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Research Paper

Movement patterns and habitat preference of Oilbirds (*Steatornis caripensis*) in the southern Andes of Colombia

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ABSTRACT. Habitat use and movement patterns in animals are usually determined by the availability of food, morphological and physiological traits, social systems, and safe sites to complete vital cycles. The objective of this study was to estimate the home-range area, daily traveled distance, and patterns of space use by Oilbirds (*Steatornis caripensis*), and the factors that can affect them in Cueva de Los Guacharos National Park (Huila, Colombia). We attached GPS devices to five individuals and recovered information from three. Home ranges were estimated by minimum convex polygon (MCP), 95 and 50% kernel methods. Traveled distances were estimated as the sum of the linear distances between sampling points (every 30 min), and patterns of habitat use were evaluated through ecological-niche factor analysis (ENFA), including forest cover, altitude, and degree of fragmentation. Analysis of habitat preference was done using 25 vegetation plots established in frequently used areas and species richness, and the proportion of consumed plants was compared with other locations within their distribution range. Home-range area was estimated to be 4517 km², possibly an underestimation due to reduced sample size. The average traveled distance per night was 55 km (range: 0-112 km). Analyses of habitat use showed a clear preference for areas with higher forest cover. Height above sea level was also largely associated with frequencies of habitat use, indicating a low use of areas above 3000 m, while the degree of fragmentation was not a strong predictor of habitat use. Finally, vegetation plots in frequently used areas showed a higher abundance of fruiting trees consumed by Oilbirds than control plots. Overall, Oilbirds have amazing movement capacity, being able to use distant landscape elements, and showing a clear preference for areas with forest cover, lower altitude, and areas with a high representation of the plant species they consume.

Habitudes de déplacement et préférence en matière d'habitat des Guacharos des cavernes (*Steatornis caripensis*) dans les Andes du sud de la Colombie

RÉSUMÉ. L'utilisation de l'habitat et les habitudes de déplacement chez les animaux sont généralement dictées par la disponibilité de ressources alimentaires, les traits morphologiques et physiologiques, les systèmes sociaux et les sites sécuritaires pour compléter les cycles de vie. L'objectif de cette étude était de calculer la superficie du domaine vital, les distances parcourues quotidiennement et les profils d'utilisation spatiale des Guacharos des cavernes (Steatornis caripensis), et cerner les facteurs qui peuvent agir sur eux dans le parc national Cueva de Los Guacharos (Huila, Colombie). Nous avons posé des unités GPS sur cinq individus et avons obtenu des informations sur trois d'entre eux. Les domaines vitaux ont été calculés au moyen des méthodes du polygone convexe minimum (MCP) et des kernels à 95 et à 50 %. Les distances parcourues ont été calculées en sommant les distances linéaires entre les points d'échantillonnage (toutes les 30 min), et les profils d'utilisation de l'habitat ont été établis par l'analyse des facteurs de niche écologique (ENFA), y compris le couvert forestier, l'altitude et le degré de fragmentation. L'analyse des préférences en matière d'habitat a été réalisée en inventoriant les espèces végétales dans 25 parcelles réparties dans des endroits fréquemment utilisés, et la proportion des plantes y ayant été consommées a été comparée avec celle d'autres endroits situés dans leur aire de répartition. Le domaine vital a été établi à 4 517 km², sans doute une sous-estimation en raison de la faible taille de l'échantillonnage. La distance moyenne parcourue par nuit était de 55 km (étendue : 0-112 km). Les analyses de l'utilisation de l'habitat ont montré une nette préférence pour les endroits avec un couvert forestier dense. L'altitude au-dessus du niveau de la mer était aussi grandement associée avec la fréquence d'utilisation de l'habitat, les endroits au-dessus de 3 000 m étant peu utilisés, alors que le degré de fragmentation ne s'est pas avéré une bonne variable explicative de l'utilisation de l'habitat. Finalement, les parcelles de végétation dans les endroits fréquemment utilisés avaient une abondance plus grande d'arbres fruitiers consommés par les guacharos que les parcelles témoin. Dans l'ensemble, les Guacharos des cavernes ont une capacité de déplacement incrovable, étant capables d'utiliser des éléments distants du paysage, et montrent une préférence certaine pour les endroits offrant couvert forestier, faible altitude, et abondance des espèces végétales qu'ils consomment.

Key Words: birds; daily travel distance; habitat use; home range; movement ecology

INTRODUCTION

For animals with the capacity of individual movement, their location in space usually depends on habitat characteristics, including a wide range of ecological factors (Nathan 2006, Scharf et al. 2018). Among the most important is the availability of nutritional resources, adequate zones to carry out reproductive events, and places with low predation risk (Fahrig 2007, Gillies and St. Clair 2010). Other parameters included in the study of movement consider topographic elements along the trajectory, travel length, and the ability to use different habitat types (Andrén 1994, Fritz et al. 2003, Frair et al. 2005). The relevance of these limiting factors is variable depending on the species (Villard et al. 1999, Johnson et al. 2002, Fritz et al. 2003) because movement capacity in birds depends on traits such as morphology, diet, foraging behaviors, body size, and habitat specialization (Neuschulz et al. 2013, Díaz Vélez et al. 2015). The most extreme cases of long-distance movement have been reported for birds that migrate from pole-to-pole (Gill et al. 2008). Still, some frugivorous species such as hornbirds, quetzals, and toucans travel long distances to find food resources that are unevenly distributed (Symes and Marsden 2007, Holbrook 2011, Mueller et al. 2014, Díaz Vélez et al. 2015). On the other hand, species such as some passerine birds, from the Furnariidae family, are incapable of crossing between forest fragments or barriers such as rivers because their movement is strongly limited by open areas (Hayes and Sewlal 2004). Therefore, anthropogenic factors such as fragmentation, edge-effects, and changes in the matrix have a heavy impact on some species (Hobbs and Yates 2003), and their movement patterns can be affected depending on factors such as fragment connectivity and size (Gobeil and Villard 2002, Gillies and St. Clair 2010, Herrmann et al. 2016). This could lead, in a cascading effect, to alterations in some ecosystem processes that depend on movements, such as seed dispersal and the movement of nutrients (Howe and Smallwood 1982, Holbrook and Smith 2000, Gosper et al. 2005, Levey et al. 2005, Stevenson and Guzmán-Caro 2010). Therefore, knowledge on how landscape changes can affect these processes is important for the conservation of populations, their interactions within communities, and ecosystem processes (Holland et al. 2009, Gillies and St. Clair 2010, Maniguaje et al. 2011).

Oilbirds (Steatornis caripensis) are nocturnal frugivorous birds distributed in the Neotropics (southern Central America, northern South America, and the tropical Andes). During the day, these birds usually sleep inside caves and canyons of both lowland and montane forests, and during the night, they travel long distances (Roca 1994, Thomas 1999, Bosque 2002, Tello et al. 2008, Holland et al. 2009). Foraging patterns in Oilbirds have only been studied in Venezuela, showing that the farthest distances from the cave are on average 44 ± 10.7 km (Holland et al. 2009). Oilbirds feed on fruits of numerous plant species (Tannenbaum and Wrege 1978, Bosque and de Parra 1992, Bosque 2002, Rojas-Lizarazo 2016, Stevenson et al. 2017), swallowing the entire fruit and digesting the pulp to later expel whole seeds in feces or through regurgitation (Bosque and de Parra 1992, Amico and Aizen 2005). Therefore, these birds have the potential of being important vectors for long-distance seed dispersal between isolated fragments (Holland et al. 2009, Karubian et al. 2012a. Stevenson et al. 2017) and could be keystone species for regeneration processes in fragmented forests. However, little is known about this species' habitat requirements outside their caves, or about the availability of appropriate areas for them within the landscape.

The objective of this study was to determine which factors, at a landscape level such as cover types, degree of fragmentation, plant diversity, and tree composition are associated with habitat use by Oilbirds. Additionally, the home range, daily traveled distance, and flight speed of three individuals were estimated. The information on habitat use was used to understand which landscape configuration can lead to the maintenance of the Oilbirds' movement patterns (Holland et al. 2009, Rojas-Lizarazo 2016). It was hypothesized that the Oilbirds would prefer the use of coverage that provides food resources and places to complete their life cycles. We also expected that at the landscape scale, they would use more often elevations near the main cave (1500-2500 masl), places with greater forest cover to find feeding trees, and would be indifferent to fragmentation given the long flight distances so far reported (Holland et al. 2009). On a local scale, it was expected that the abundance of plants consumed would be higher in frequently used areas than in control areas (i.e., where they have not been reported).

METHODS

Study area

The study area was defined as the minimum rectangle (ca. 8000 km²) enclosing all known movements of the colony of Oilbirds in the southern Andes of Colombia (Fig. 1). The studied Oilbirds based their activities in the main cave at Cueva de Los Guacharos National Park (NP), but their moving ranges included three additional national parks (Alto Fragua Indi Wasi, Serranía de los Churumbelos, and Puracé), regional reserves, private farms, and some urban areas. The main cave, in which nesting takes place, is located at 2000 masl (Fig. 1). The forests at Guacharos NP are classified into three groups: sub-Andean forests located between 1100 and 2400 masl, which include primary and secondary forests; Andean forests, located from 2400 to 2700 masl; and subparamo above 2700 masl (MINAMBIANTE 2005). At least 74 families of woody plants have been found in the park (Prada and Stevenson 2016). Also, there are forests dominated by oak trees, which are distributed in the upper limit of sub-Andean forests and the lower limit of Andean forests (MINAMBIENTE 2005).

Data collection

GPS telemetry devices of approximately 23 gm (e-obs GPS-Tags WGS84-Height, Global Positioning System of e-obs digital telemetry \bigcirc) were attached to five individuals Oilbirds captured at the main cave of Cueva de Los Guacharos NP. The devices generate radio wave transmissions at a specific radio frequency that were received with a Yagi-Uda-antenna (provided with the devices for that specific task) in the cave, allowing the downloading of the data. GPS tags corresponded to approximately 6% of the individual's body weight (mean body weight = 419 gm; Holland et al. 2009) and were attached to the back of the birds through a harness-type system using an elastic thread of 0.6 mm wide, which surrounded the individual's wings and the chest in a T form (Roshier and Asmus 2009). Devices were located close to the individual's center of gravity, so that the installation would not affect their mobility. Captures were

performed using mist nets in the cave's entrance during two different seasons. Birds of unknown sex greater than 200 gm were selected. Devices labeled G29 and G30 were installed in the nonbreeding season, beginning data collection on December 2015; and devices G31, G32, and G33 were placed during the breeding season, beginning data collection on March 2016. Data were recovered for 3 out of 5 individuals: 56 and 31 nights were sampled for devices G32 and G33, respectively, and 17 nights were sampled for device number G29. Two Oilbirds in the nonbreeding period provided no data because they did not return to the cave, at least when we downloaded data at proximity. Even with low sample sizes for both the nonbreeding and the breeding season, we present some data separately. Information on location (WGS-84), flight speed, elevation, and flight direction were collected for each bird at 30-minute intervals, from 18:00 to 6:00 h COT. A total of 2266 records were obtained for the 3 individuals, of which 29% reported coordinates and speeds of zero. Because the GPS signal is lost within the cave, coordinates of the cave were assigned when the trajectory showed an approach to that point. All location data generated by the telemetry devices were converted to UTM (universal transverse mercator) coordinates.

Fig. 1. Study area and the location of Cueva de Los Guácharos National Park in which the Oilbird colony under study was located.



Home range and movements

The home range was estimated for each individual and all three, using 100% minimum convex polygon (MCP) because it allows comparisons with other studies. Also, within the home range established for each individual, a grid (5 x 5 km) was built to estimate the number of times a quadrat was used and thus determine if the cumulative sampling effort per individual was sufficient. Furthermore, Kernel UD analyses were performed to estimate the home-range size of the studied individuals, using 95% and 50% of probability of spatial occurrence as indicators of the total range and core areas, respectively. The home ranges were estimated and visualized using the extension Spatial Analysis for ArcGIS 10.3 and R software, using the package adehabitatHR (Calenge 2006, 2011, R Development Core Team 2012). Daily straight-line distances were calculated as the sum of the linear distances between sampling points every 30 minutes. Flight-speed

data were downloaded as instantaneous samples (not calculated from a distance moved over time between consecutive GPS locations) to establish at which time of the night individuals used different movement patterns, indicating the hours when the Oilbirds engaged in fast or slow movements. Kruskal-Wallis tests were used to examine differences in flight speed between individuals and night hours.

Landscape elements and habitat use

Geographic information analyses were performed with the software QGis, ArcGis, and the packages raster, rgdal, sp, and gdistance in R (Pebesma and Bivand 2005, Hijmans and van Etten 2014, Bivand et al. 2016, OSGEO 2018). A vegetation map was generated to define the different habitat types available for the Oilbirds, including those known to be used by the species in previous studies (Snow 1961, Tannenbaum and Wrege 1978, Roca 1994, Bosque et al. 1995, Bosque 2002, Holland et al. 2009, Karubian et al. 2012a). Following CORINE land-cover classification, habitat types were grouped as (1) dense forest, (2) fragmented or disturbed forest, (3) coffee plantations, (4) mosaic of crops and natural forest, (5) mosaic of grass with natural forest, (6) pastures and crops, (7) burnt zones, naked, and degraded lands, (8) rivers and lagoons, (9) secondary vegetation, (10) shrublands, (11) forest plantations, and (12) urban zones. Additionally, the central cave was included as a cover category to avoid overestimating the use of dense forest, in which the main cave is located.

To identify which variables affect the frequency of habitat use, an ecological-niche factor analysis (ENFA) was performed using the package dehabitatHS in R 3.4.1, which estimates the degree of marginality and specialization using data on presence relative to the habitat availability in the study area (7.961 km²). Marginality is defined as the environmental distance between the species? optimum and available habitat, and specialization is the relationship between the ecological variance of the habitat and that of the species. In other words, specialization is opposite to tolerance and suggests how specialized individuals can be to specific variables (Hirzel et al. 2002). The following factors were used as explanatory variables: forest cover (percentage of trees per pixel, 30 x 30 m, in raster format; Hansen et al. 2013), height above sea level from a digital model of elevation (Amatulli et al. 2018), and degree of fragmentation, associated to the degree of continuity between the forest fragments in the study area, obtained from the forest cover map. To quantify the degree of fragmentation (F) four parameters were used: n = the quantity of cells with forest cover within the analysis window; c = the number of cells that have at least another contiguous cell with forest cover, meaning that it shares one of its sides completely; g = the number of groups of cells of the forest cover that are formed within the window; and N = the total number of cells. From these data, a fragmentation index was estimated according to González-Caro and Vasquez (2017) with values of zero when fragmentation is high and values close to one when fragmentation is low.

$$\mathbf{F} = \frac{nc+n}{gN^2} \tag{1}$$

From these analyses, a raster is obtained, indicating the index of fragmentation for every pixel, and then used as a niche factor. The analysis was performed with 999 random data replicates. To

test for spatial pseudoreplication, an estimation of Moran's Index 1 was included (Dutilleul et al. 1993).

Influence of vegetation

To evaluate if plant diversity and the proportion of species consumed by Oilbirds are associated with habitat use frequency, a comparison was made between the characteristics of the most frequently used areas by the individuals equipped with the tracking devices, and other plots in which Oilbirds were not reported. Frequently used areas (N = 30) were selected based on a high number of independent visits (more than 6). The minimum distance between sites was 300 m to avoid spatial pseudoreplication. A total of 25 locations were surveyed because of accessibility and security.

At each of the frequently used locations, 0.1 ha circular vegetation plots were established in which all trees, palms, and lianas with a diameter at breast height (DBH) > 10 cm were marked, identified, and measured. Because GPS points can have between 2-5 m of error, circular plots were established to increase the chance of including feeding trees. A GPS fix was taken as the center of the plot, and vegetation within 20 m was sampled. These plots in the frequently used locations were compared with plots within the PNN Cueva de Los Guacharos, other places in the south of Huila, and in the foothills of Caquetá, that were within the sampling window (Fig. 1), but with no reports of visits by Oilbirds. These plots were taken as controls (N = 46), even though it cannot be guaranteed that these are zones are not used by the Oilbirds, and their location was determined to represent the floristic composition of different forest types in the region (e.g., Prada and Stevenson 2016).

The DBH and the species (or morphospecies) were recorded for each plant within plots. Based on secondary literature, plant species potentially consumed by the Oilbirds of the PNN Cueva de Los Guacharos were determined (i.e., all species from the Lauraceae family, various palms such as Euterpe precatoria, Prestoea acuminata, Geonoma undata, Oenocarpus spp., Socratea exhorrhiza, Aiphanes horrida, and Chamaedorea linearis; and few other plants in the genera: Dacryodes, Trattinnickia, Dendropanax, Turpinia, Guarea, Viburnum, and Symplocos). The number of individuals of the potentially consumed species was registered, as well as their proportion in each plot, and the proportion of their basal area (BA) estimated from DBH measurements. To estimate the diversity of plants in each plot, species richness was determined as the index of species per stem, correcting the richness value for the number of individuals (Hubbell et al. 1999), which was highly variable (8-281). In fact, fewer individuals were found in frequently used areas than in control plots (ANOVA $F_{1,69}$ = 27, p < 0.001; Appendix 1, Table A1.1). The number of species per stem, the number of individuals of consumed species, their proportion, and basal area were compared between frequently used and control sites using ANOVA tests, given the parametric nature of the data.

RESULTS

Home range and movements

According to the MCP, the three Oilbirds occupied a home range of at least 4517 km² (580.6 km² for individual G29, 1866.8 km² for individual G32, and 2295.5 km² for individual G33), whereas

the 95 and 50% kernel were 2567.9 km² and 481.7 km², respectively. However, for all three individuals, rarefaction curves showed that the sampling effort was not enough to obtain a reliable estimation of the home-range area (Fig. 2), which suggests more extensive ranges. The individual sampled in the nonbreeding season spent more days outside the cave (58%) than those tracked during the breeding season (6 to 17.6% of days outside the cave), which also tended to remain closer to the cave than the other birds. Core areas included the region around the cave and grouped points in foraging areas separated by a maximum distance of 40.7 km (Fig. 3), which agrees with the Moran Index indicating spatial clustering.

Fig. 2. Rarefaction curves indicating the number of quadrats used by three Oilbirds as function of the cumulative sampling days in the PNN Cueva de Los Guácharos (Huila, Colombia). Values for G29 are shown in red (nonbreeding season), for G32 in green, and for G33 in blue.



Fig. 3. Estimated home range for the Oilbirds studied in the PNN Cueva de Los Guácharos (Huila, Colombia), according to Kernel estimates of 95%, blue; and 50%, purple. Points correspond to the locations of instantaneous records every 30 minutes, and the green triangle represents the cave in which birds were captured and fitted with GPS tags.





Fig. 4. Boxplots of instantaneous flight speed recorded during night hours for three Oilbirds captured in PNN Cueva de Los Guácharos (Huila, Colombia): (a) Oilbird G29 (nonbreeding season), (b) Oilbird G32, and (c) Oilbird G33.

The most distant point from the cave was located at 58.2 km. Tracked Oilbirds moved on average 54.7 km per night, ranging from an average of 19.0 km (nonbreeding season) to 52.0 and 79.1 km (individuals tagged during the breeding season; Appendix 1, Table A1.2). Maximum flight distances per night were of 101.3 and 112.4 km for individuals monitored during the breeding season, and 48.2 km for the individual monitored in the nonbreeding season. Oilbirds monitored during the reproductive season did not move away from the cave some nights, whereas the minimum flight distance for the other individual was 0.9 km.

The mean overall movement speed was 9.2 km/h (including travel and foraging speeds), but the maximum speeds registered were between 54.9 and 59.7 km/h (Appendix 1, Table A1.3). In general, higher movement speeds were recorded at the beginning and at the end of the night ($X^2 = 197.9$, df = 11, P < 0.0001; Fig. 4). The Oilbird sampled in the nonbreeding period showed the lowest speeds (Appendix 1, Table A1.3).

Landscape elements and habitat use

The most frequently used area was the cave (28% of the records), followed by dense forest (21%), a mosaic of crops and natural vegetation (15%), and coffee plantations (12%). The available places that did not show records included urban zones, exotic tree plantations, shrublands, and degraded, burnt, and exposed soils.

According to ENFA, there was a marginality of 0.3 (axis X in Fig. 5A), indicating that the monitored Oilbirds used specific places relative to the available habitat within the study window. Specialization (axis Y in Fig. 5A) was 4.09, showing that the variance of the available habitat was four times higher than the variance of used habitat. Considering the computation of the marginality and the specialization, there was a significant difference between the areas used and the available habitat (P = 0.001, Fig 5A). Results showed that the most influential variables

of habitat use were elevation and tree cover, which showed high levels of specialization and showed tolerance to fragmentation (axis Y in Fig. 5A). There was a preference for the use of intermediate elevations of 1000-2000 m, compared to the 200-3500 m range available in the study area (Fig. 5Ba), showing intolerance to altitudes with no birds visiting elevations above 3000 m. Similarly, they chose areas with high tree cover (Fig. 5Bb), which does not imply that they do not travel across pastures, agricultural, or urban zones, but indicates a higher permanence in areas with forest cover. Oilbirds were detected in places with all possible degrees of fragmentation, but showed a peak at relatively low fragmentation scores (Fig. 5Bc). Several of the frequently used areas were located within transformed matrices, including coffee plantations and visits to isolated trees in pastures. Based on this information, we could suggest that the current degree of fragmentation is not a determining factor in the distribution and landscape use by the Oilbirds.

Influence of the vegetation

When controlling for the number of plant individuals, the proportion of basal area (BA) of plants consumed by Oilbirds was higher in frequently used areas. When examining the index of species per stem, no differences in diversity were found between plots in frequently used areas and control plots ($F_{1,69} = 0.11$, P = 0.74). On the other hand, the proportion of individuals that were included in the Oilbirds' diet was higher in the frequently visited plots ($F_{1,69} = 9.8$, P = 0.002; Fig. 6a), as well as the proportion of BA of consumed plant species ($F_{1,69} = 4.23$, P = 0.04; Fig. 6b). Moreover, to evaluate if this difference was due to the presence of particular forest types, the same comparison was made removing plots from forests that do not have many elements consumed by the Oilbirds, such as those dominated by species of white oak (*Quercus humboldtii*), black oak (*Trigonobalanus excelsa*), and *Alfaroa colombiana*. These species are not part of

Fig. 5. Ecological-niche factor analysis (ENFA) for Oilbirds in the southern Andes of Colombia: (A) Biplot of ENFA, where the x-axis represents marginality and the y-axis represents specialization. The length of vectors shows the contribution of the variable and its influence in the position of the ecological niche (dark gray) relative to the available habitat (light gray). (B) Histograms for three variables in the ENFA, in which the habitat available in the area used by Oilbirds is shown in white, and gray events of presence obtained through GPS tags.



the Oilbirds' diet and in 6 control plots represented between 60 and 90% of the total BA, which when removed from the analyses, the difference in the proportion of BA of consumed individuals was no longer significant ($F_{1,63} = 2.35$, df = 63, P = 0.13). This suggests the avoidance of this highly dominated type of forest by Oilbirds because none of the frequently used plots presented dominance of these plants.

Fig. 6. Comparison between (a) the proportion of trees and palms that may be consumed by Oilbirds and (b) the proportion of basal area (BA) of those plants, in plots frequently used by Oilbirds fitted with GPS tags, and plots in which they have not been reported, established in the departments of Huila and Caquetá.



DISCUSSION

Results show long travel distances and large home ranges for Oilbirds in the PNN Cueva de Los Guacharos, showing larger estimates than most continental Neotropical birds (Appendix 2, Table A2.1). From a review of resident neotropical birds, the largest home ranges studied occur in raptors and scavengers, such as eagles and condors. Among frugivorous, those with more extensive ranges are parrots, which are considered fruit predators. In previous studies, it was reported that Oilbirds could fly up to 73.5 km away from the central cave (Holland et al. 2009), a value similar to the one reported in this study of 58.2 km. Even though the results from this study underestimate home-range values, they suggest that the magnitude of the areas these birds can cover is considerable. For other frugivorous Neotropical species, such as Ramphastos tucanus, R. vitellinus, and Pteroglossus pluricinctus (Ramphastidae), home ranges of 0.8-9.66 km² (Holbrook 2011) have been estimated, which is about 7 times lower than the values found for Oilbirds in this study. Ceratogymna atrata and Ceratogymna cylindricus (now Bycanistes cylindricus), frugivorous birds, considered to be important seed dispersers in Africa from the Bucerotidae family (Holbrook and Smith 2000, Mueller et al. 2014), have home ranges between 9.25-44.72 km2 (Holbrook and Smith 2000) and traveled distances of up to 15 km for Bycanistes bucinator (Mueller et al. 2014), which are also lower than the values reported for the Oilbirds.

Another interesting fact is the confirmation that these birds can spend several days outside the cave, as has been previously reported in Venezuela (Holland et al. 2009). Given their broad home range, they may play an important role as long-distance seed dispersers, even more so when they do not return to the cave every night. If this is so, Oilbirds would be dispersing seeds far from their parent trees, allowing them to escape possible pathogens, to avoid competition, and to colonize new habitats, thus giving them an advantage for establishment (Howe and Smallwood 1982, Kellner and Hubbell 2018).

Considering the low number of Oilbirds providing data from GPS devices, it is difficult to infer definitive conclusions. However, the results suggest that movement patterns might differ between breeding and nonbreeding seasons. During the reproductive season, birds showed higher flight speeds, longer daily traveled distances, and more extensive home ranges compared to the individual monitored outside the reproductive season. At the same time, they spent a lower proportion of days outside the cave, compared to the individual monitored in the nonbreeding season. This could be related to the fact that during the reproductive season birds are forced to return to their nests in the cave to take care of the chicks, whereas outside the reproductive season, birds can spend several days outside the cave near foraging sites, as reported by Holland and collaborators (2009). This would also explain patterns of high flight speeds at the beginning of the night, when they leave the cave, and early in the morning when they must return to the cave, especially during the breeding period. The median overall speed was low, probably because Oilbirds tend to forage for fruits in flight, and these foraging movements require low velocity.

Our results indicate that caves were the most frequently used habitat, which is vital to complete reproductive cycles, and habitats with high tree cover were the second most important, allowing Oilbirds to find feeding sources. However, high levels of fragmentation did not seem to limit their movements because they could overfly above crop and pasture matrices, using the whole range of fragmentation scores in the matrix studied. It is known that for several bird species, long distances between desired covers (such as forests), mountains, rivers, roads, and even behavioral limitations can restrict their movement (Bélisle and St. Clair 2002, Harris and Reed 2002, Laurance et al. 2004). For the Oilbirds we tracked, long distances were traveled both over continuous forest cover, and over severely fragmented areas (at least 10 km flying over pastures), suggesting that they may not require stepping stones to cover long distances. Long-wattled Umbrellabirds (Cephalopterus penduliger) can fly over open zones in Ecuador, allowing seed dispersal and gene flow between plant populations of different forest fragments (Karubian et al. 2012b). Oilbirds could be playing similar roles in their distribution range, even at broader spatial scales, and generating opportunities for plants to colonize new habitats, taking seeds to isolated places. Even though they were detected mainly in areas with high forest cover, they also forage in pastures and crops, in which they may find fruit sources (for instance, Nectandra acutifolia was found in open habitats). It is not clear how they know where these fruit trees are located, but their relatively unidirectional and nonerratic movement patterns suggest a previous knowledge of their location. This could be explained by mental maps and/or the sharing of information among colony members, which could be a topic for future studies.

At the scale of plots, it was evident that feeding trees are associated with the habitat-use frequency. The number, proportion, and basal area of consumed species were higher in the frequently used areas than in control plots (Appendix 1, Fig. A1.1), showing a prevalent role of fruit productivity rather than diversity. The diet of Oilbirds includes species with high contents of lipids such as laurels and some palms (Stevenson et al. 2017) and the sites that they visit present an abundance of consumed species. We also evidenced that frequently used sites had a high density of feeding trees, and within the study area, 58% of the frequently used plots had at least one large individual of consumed species (which possibly determined use). However, these species are also present in some control plots that might also be visited by the Oilbirds. A more considerable sampling effort would be required to confirm that Oilbirds would visit control sites when these species are fruiting. The analysis of vegetation differences between frequently used and control plots showed that when plots placed in oak forests were excluded (dominated by Trigonobalanus excelsa, Quercus humboldtii from the Fagaceae family and Alfaroa colombiana from the Juglandaceae family), differences were not significant. This suggests that Oilbirds avoid these zones in which there are fewer food resources for them.

Given the large home-range size found, the conservation of this colony very likely depends on the protection of forests in the whole region. Fortunately, in this region of Colombia, there is a network of national (Cueva de Los Guacharos, Churumbelos, Alto Fragua-Indi Wasi, and Puracé) and regional natural parks (e.g., Corredor Oilbirds in Puracé) that favor the maintenance of forest ecosystems. However, it was estimated that only 39.5% of the original cover remained by 2000 in the Andean territory of Colombia (Rodríguez et al. 2006) and annual deforestation in a recent year was 26,014 ha (Galindo et al. 2014). Although Oilbirds can tolerate open zones because of their wide home ranges, it is necessary to know which fragmentation threshold sustains appropriate resources and how far they can travel between forest patches. To overcome this and given the reports of individuals of this species using isolated trees, we suggest that the maintenance of forest cover in other landscape elements is necessary (as long as they include trees of the species consumed by the Oilbirds). It is also important to outline that not all types of forest cover are adequate for the species because commonly occurring vegetation types in the study area such as oak forests, and the forested plantations do not offer many resources.

Our results indicate that the elevation is also a variable that restricts habitat use by the Oilbirds, keeping their activities within an altitudinal range of 200-3000 masl, but with a higher frequency between 1000-2000 masl. Avoiding high elevations is likely a product of the fact that in this region at high altitudes, there is a preponderance of oak forests (Prada and Stevenson 2016). Besides, most flight paths to lowlands in Caquetá went through a narrow, low altitude area in the edge of the Eastern Cordillera, which could be associated with a preference for routes that minimize climbs and maintain relatively straight movements.

CONCLUSION

Landscape composition such as cover types, elevation, and plant composition play significant roles in habitat selection and movement patterns in Oilbirds. Oilbirds use caves very frequently, nesting in conditions that may minimize predation rates, and they prefer forest cover, in which they visit a particular set of fruiting plants. Our findings show that they move widely, visiting distant fragments or even isolated trees to find feeding resources in areas of at least 4517 km², avoiding high elevation areas, where their preferred food plants are scarce. Although Oilbirds are capable of inhabiting fragmented landscapes, our results highlight the importance of forests to maintain their nutritional needs. Because they use different habitats such as plantations, crops, and grass mosaics (as long as they have available resources), it is essential to maintain their feeding trees in the landscape to assure Oilbirds' visits, and thus, their ecosystem services.

Responses to this article can be read online at: http://www.ace-eco.org/issues/responses.php/1564

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Appendix 1. Field data.

Table A1.1. Number of individuals, species richness, diversity (ind./spp), consumed plant individuals and their proportion (Ind. Prop.), total basal area (BA) of consumed species, and their proportion (Prop. AB) within vegetation plots. Plots beginning with Pufe. correspond to frequently used areas, and the other ones represent other places in Huila and Caquetá.

Plot	# trees	Species	Ind/spp	Consumed individuals	Prop. Ind.	BA Consum	Total BA	Prop. BA	Control
Δ1 - 900	83	57	1.46	7	0.08	1571	50320	0.03	1
A1 = 500 A2 = 1100	02	57	1.40	, 11	0.08	10010	50520 62056	0.03	1
A2 -1100	92 75	40	1.59	0 0	0.12	10010	64022	0.17	1
A3 -1300	151	49	2.28	0 10	0.11	1827	20704	0.04	1
CP1	131	40	5.20 2.52	10	0.07	2826	10778	0.03	1
	57	40	2.32	10	0.10	3830 460	49220	0.10	1
GK2 CT1	57	24	2.30	2 5	0.19	400	22333	0.19	1
CT2	150	22	4.20	5 12	0.21	5206 9190	52275 70665	0.22	1
GUAC1	130 94	22	4.29	12	0.12	0100 2601	25600	0.15	1
GUACI CUACIO	84 07	20 20	2.33	18	0.21	3081 10912	53009	0.10	1
GUACIU	97	50 40	5.25 2.29	13	0.13	5022	52425	0.21	1
GUACI1	95 104	40	2.38	17	0.18	5082	01021	0.10	1
GUACI2	104	47	2.21	24	0.23	5082 1022	42423	0.12	1
GUACI3	100	42	2.38	20	0.07	1923	25015	0.08	1
GUACI4	106	29	3.66	20	0.19	14035	3608/	0.39	1
GUACIS	83	34	2.44	17	0.20	8933	3//42	0.24	1
GUACI6	108	34	3.18	5	0.05	1349	30690	0.04	l
GUACI7	104	44	2.36	14	0.13	1648	25257	0.07	l
GUACI8	78	42	1.86	10	0.13	1861	28891	0.06	l
GUAC19	74	6	12.33	1	0.01	104	75751	0.00	l
GUAC2	281	53	5.30	75	0.27	7838	35526	0.22	l
GUAC20	64	19	3.37	1	0.02	115	11706	0.01	1
GUAC3	85	12	7.08	2	0.02	342	73096	0.00	1
GUAC4	99	33	3.00	11	0.11	4579	37298	0.12	1
GUAC5	88	37	2.38	12	0.14	3669	55948	0.07	1
GUAC6	91	40	2.28	12	0.13	4662	38181	0.12	1
GUAC7	98	21	4.67	9	0.09	1121	34585	0.03	1
GUAC8	130	49	2.65	12	0.09	2579	37667	0.07	1
GUAC9	92	32	2.88	5	0.05	1182	37266	0.03	1
P1	35	21	1.67	3	0.29	1234	7803	0.49	1

P2	49	9	5.44	4	0.37	1169	26829	0.40	1
PJ1	71	35	2.03	7	0.15	2561	37604	0.11	1
PJ2	44	16	2.75	2	0.24	1220	15574	0.26	1
1°1Penc	100	44	2.27	24	0.24	11402	48614	0.23	1
1°2Penc	81	22	3.68	7	0.09	2231	36992	0.06	1
PUFE092	72	56	1.29	12	0.17	13927	44987	0.31	0
PUFE126	8	3	2.67	1	0.13	94	2697	0.03	0
PUFE140	17	6	2.83	1	0.06	1645	13332	0.12	0
PUFE154	81	29	2.79	21	0.26	4264	22905	0.19	0
PUFE160	47	19	2.47	13	0.28	6104	33691	0.18	0
PUFE173	74	28	2.64	18	0.24	7213	29084	0.25	0
PUFE186	85	29	2.93	18	0.21	5104	38272	0.13	0
PUFE276	16	4	4.00	1	0.06	849	4676	0.18	0
PUFE279	32	13	2.46	1	0.03	2370	29465	0.08	0
PUFE311	84	29	2.90	8	0.10	2707	30598	0.09	0
PUFE329	40	15	2.67	1	0.03	207	16689	0.01	0
PUFE347	10	8	1.25	1	0.10	608	2860	0.21	0
PUFE562	54	17	3.18	13	0.24	5302	23566	0.22	0
PUFE579	28	4	7.00	23	0.82	56636	62522	0.91	0
PUFE597	84	26	3.23	34	0.40	10056	40928	0.25	0
PUFE728	16	10	1.60	4	0.25	2069	7460	0.28	0
PUFE780	46	30	1.53	8	0.17	2744	21371	0.13	0
PUFE79	61	15	4.07	1	0.02	46	21200	0.00	0
PUFE81	31	3	10.33	0	0.00	0	4722	0.00	0
PUFE840	15	12	1.25	5	0.33	3672	7804	0.47	0
PUFE842	18	8	2.25	0	0.00	0	17434	0.00	0
PUFE9	88	29	3.03	16	0.18	10509	115457	0.09	0
PUFE128	74	58	1.28	11	0.15	4491	34988	0.13	0
PUFE602	40	13	3.08	20	0.26	5780	10545	0.37	0
Q1 -900	87	50	1.74	4	0.05	1692	32693	0.05	1
Q2 -1100	71	49	1.45	5	0.07	1044	34847	0.03	1
Q3 -1300	75	37	2.03	0	0.00	0	52410	0.00	1
Q4 -1500	122	51	2.39	8	0.07	6648	43380	0.15	1
R1	89	27	3.30	14	0.13	6682	35779	0.13	1
R2	49	19	2.58	4	0.23	836	16423	0.28	1
RC1	45	20	2.25	2	0.27	304	32322	0.21	1
RC2	64	18	3.56	7	0.21	2656	27160	0.17	1

Ro1Penc	101	15	6.73	2	0.02	296	33835	0.01	1
2°1Penc	59	21	2.81	3	0.05	513	10493	0.05	1
2º 2Penc	118	34	3.47	13	0.11	2784	48335	0.06	1

Table A1.2. Daily traveled distances and home range for three Oilbirds fitted with GPS tags captured in the PNN Cueva de Los Guácharos (Huila, Colombia).

	G29	G32	G33	Total
Average	19.0	52.0	79.1	54.7
Standard Deviation	15.4	26.4	24.5	31.3
Max. Distance/night	48.2	101.3	112.4	112.4
Min. Distance/night	0.9	0.0	0.0	0.0
50% Kernel Home Range (km ²)	72.8	286.5	315.3	481.7
95% Kernel Home Range (km ²)	469.2	1747.0	1965.3	2567.9

Table A1.3. Mean movement patterns (i.e., overall velocity in km/h, including foraging movements) recorded for three oilbirds captured in the PNN Cueva de Los Guácharos (Huila, Colombia). We found differences in average speed between individuals (KW test: $X^2 = 16.8$, df = 2, P = 0.002). Letters represent similar groups, showing that the oilbird on the non-breeding season had the lowest values.

	G29	G32	G33	Mean
Average (km/h)	3.5 b	10.1 a	11.6 a	9.2
Standard Deviation	9.5	15.3	16.0	14.8
Max. Speed (km/h)	54.9	56.3	59.7	57.0



Fig. A1.1. Comparison between (a) plant species richness ($F_{1,64} = 14.8$, P = 0.0003) and (b) the proportion of consumed plant species ($F_{1,69} = 12.25$, P = 0.0008) in frequented areas (1) and where oilbirds have not been reported (0), in plots established in the Huila and Caquetá departments.

Appendix 2. Data from a literature search.

Table A2.1. Home range data and daily distances for Neotropical birds. The search was done in *google scholar* and *web of science* using the words "neotropical" AND "bird*" AND "home range" AND "daily distance*". Only species from neotropical countries were included. The numbers following species names correspond to the references below the table.

Species	Common name	Home Range (km ²)	Flight path	Site
1			distance (km)	
Harpyhaliaetus coronatus ³⁸	Crowned Eagle	12845		Brazil/Argentina
Aramides Wolfi ¹⁸	Brown Wood-Rail	1350		Bilsa Biological Station,
				Ecuador
Rhynchopsitta terrisi ²⁶	Cotorra serrana oriental	123.8 - 47.4	23.62 - 23.71	Sierra Madre Oriental, México
Vultur gryphus ²⁷	Andean condor	14.169 - 66.624		Andes centrales de Chile y Argentina
Amazona auropalliata ³⁰	Yellow-naped Amazon	10.414 ± 2.515		Guanacaste
Crax globulosa ²⁰	Wattled Curassow	8.04 ± 5.56		Uacari Sustainable Development Reserve
Ara rubrogenys ²⁴	Red-fronted Macaw	3.3 - 57.38	9 - 28	Andean dry forests, Bolivia
Pteroglossus pluricinctus ¹³	Many-banded Araçari	1.91		Yasuní, Ecuador
Crax alector ²	Black Curassow	1.85		Tinigua National Park
Mitu salvini ³¹	Salvin's Curassow	1.55		Tinigua National Park
Rupornis magnirostris ²⁵	Roadside hawk	1.43		Sao Paulo, Brazil
Ramphastos sulfuratus ¹⁰	Keel-billed Toucans	0.97 ± 0.33		Los Tuxtlas, Mexico
Ramphastos vitellinus ¹³	Channel-billed	0.86		Yasuní, Ecuador
Ramphastos tucanus ¹³	Toucan White-throated Toucan	0.86		Yasuní, Ecuador

Megascops choliba ¹	Screech-Owl	0.808 ± 0.402		Brazilian Cerrado
<i>Tyrannus melancholicus</i> ¹⁴	Tropical Kingbird	males (0.430 ± 0.226) ,		Brazilian Cerrado
		females (0.456 ± 0.455)		
Nothoprocta ornata ⁹	Ornate Tinamou	0.438 ± 0.216		Qurpa
Grallaria ridgelyi ¹⁶	Jocotoco Antpitta	0.411 ± 0.053		Reserva Tapichalaca
Cyanocorax chrysops ³⁷	Plush-crested Jay	0.2 - 0.3		Brazil
Amazona leucocephala ³³	Bahama Parrot	0.186 (SE = 19.47)		Great Abaco Island
Grallaria varia ¹⁵	Variegated Antpitta	0.176		Amazonia
Colinus cristatus ³⁶	Crested bobwhites	0.161 ± 0.116	0.360 ± 0.241	Estación Experimental La
				Iguana
Poospiza cinerea⁴	Cinereous Warbling- Finch	0.150 and 0.166		Alto da Boa Vista
Suiriri affinis ²²	Campo Suiriri	0.14 ± 0.02		Central Brazil
<i>Poospiza cinerea</i> ²³	Cinereous Warbling- finch	0.136 - 0.213		Paredão da Serra do Curral City Park
Suiriri islerorum ²²	Chapada Flycatcher	0.112 ± 0.006		Central Brazil
Cipo espinhacensis ⁶	Cipo Cinclodes	0.093		Serra do Breu
Sclerurus scansor ¹²	Rufous-breasted	0.054 - 0.133	0.059 - 0.279	Atlantic forest
	leaftosser			
Centronyx bairdii ³²	Baird's sparrow	0.048 ± 0.019 IC 95 %	$0.203 \pm DE \\ 0.187$	Rancho Santa Teresa
Ammodramus savannarum ³²	Grasshopper sparrow	0.044 ± 0.023 IC 95 %	0.134 ±DE 0.106	Rancho Santa Teresa
Asthenes luizae ⁷	Cipo Canasteros	0.04	1.238 , 0.780 and 1.056	Espinhaco Range
Mixed flocks ¹⁷	Mixed flocks	0.032 - 0.133		Noragues
Parkesia motacilla ¹¹	Louisiana Waterthrush	0.03		Caribbean National Forest
Aulacorhynchus	Blue-throated	0.02		
caeruleogularis ²⁸	Toucanet			

Chiroxiphia caudata ¹²	Swallow-tailed manaki	0.024 - 0.175 (max = 4.60)	0.053 - 0.201	Atlantic forest
Seiurus aurocapilla ¹⁹	Ovenbirds	0.01 - 0.07		Belize
Dixiphia pipra ³⁴	White-crowned Manakin	0.012 - 0.057		Tiputini Biodiversity Station
Pyriglena leucoptera ⁵	White-shouldered fire- eye	0.013 ± 0.006		Manancial do Barreiro
Amazona vittat ²¹	Puerto Rican parrots	0.011 ± 1.35		Puerto Rico
Thamnophilus caerulescens ⁵	Variable antshrike	0.010 ± 0.003		Manancial do Barreiro
Catharus bicknelli ³⁵	Bicknell's Thrushes	0.007-0.032		Sierra de Bahoruco National Park
Dysithamnus mentalis ⁵	Plain antvireo	0.007 ± 0.002		Manancial do Barreiro
Several species ²⁹	Several iinsectivorous birds	0.005 - 0.075		Vicosa region
Arremon assimilis ³	Gray-browed brush finch	0.005 ± 0.003		Andes, Colombia
Pyriglena leucoptera ⁵	White-shouldered fire- eye	-	0.351 - 0.498	Atlantic forest
Otus nudipes ⁸	Puerto Rican Screech Owl	2.2925e-5 - 4.4675e-5		Puerto Rico

*Home rage were mostly reported using the MCP method of 100% and 95% and in occasions by Kernel UD of 50% and 95% method

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