only *C. alba* presence was significantly higher in foliage profiles of warbler 95% AK outlier plots than reference plots (72% vs. 35.3%; $G = 17.98$, $df = 1$, $P < 0.001$), whereas differences between 95% AK outlier and reference plots were not significant for *E. fruticosa* (22.1% vs. 13.7%; $G = 1.447$, $df = 1$, $P = 0.219$) and *L. involucrata* (18.6% vs. 25.5%; $G = 0.895$, $df = 1$, $P = 0.344$). Corresponding to higher proportional presence of *C. alba* foliage in 95% AK outlier plots relative to reference plots, the presence of at least one principal fruit species was higher in foliage profiles of outlier than reference plots (83.7% vs. 60.1%; $G = 8.80$, $df = 1$, $P = 0.003$).

Analyses of five habitat traits (Appendix 2) of core, 95% AK outlier, and reference plots in a combined multivariate analysis indicated that the three groups were significantly different (PMANOVA: $n = 218$, $F = 4.00$, $P = 0.005$; core vs. outlier: $P = 0.002$, core vs. reference: $P = 0.002$, outlier vs. reference: $P = 0.01$). However, there was some overlap in multivariate space using discriminant analyses (Appendix 3). The first discriminant function was negatively associated with principal fruit shrub foliage and positively associated with mean canopy height in plots (Appendix 2). The second discriminant function was not strongly influenced by any of the variables. The vegetation structural variables and age since disturbance did not have strong influences on either discriminant functions, although there were some correlations between these variables, mean height, and principal fruit plant foliage (Appendix 4). Overall, core plots were more likely to have more foliage of the principal fruit shrubs and lower mean canopy heights, compared to 95% AK outlier and reference plots, but were within the multivariate space of the other two types of plots. The 95% AK outlier plots also had more principal plant foliage and lower mean canopy height compared to reference plots, but were also mostly within the multivariate space of the reference plots.

DISCUSSION

Large home range size of Kirtland's Warblers in Eleuthera

We found that the warbler's sedentary (~21-day, 95% AK) nonbreeding home range was larger than most other wintering Nearctic-Neotropical migratory passerine birds tracked for similar time durations (Cooper et al. 2014, 2021, Townsend et al. 2010, Winker et al. 1990). While the warbler's range sizes were relatively large, methodological differences with other migrant birds (Kernohan et al. 2001, Anich et al. 2009, Can et al. 2019) and absence of examples from the same foraging guild (Brunner et al. 2022) constrain comparisons. Even with these limitations the sedentary nonbreeding home range of the Kirtland's Warbler (95% AK home range: 0.53–39.79 ha) was comparable in size to that of the Swainson's Warbler (*Limothlypis swainsonii*) estimated with telemetry (95% autocorrelated kernel density estimate home range = 2.18–20.24 ha) in dry-scrub and scrub-mangrove habitats in Jamaica (Brunner et al. 2022). As food (sub-leaf litter arthropods) increased following rainfall, wintering Swainson's Warblers constricted their space use or shifted from food-poor to food-rich sites. This flexible space use response to rainfall-mediated change in food abundance is similar to that of wintering Kirtland's Warblers foraging on ground and foliage surface arthropods and fruit. Although not examined in our current study, Kirtland's Warbler shifts between sedentary home ranges in response to fluctuations in food abundance within a winter can be of considerable extent ($\bar{x}$ maximum distance between locations = 3.3 ± 3.3 km SD; Wunderle et al. 2014), suggesting that the warbler may use a relatively large area over the course of a winter, even larger than the sedentary home ranges studied here.

The relatively large size of the warbler's winter home range compared to most Nearctic-Neotropical migrants is attributed to its occurrence on drought-prone shallow soils on limestone substrates, which contribute to high spatiotemporal variation in arthropod and fruit availability (Wunderle et al. 2010, 2014). For the warbler's ground and foliage arthropod prey, biomass measures are low and comparable to values sampled similarly in Jamaican dry limestone habitats, which are among the lowest measures of arthropod biomass for any habitat sampled on Jamaica (Strong and Sherry 2000, Johnson and Sherry 2001). Arthropod availability also varies with rainfall and moisture (Palacios-Vargas et al. 2007, Wilson et al. 2013, Wunderle et al. 2023). The distribution of the warbler's favored fruit shrubs is limited by interactions between successional stage, disturbance type, and edaphic conditions and phenologies that vary among sites and shrub species (Wunderle et al. 2010, 2014, Fleming et al. 2015). Furthermore, fruit availability can change with rainfall, fruit desiccation, and consumption by other frugivores (Wunderle et al. 2014, Fleming et al. 2024). Further, as the winter dry season progresses, moisture and food availability become patchier across the landscape (Smith et al. 2010, Wunderle et al. 2014), becoming disproportionately abundant at sites with shallow water tables (Fleming et al. 2024). Consequently, the warbler's food resources are spatially and temporarily unpredictable, favoring wide-ranging foraging over a large home range in response to fluctuations in food availability over the course of the winter.

Home range size variation: Intraspecific factors and food resources

We expected that sedentary home range and core sizes would differ between age classes and sexes due to intraspecific competition and experience (Wunderle et al. 2014), but our results were mixed. Although we found no age or sex differences in home range size, core areas of females were significantly smaller in adults than juveniles. Age class differences in female core area size were consistent with the notion that greater experience (a) may lead to greater foraging efficiency (Wunderle 1991) and thus smaller home ranges, (b) ability to find scattered food patches known from previous winter(s) (Smith et al. 2011), and (c) familiarity with the fruiting shrubs (high quality food patches) relegating younger individuals to lower quality patches requiring larger areas to obtain adequate food resources (Marra 2000). By contrast, there was no age difference in core area size in males. Between the adult sexes, however, the smaller mean core size of females, given that they are the subordinate sex (Wunderle et al. 2014), compared to males did not fit our expectation of smaller core areas in dominant individuals. Possibly there is an advantage to a larger core area for males as a hedge against a change in food availability and thus capacity for maintaining good body condition, facilitating the prompt weight gain needed for early spring migration departure which is associated with enhanced reproductive success (Rockwell et al. 2012, Cooper et al. 2015, Ouwehand et al. 2023). Females normally depart later than males; prompt weight gain may be less urgent (Rushing et al. 2016, Akresh et al. 2019b).

The warbler maintains a mixed diet of fruit and arthropods consistently throughout the winter and arthropod biomass has been shown to be correlated with warbler abundance and site fidelity (Wunderle et al. 2014). Neither home range nor core size were correlated with fruit biomass or fruit shrub foliage abundance. Although the absence of an association between food abundance and home range size has been found in other wintering migrants (e.g., Ovenbirds, *Seiurus aurocapilla*; Brown and Sherry 2008), it is also possible that our sampling design did not accurately assess fruit availability. Our three randomly-placed vegetation plots per core area may not have adequately sampled fruit biomass or foliage as they can be heterogeneous and patchy. Also, ripe fruit biomass may have been undercounted if fruit was lost during the 1 to 3-week delay between cessation of telemetry and initiation of sampling. Perhaps arthropod availability is at least a factor that drives variation in home range and core area size even though other measures suggest fruit availability influences warbler distribution. Therefore, sedentary nonbreeding home range size might be adjusted to abundance of both fruit and arthropods. Samples of fruit abundance alone may be insufficient to detect a relationship between space use and food availability.

Home range and core size both increased with site disturbance age. In addition, mean canopy height and presence of principal fruit shrub foliage were important in the first linear discriminant function for distinguishing among warbler core, warbler 95% AK outlier, and reference plots. These relationships align with an observed decrease in fruit abundance with succession on Eleuthera, where fruit abundance is greatest on younger post-disturbance sites (Fleming et al. 2024), as found elsewhere (Martin 1985, Levey 1988, Blake and Loiselle 1991). Insofar as

disturbance age is a proxy for fruit abundance, our findings are consistent with increased warbler space use with decreased fruit abundance. Pioneer species tend to fruit over longer periods and produce larger fruit crops relative to those found in shaded forest understory (Croat 1975, Denslow et al. 1986, Levey 1988). Light limitation contributes to these differences as demonstrated by higher fruit production within a species in sun-exposed than in shaded sites (Jordano 1982, Clark and Clark 1987, Smith 1987). The warbler core area expansion with canopy height was consistent with reduced fruiting in shade beneath tall canopies, compelling warblers to increase the area searched for fruit. By contrast, arthropod abundance and diversity have been found to be higher in mid to mature forest than in early series (Smith and Robertson 2008), especially in the dry season (Parrish and Sherry 1994, Silveira et al. 2010) a pattern suggesting that arthropod availability alone is unlikely to explain the observed increase in space use with disturbance age.

Variation in home range size and overlap by winter period and site

The warbler's largest home range and core areas were found in early (Fig. 5) and midwinter 2005–2006 in MR. In contrast, the smallest occurred in late winter at OH in 2004–2005 (Fig. 4). Conditions were wetter, and principal fruits and ground arthropods had higher biomass at MR in early winter to midwinter as compared with OH in late winter where fruit distribution was highly clumped (Wunderle et al. 2014). The abundant and widely scattered principal fruit shrubs (especially *C. alba* and *E. fruticosa*) in MR likely contributed to the broad dispersion of home ranges with minimal overlap of neighboring core areas ($\bar{x} = 0.55\%$), including a banded, but untagged, individual observed outside the core areas of the early MR radio-tagged birds. In addition, the overall wetter conditions in early and midwinter MR may have not only have contributed to abundant food resources at MR, but also elsewhere, possibly reducing intrusion by wandering frugivores. Therefore, the warbler's core areas in MR were likely economically defensible resulting in low core area overlap in early winter.

Although mean pairwise home range overlap was considerable (16%), the average overlap was less for core areas (3%), especially for the early (Fig. 3) and midwinter sites. The limited core area overlap is consistent with exclusive use, suggesting that neighboring warblers were territorial or avoided interacting with conspecifics. This pattern of space use is similar to that of Ovenbirds wintering in Jamaica (Strong and Sherry 2000, Brown and Sherry 2008). The exclusive use of a core area may arise when chance encounters cause individuals to actively move away from each other (Strong 1999) as also observed in wintering Black-throated Blue Warblers (*Setophaga caerulescens*; Wunderle unpublished data), which is typical for spatiotemporal territories (*sensu* Wilson 1975). Agonistic displays, including vocalizations and chases occurred in early winter at RS and MR (Wunderle et al. unpublished data), as observed in other migrant species during winter territory establishment (Brown et al. 2000, Marra 2000).

In contrast to early winter, warbler vocalizations and chases were infrequent in late winter OH in 2004–2005. Here, despite occurrence of a high density of warblers with relatively small core areas we found high levels of pairwise overlap ($\bar{x} = 8.56\%$) relative to the other site-periods. The OH overlap values represent minimum values, as two additional color-banded warblers

(without radio tags) occurred in the core areas of the five radio-tagged birds, but were not included in overlap calculations. We attribute the small core areas and high overlap in late winter OH to the warblers' consumption of abundant *L. involucrata* fruit clumped in a small (< 0.8 ha) patch in the southeast corner of the study site where the birds concentrated and fruit was also most abundant as occurred in the previous late winter 2003–2004 (Wunderle et al. 2014). Outside their core areas, however, the OH warblers were mostly foraging on arthropods as ripe fruit was scarce or absent in the remainder of the home range (Wunderle et al. unpublished data). The relatively high degree of core overlap in OH occurred in both late winters (based on resighting data) despite less than half the number of warblers (7 versus 16) present on site in late 2004–2005, but with equivalent biomass of live fruit in the fixed site transects. As concluded previously from the extensive core area overlap in late winter OH in 2003–2004 (Wunderle et al. 2014), warblers were not defending home range or core boundaries, but rather, only the space in the vicinity of an individual. Frequently, intrusion of a core area by another warbler occurred while the occupant was foraging elsewhere (Wunderle et al. unpublished data). Because of the high visitation rate by the warblers and other frugivores to OH's small isolated *L. involucrata* fruit patch in late winter, the OH core areas were perhaps not economically defensible (e.g., Brown 1964, Gill and Wolf 1975). This high degree of core area overlap in late winter OH suggests the potential for fruit competition and a reduction in territoriality (e.g., Latta and Faaborg 2001, 2002) at high density sites during the late winter especially in drought years when overall food resources are sparse elsewhere.

Conservation implications

The relatively large size of sedentary home range documented in this study and the distances over which wintering Kirtland's Warblers move when abandoning food-depleted locations and shifting elsewhere to richer food patches reinforce previous recommendations (Wunderle et al. 2014) that management at a landscape scale is required to sustain sufficient early-succession patches with food resources used by the warbler. The concentration of warbler space use in areas with favored fruit species re-emphasizes the importance of fruit, a resource highly vulnerable to spatial-temporal variation in availability; disturbance type, successional stage, phenology, rainfall, and moisture availability all contribute to a temporally and patchy distribution of fruit (Wunderle et al. 2010, Wunderle et al. 2014, Fleming et al. 2024). As the winter dry season progresses, ripe fruit patches diminish resulting in increased distances between ripe patches scattered across the landscape. By late winter of drought years, fruit availability and warbler body condition declines, which negatively affects the warbler's survival and reproduction in North America (Rockwell et al. 2016). Therefore, conservation should emphasize the least drought-prone sites such as those with shallow freshwater tables where fruit production and arthropod abundance are least affected by late winter droughts (Wunderle et al. 2014, Fleming et al. 2024).

Habitat patches for the warbler should be augmented by including sites where reoccurring disturbance occurs (e.g., sites prone to storm surge flooding, goat farms, and utility rights-of-ways) providing conditions for primary or favored fruit shrub establishment naturally or manually planted or dispersed via seeds (Fleming et al. 2015, 2019). Shrubby edges (such as natural breaks

in the canopy or along small, undeveloped forest roads) may also provide suitable habitat with higher light levels and correspondingly more fruit. These recommendations instituted at landscape scales on several islands in the central archipelago are especially important as spatiotemporal variation in the warbler's food resources are likely to increase with extreme weather associated with global climate change (Rauscher et al. 2008, Biasutti et al. 2012).

Author Contributions:

JMW, DC, EHH, and DNE conceived and refined the study design. EHH provided remote sensing data and ground truthing from her disturbance map. Warbler telemetry fixes were obtained by DC, JMW, and DNE. JEM plotted telemetry data, calculated home ranges, and randomly selected core and outlier plots for habitat measures. Field habitat measures were obtained by JMW, DC, and DNE. Statistical analyses and interpretation were provided by MEA and DC. Drafts of methods and results were produced by JMW, DC, and MEA. Final manuscript drafted by JMW with editing assistance from all authors.

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Data Availability:

Data not archived as field work was conducted on Commencement or communal lands and private property.

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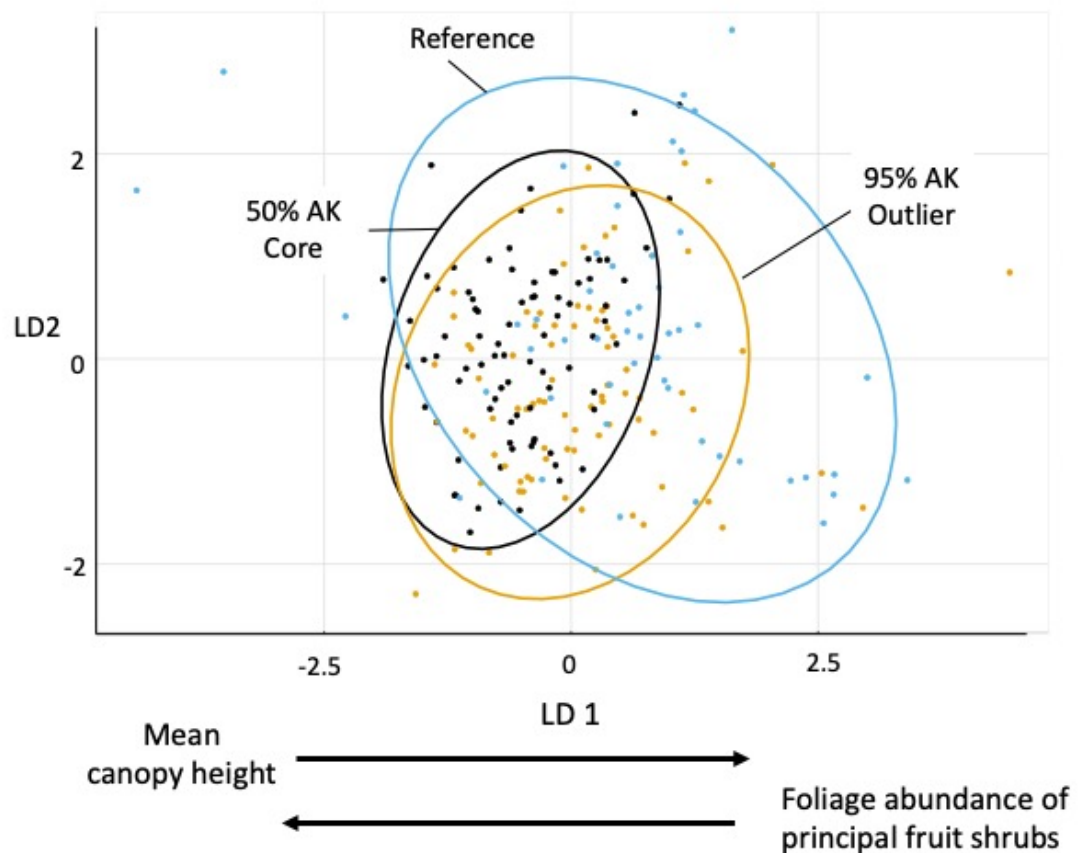
Appendix 1. Movement parameters for 27 radio-tagged Kirtland's Warblers (*Setophaga kirtlandii*) followed for approximately 3 weeks in southern Eleuthera, The Bahamas in winters 2004 – 2005 and 2005 – 2006. Number of fixes refers to locations or sites (points) where a warbler was found with telemetry. Distance/hour refers to the average distance (m) moved between successive fixes in a day and maximum distance refers to the maximum linear distance between two fixes for an individual. Home range sizes (ha) are shown for the 95% adaptive kernel (AK), 50% adaptive kernel (AK), 95% minimum convex polygon (MCP) and 50% minimum convex polygon (MCP). Note individual RX- was radio tagged twice. See text for methods.

Bird	Sex	Age	Study Site	Capture Date	Days Track	No Fixes	Distance (m)/hr	Max Distance (m)	95% AK (ha)	50% AK (ha)	95% MCP (ha)	50% MCP (ha)
WX-RR	F	SY	RS-DD	25/10/04	22	112	87.7	1,409	33.4	4.51	34.5	11.4
YR-XY	M	ASY	RS-DD	03/11/04	18	98	123.6	1,080	39.8	1.7	20.9	1.2
BY-WX	F	ASY	RS	04/11/04	23	113	63.1	214	2.1	0.5	1.9	0.7
BB-BX	M	ASY	RS	07/11/04	20	110	118.2	1,213	14.4	1.7	8.1	1.2
BW-XW	M	SY	DD	13/11/04	20	96	202.7	1,330	2.5	0.3	1.4	0.2
PX-GO	M	ASY	WB	21/11/04	21	114	58.4	789	17.1	3.1	14.8	6.2
XB-WW	F	SY	WB	23/11/04	21	115	180.8	3,067	11.8	1.2	12.0	0.6
YB-YX	M	SY	WB	25/11/04	20	114	44.9	506	31.6	3.8	22.7	3.9
BB-XR	M	SY	OH	14/03/05	21	126	42.5	220	2.1	0.1	1.2	0.1
BW-BX	F	ASY	OH	14/03/05	21	127	30.2	120	0.6	0.1	0.4	0.1
XB-BW	F	SY	OH	14/03/05	20	115	92.1	972	2.4	0.7	1.5	0.5
XY-RW	M	ASY	OH	14/03/05	21	124	74.1	1,959	78.1	12.7	99.9	9.3
YW-XY	M	SY	OH	14/03/05	20	117	25.1	163	0.5	0.1	0.3	0.1
OO-RX	M	ASY	RS	21/11/05	22	123	42.5	1,114	8.0	0.6	3.6	0.7
XR-RR	F	ASY	MR	26/11/05	16	79	64.6	179	3.0	0.6	2.2	0.7
Y-X	M	ASY	MR	26/11/05	20	130	76.8	406	6.7	0.9	4.4	0.9
XY-RY	F	SY	MR	27/11/05	23	113	100.8	947	11.1	2.1	6.8	1.5
YR-RX	M	ASY	MR	28/11/05	22	122	114.1	475	16.4	2.4	12.9	2.6
RX-	M	ASY	MR	29/11/05	21	113	62.1	199	6.1	2.8	2.1	0.6
YY-YX	F	ASY	MR	29/11/05	21	120	87.0	662	9.7	0.7	7.8	0.5
XY-YY	M	ASY	MR	01/02/06	25	146	96.1	354	11.1	2.7	8.9	3.1
RY-XR	F	ASY	MR	02/02/06	27	155	71.3	312	7.1	0.7	4.6	0.5
RR-YX	M	ASY	MR	04/02/06	18	105	74.5	356	13.5	0.9	8.1	0.8
YX-RY	M	SY	MR	04/02/06	19	96	61.7	1,379	118.5	1.3	66.9	0.6
RX-	M	ASY	MR	05/02/06	21	122	54.0	193	4.3	0.6	2.2	0.6
YR-YX	F	ASY	MR	06/02/06	22	114	77.4	328	5.7	0.7	4.3	0.6

Appendix 2. Standardized coefficients of linear discriminant functions 1 and 2 for five habitat variables measured in 0.03 ha circular plots in radio-tagged Kirtland's Warbler (*Setophaga kirtlandii*) core areas (50% adaptive kernel) outlier areas (outside the 95% adaptive kernel), and in randomly selected reference plots in southern Eleuthera, The Bahamas. Variables are defined in the text and in Wunderle et al. (2010). Bold numbers highlight the most important variables in the discriminant functions.

Variable	LD1	LD2
Foliage 0- 0.5 m	0.015	0.028
Foliage 0.5-1.0 m	0.001	0.019
Foliage of Principal Fruit Shrubs	-0.240	0.011
Age of Patch	-0.034	-0.034
Mean canopy height	0.559	-0.043

Appendix 3. Graph of linear discriminate function 1 against linear discriminate function 2 based on five habitat variables measured in 27 Kirtland's Warbler (*Setophaga kirtlandii*) core area plots (50% adaptive kernel) and outlier plots (outside the 95% adaptive kernel) and 51 randomly selected reference plots in southern Eleuthera, The Bahamas. Black dots and ellipses indicate warbler core areas, orange represents warbler outlier plots, and blue represents random reference plots. Ellipses represent 95% CIs of the groups.



Appendix 4. Correlation matrix of the five habitat variables included in the DA.

Foliage 0- 0.5 m	Foliage 0.5-1.0 m	Foliage of Principal Fruit Plants	Age of Patch
0.47			
0.05	0.29		
-0.39	-0.18	0.14	
-0.30	-0.11	0.11	0.60