



Patterns of territorial space use by Shining Sunbeams (*Aglaeactis cupripennis*), tropical montane hummingbirds

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ABSTRACT. For many territorial hummingbirds, habitat use is influenced primarily by the interaction between resource acquisition and non-foraging behaviors such as territory advertisement and defense. Previous research has highlighted the importance of foraging-associated habitat features like resource density and distribution in determining the space-use patterns of hummingbirds. Less is known, however, about how habitat selection associated with non-foraging behaviors influences space use by territorial species. We used radio telemetry to examine patterns of territorial space use by Shining Sunbeams (*Aglaeactis cupripennis*) in high Andean montane forests near Manu National Park, Peru, and Bosque Comunal “El Carmen” near Chordeleg, Ecuador. We quantified within-territory habitat characteristics related to resource acquisition and non-foraging behaviors such as territory advertisement and defense. We found that Shining Sunbeams showed high use of core areas in territories where foraging effort was relatively low. We found no relationship, however, between the position of core areas and habitat characteristics associated with territory defense, predator avoidance, or other non-foraging behaviors. We also found no relationship between use of non-core areas and habitat use based on resource acquisition. Thus, patterns of territorial space use by Shining Sunbeams may be characterized by core areas not determined by foraging behavior. Further studies examining territorial behaviors and the influence of intrusion pressure will help identify the underlying determinants of territory space use by this and other species of Andean hummingbirds.

RESUMEN. Patrones de uso del espacio territorial por el Colibrí cobrizo (*Aglaeactis cupripennis*), colibrí montano tropical

Para muchos colibríes territoriales, el uso del hábitat está influenciado principalmente por la interacción entre la adquisición de recursos y los comportamientos no forrajeros, como el anuncio y la defensa territorial. Investigaciones previas han resaltado la importancia de las características del hábitat asociadas con el forrajeo, como la densidad y la distribución de los recursos para determinar los patrones de uso del espacio de los colibríes. Sin embargo, se sabe menos acerca de cómo la selección del hábitat asociada con los comportamientos de no alimentación influye en el uso del espacio por parte de las especies territoriales. Utilizamos la radiotelemedría para examinar los patrones de uso del espacio territorial por el Colibrí cobrizo (*Aglaeactis cupripennis*) en los bosques montañosos altoandinos cerca del Parque Nacional Manu, Perú, y el Bosque Comunal “El Carmen” cerca de Chordeleg, Ecuador. Cuantificamos las características del hábitat dentro del territorio relacionadas con la adquisición de recursos y los comportamientos no forrajeros, como el anuncio y defensa territorial. Descubrimos que el Colibrí cobrizo mostraba un alto uso de áreas centrales en territorios donde el esfuerzo de búsqueda de alimento era relativamente bajo. Sin embargo, no encontramos relación entre la posición de las áreas centrales y las características del hábitat asociadas con la defensa del territorio, la evitación de depredadores u otros comportamientos que no son de forrajeo. Tampoco encontramos relación entre el uso de áreas no centrales y el uso del hábitat basado en la adquisición de recursos. Por lo tanto, los patrones de uso del espacio territorial por el Colibrí cobrizo puede caracterizarse por áreas centrales no determinadas por el comportamiento de búsqueda de alimento. Otros estudios que examinen los comportamientos territoriales y la influencia de la presión de intrusión ayudarán a identificar los determinantes subyacentes del uso del espacio territorial por esta y otras especies de colibríes andinos.

Key words: Andes, montane forest, Manu National Park, Neotropics, *Oreocallis*, radio telemetry, Trochilidae

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The territorial behavior of hummingbirds can be influenced by factors such as resource abundance and quality, prior-residence effects, and the identity and density of co-occurring competitors (Norton et al. 1982, Marcheseault and Ewald 1991, Temeles et al. 2004,

Kokko et al. 2006, Rousseu et al. 2014, Mendiola-Islas et al. 2016). The results of previous studies have highlighted how these factors can influence territory size, or the thresholds needed to maintain territorial behavior in some species (Norton et al. 1982, Eberhard and Ewald 1994, Justino et al. 2012). For example, natural variation and experimental manipulation of competitor density, flower abundance, nectar volume, and nectar quality have been used to demonstrate that territorial hummingbirds respond to environmental cues by adjusting the size of defended areas (Ewald and Carpenter 1978, Hixon 1980, Hixon et al. 1983, Tamm 1985, Marchesseault and Ewald 1991, Eberhard and Ewald 1994, Temeles et al. 2004, Hazlehurst and Karubian 2018). Such effects can interact with reduced resource availability and lead to territory expansion and increased intrusion pressure that may impose limits on the upper bounds of territory size (Hixon 1980, Tamm 1985, Eberhard and Ewald 1994).

In addition to their impact on territory size, similar environmental factors can influence the within-territory dynamics of hummingbirds (Tamm 1985, Temeles et al. 2004, García-Meneses and Ramsay 2012, Justino et al. 2012). The relationship between resource acquisition and territory defense may produce different space-use patterns by territory owners. For example, elevated levels of aggression and high visitation rates by resident owners are correlated with patches containing many flowers (Stiles 1971, Wolf and Hainsworth 1991, García-Meneses and Ramsay 2012, Missagia and Alves 2016). Territorial aggression also depends on the size of competitors and the extent of resource overlap (Lyon et al. 1997, Dearborn 1998), which may vary across seasons or with time of day (Stiles 1971, Paton and Carpenter 1984). For example, some species of hummingbirds spend more time near territory boundaries during peak activity hours to aid in territory defense and then later consolidate foraging efforts near territory cores (Paton and Carpenter 1984). Ultimately, overall patterns of space use by territorial hummingbirds are related to resource acquisition, territory defense, and how these factors interact with features of the habitat.

To describe space-use patterns by territorial hummingbirds, understanding how different

behaviors might be associated with particular habitat characteristics is necessary. Previous studies of the relationship between habitat and territoriality have largely focused on foraging behavior, correlating hummingbird visitation rates to resource-dense patches (Justino et al. 2012, García-Meneses and Ramsay 2012, Jiménez et al. 2012). However, less is known about how non-foraging behaviors and related habitat features might influence patterns of space use, particularly structural habitat characteristics. For example, some vegetation in territories may provide greater visibility or maximize signal transmission in territory advertisement (García-Meneses and Ramsay 2012, Jiménez et al. 2012, Justino et al. 2012, Rousseu et al. 2014). Incorporating such data into our understanding of the territorial behavior of hummingbirds has been challenging due to the difficulty of tracking individual hummingbirds and obtaining precise, behaviorally explicit data on space use in hummingbird territories.

We used radio telemetry to address this limitation and describe patterns of space use by Shining Sunbeams (*Aglaeactis cupripennis*), a territorial hummingbird found throughout high-elevation regions in the tropical Andes (Schulenberg et al. 2007). Although not obligate specialist nectarivores (i.e., feeding from few flower species), much of their diet consists of nectar from the flowering tree, *Oreocallis grandiflora* (Proteaceae), in regions where their ranges overlap (Céspedes et al. 2019). This system provides a unique opportunity to examine foraging and non-foraging determinants of territory space use by allowing quantification of resource availability while simultaneously tracking individuals to describe the spatial distribution of behaviors (e.g., foraging, vocalizations, and territorial aggression). Using this approach, we correlate hummingbird behaviors with habitat features, specifically resource density and vegetation structure, to evaluate space use in non-breeding territories. By considering habitat structure, our goal was to describe the relative contribution of non-foraging behavior in determining patterns of hummingbird territoriality. Specific objectives were to determine (1) if there are core areas in territories that are used more frequently and, (2) if so, whether core areas and non-core areas have different habitat structural features and

patterns of use. An important goal of our study was to evaluate new ways to quantify the local distribution of and habitat use by hummingbirds, which can help us better understand interactions among species, forces structuring local communities, and consequences for pollination in flowering plant communities in the high Andes.

METHODS

Study site and focal species. Our study was conducted on the eastern slope of the Andes at the Wayqecha Biological Station located at the southern edge of Manu National Park in Peru (13°10′29.6″S 71°35′13.8″W), and the Bosque Comunal “El Carmen” in the Azuay province of central Ecuador (2°59′05.1″S 78°44′45.2″W). Both sites are at the boundary between tropical montane forest and either high-elevation Andean *puna* (Peru) or *páramo* (Ecuador). In these transitional regions, habitat structure was relatively heterogeneous, with distinct patches of montane forest separated by open grasslands. These isolated patches of forest were composed of trees belonging to common montane forest genera, such as *Eugenia* and *Weinmannia*, and *Chusquea bamboo*. *Oreocallis grandiflora* was the most abundant ornithophilous flowering species at both locations and, in many areas of our study sites, was the only available floral resource during our study.

Shining Sunbeams were the most common hummingbird observed during our study at both locations. All individuals captured during our study displayed territorial behavior, but their sex was not determined. Flight displays, vocalizations, and aggression toward other hummingbirds were observed for all tracked individuals. Territorial behavior was often initiated from perches in defended *O. grandiflora* trees (L. Pavan, pers. observ.). Many Violet-throated Starfrontlets (*Coeligena violifer*) and Sparkling Violetears (*Colibri coruscans*) were present at our Peruvian study site, whereas Green-tailed Trainbearers (*Lesbia nuna*) and Purple-throated Sunangels (*Helianthangelus viola*) were present at the Ecuadorian site. Tyrian Metaltails (*Metallura tyrianthina*) were common at both locations. All non-target species were observed intruding into the territories of Shining Sunbeams and feeding on *O. grandiflora* flowers, but territorial intrusions by conspecifics were more common

than intrusions by the non-target species (Céspedes et al. 2019).

Behavioral space use. We used radio telemetry to obtain data on the distribution of feeding and non-feeding activities in territories. Shining Sunbeams ($N = 19$) were captured using mist-nets between 15 August 2013 and 9 December 2015 (11 in Peru and 8 in Ecuador). Territory owners were targeted by placing mist-nets in areas where individuals exhibited territorial behavior (e.g., vocalizations, visual displays, and aggression toward other hummingbirds). All 19 birds were likely adults based on plumage and the degree of corrugations on their bills. Radio-transmitters (0.25 g; Blackburn Transmitters, Nacogdoches, TX) were attached ~1 cm below the interscapular space on the back by applying eyelash adhesive to the skin (DUO, American International Industries, Los Angeles, CA), allowing transmitters to fall off and be retrieved when feathers started to regrow. No apparent behavioral or flight differences were observed between individuals with and without transmitters; other investigators using radio telemetry to study hummingbirds have also reported no apparent negative effects (Hadley and Betts 2009, Zenzal et al. 2014, Volpe et al. 2016, Zenzal and Moore 2016). Shining Sunbeams are relatively large hummingbirds (mean = 7.04 ± 0.37 [SD] g, $N = 19$), and tags were only placed on birds if the weight of tags was < 5% of their body mass (Kenward 2001).

Tracking began one day after transmitter deployment, and birds were then tracked for 2–4 days using a TRS-10X receiver with a 0.1-MHz bandwidth and 3-element Yagi antenna (Wildlife Materials). Tracking took place in two sessions each tracking day, either from 6:30 to 8:30 and 13:00 to 15:00, or from 9:00 to 11:00 and 15:30 to 17:30. All birds were tracked on consecutive days and during the same time period each day. GPS locations, elevation, and behavioral observations were recorded every 10–15 min during the 2013 field season, and every 5 min in 2014 and 2015. Behaviors were categorized as feeding, vocalizing, displaying, aggression, or perching/movement (movement refers to individuals observed moving between perches when the start and end locations were not observed). Visits to either individual flowers or inflorescences were recorded as feeding

behavior. Displays were defined as non-vocal territory advertisement and were most often observed as flight displays. Aggression was defined as an antagonistic interaction with another hummingbird (regardless of species) such as direct fighting or chasing behavior. All other observations were recorded as perching/movement if they could not be categorized as another behavior type. Observations were made using binoculars from no closer than 10 m to avoid disturbance. We recorded 50 locations, elevation measurements, and behavioral observations for each of the five birds tracked in 2013. Because the frequency of observations was higher for the 14 birds tracked in 2014 and 2015, we randomly selected and analyzed 50 of these observations to ensure equal sample sizes across individuals.

Microhabitat use. Vegetation surveys were conducted immediately after tracking each of the 19 individuals in this study to quantify within-territory habitat variation. In 2013, 10-m diameter sample plots were randomly positioned at 10 points in each territory, as established using tracking data. The location of each plot was determined by generating randomly intersecting UTM coordinates bounded by territory dimensions. Coordinates were restricted so that sample plots were non-overlapping and located entirely within territory boundaries. In 2014 and 2015, surveys were conducted by establishing one transect along the longest axis of each territory and a second transect perpendicular to the first. Similar 10-m diameter sample plots were established every 15 m along each axis. In total, 112 vegetation plots in 11 territories (seven from Peru and four from Ecuador) were included in our study. Due to differences in sampling methods, vegetation data from the territories of eight tracked individuals were not included in our analyses.

Environmental variables measured in each sample plot included canopy height, canopy cover, number of *O. grandiflora* inflorescences, and total number of all inflorescences with flowers larger than ~ 1 cm in corolla length. These habitat characteristics were selected based on previous studies of habitat variation and space use by songbirds (Barg et al. 2006, Anich et al. 2012, Jimenez et al. 2012). They provided a reasonable

approximation of habitat structure and resource density that allowed comparison of foraging and non-foraging (all behaviors not classified as feeding) determinants of space-use patterns. Canopy cover was visually estimated as the percentage of visible sky impeded by vegetative growth within the 10-m diameter sample circle at a point 2 m above ground. Observations were treated as a nominal variable and estimated as 5% categories. Canopy height was estimated from the base of the tallest tree in each sampling plot. We measured the distance from the ground to the highest accessible point and then visually extrapolated to the highest visible point to estimate overall canopy height. Given the conspicuousness and relatively low number of *O. grandiflora* inflorescences in each sample plot (10.8 ± 4.5 [SD]), the open habitat, and low mean canopy height (4.4 ± 0.4 [SD] m), *O. grandiflora* inflorescences were counted from the center point of each sample plot. Inflorescences of all other species (including single flower inflorescences) were counted by systematically moving in 1-m wide bands through entire 10-m diameter plots.

Statistical analysis. The total area of territories was calculated with a 90% kernel density estimate (KDE) for each of the 19 territories using the package “adehabitat HR” (Calenge 2006) in R version 3.2.3 (R Core Team 2015). The 90% isopleth (the contour line describing 90% of the observed variation in the model) was selected as the upper boundary because estimates based on isopleths $< 50\%$ and $> 90\%$ have been shown to bias area calculations (Borger et al. 2006). The smoothing parameter was calculated independently for each 90% KDE using a fixed reference bandwidth (h_{ref}). This smoothing parameter was selected because it best responds to the unimodal data distribution in our study (Worton 1989). Separate 90% kernel density estimates using smoothing parameters calculated from a least squares cross validation function (h_{LSCV}) resulted in statistically similar area estimates and so were excluded from this analysis.

Behavioral differences in use of space at varying distances from core areas were analyzed using the mean 90% KDE calculated from pooled territory sampling data. Each 90% KDE was divided into a series of

concentric rings representing 15% isopleths (contours signifying the percent variation described by the KDE model; in this case, each contour represents an additional 15% of variation explained). We calculated the area of each 15% isopleth for all individuals and compared the differences in area between successive isopleths. We defined the core area as the first point where consecutive isopleths at least doubled in area. We then took the mean across all individuals and rounded to the nearest increment of 5%. The number of occurrences of Shining Sunbeams feeding and non-feeding observations (vocalization, displaying, aggression, and perching/movement) in each 15% isopleth ring was standardized for the area of each ring by calculating an observation density. The variance between observation densities calculated for each of the six isopleths was unequal (Levene's test, $P < 0.05$ for both observation types) so we used two separate Welch's ANOVA tests with six groups each to examine differences in the density of observations at different distances from territory centroids. One test included all non-feeding observations (vocalizing, displaying, aggression, or perching/movement), and the second included observations where birds were feeding on *O. grandiflora* flowers or inflorescences. Both Welch's ANOVA analyses were followed by Games-Howell multiple comparison tests. All pairwise comparisons between feeding and non-feeding observations in both ANOVA models, however, were non-significant and so were not reported in this analysis.

To evaluate the environmental characteristics most associated with the position of core areas, measured environmental variables were analyzed using four separate general mixed effect models where individuals were treated as a random effect. Each of the four environmental variables was independently compared against the isopleth on which the center of each sample plot occurred (as determined by the KDE isopleths). The goal of this comparison was to determine whether there were significant differences in the characteristics of core and non-core areas. Specifically, this analysis was focused on whether resource abundance or habitat characteristics were more strongly correlated with the location of core areas. Each general mixed effect model was evaluated using normally distributed

residual analysis and marginal goodness-of-fit (Nakagawa and Schielzeth 2013).

Finally, to examine possible differences in patterns of habitat use inside and outside of core areas, we subsetted the total number of hummingbird observations (50 per individual) into those that directly overlapped with vegetation survey plots. Overlapping hummingbird observations were divided into those inside ($< 20\%$ KDE) and outside ($> 20\%$ KDE) of core areas. The 20% KDE threshold was selected as the core area using the previously described method outlined by Barg et al. (2005). General mixed effect models were again used to compare the relationship between the four measured habitat variables and the proportion of overlapping hummingbird observations inside and outside of the core area ($N = 80$ inside core area, $N = 33$ outside core area). Each mixed effect model was evaluated using a normally distributed residual analysis and marginal goodness-of-fit (Nakagawa and Schielzeth 2013). Values are provided as means ± 1 SD.

RESULTS

Behavioral space use. The distribution of the kernel probability densities calculated for all 19 territories indicated that space use by territorial hummingbirds was aggregated around central points or core areas (Fig. 1). The mean 90% KDE size of the 19 territories was $1559.8 \pm 465.3 \text{ m}^2$ (range = 604.4–3923.0 m^2). The mean size of core areas (20% isopleth) was $102.5 \pm 23.5 \text{ m}^2$, indicating that 20% of the variation in each kernel density estimate could be described by an average of only 7% of overall territory size (Table S1). The mean offset distance between the centroid and geometric centers of territories was $7.9 \pm 2.0 \text{ m}$. This resulted in the probability density function in each of the 19 territories being distributed asymmetrically around the center point of core areas (Fig. 1).

The mean density of non-feeding observations varied significantly at different distances from the center of territories (Welch's ANOVA, $F_{5, 747} = 38.8$, $P = 0.0001$, $N = 6$). Mean densities of non-feeding observations within the 15% isopleth were 225% higher ($0.28 \pm 0.03 \text{ observations/m}^2$) than the overall mean, whereas non-feeding observations between the 30 and 90% isopleths were

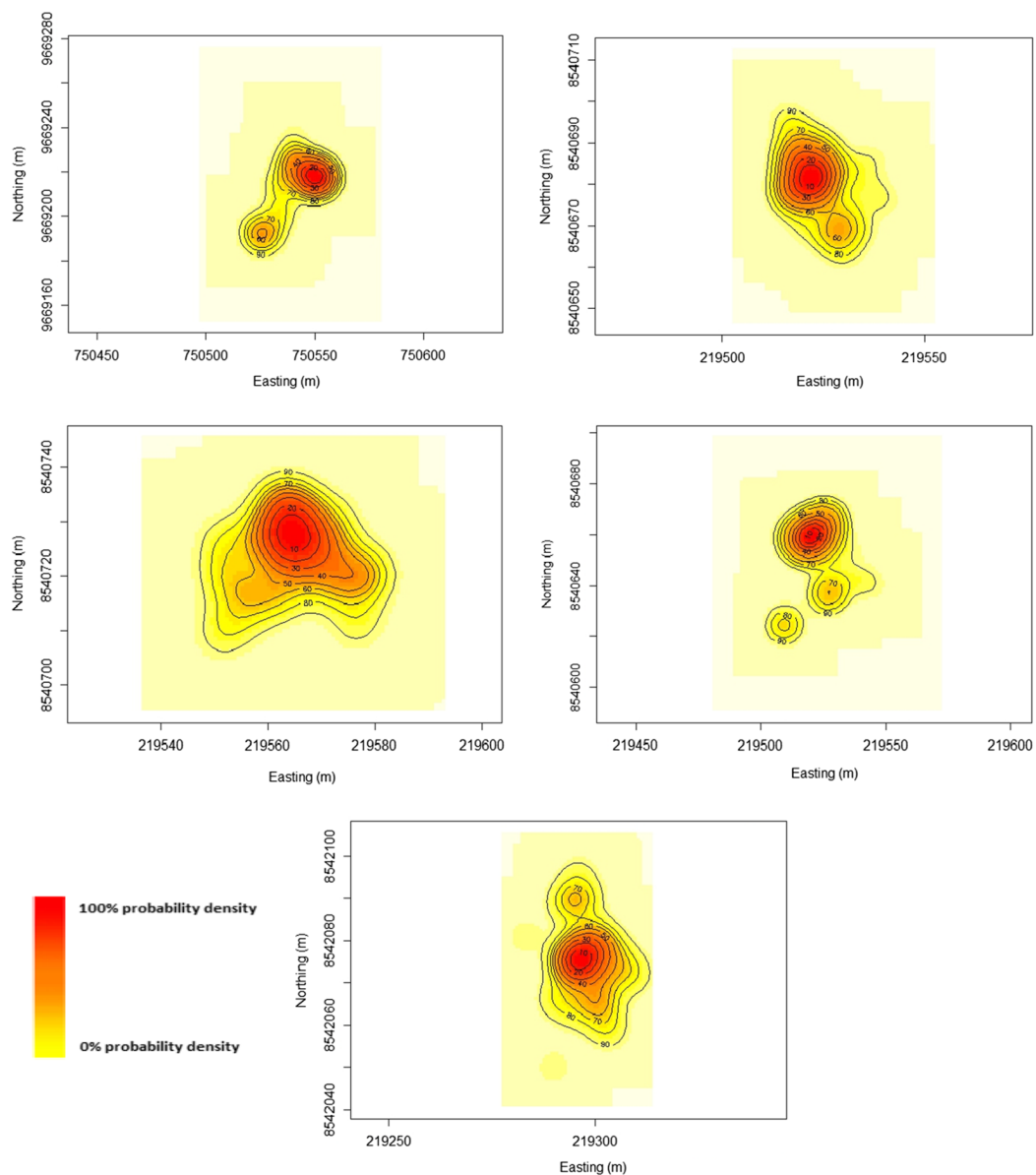


Fig. 1. Ninety percent kernel density estimates for five representative hummingbird territories out of the total 19. Territory estimates based on all observations for each radio-tagged individual (50 locations per individual). Color corresponds to probability density, with contour lines indicating 10% isopleths. An ad hoc smoothing parameter (h_{ref}) was calculated independently for each estimate. Estimate parameters, areas, and positions are summarized in Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

significantly lower (Fig. 2). We also found a significant difference in the mean densities of feeding observations at different distances from the center of territories (Welch's ANOVA, $F_{5, 120} = 3.9$, $P = 0.0027$, $N = 6$). This was driven largely by fewer feeding observations in the

90% isopleth ring; pairwise comparisons revealed no significant difference in the density of feeding observations between the 15 and 60% isopleths (Fig. 2).

Microhabitat use. Comparisons of the mean values of all four environmental

variables and the distance to territory centroids (as determined by the KDE isopleths) revealed no significant differences (Table 1). This included both abundance of *O. grandiflora* inflorescences ($R^2 = 0.16$, $t_{110} = -1.0$, $P = 0.27$, $N = 112$) and canopy cover ($R^2 = 0.04$, $t_{110} = 0.7$, $P = 0.52$, $N = 112$; Fig. 3), two habitat characteristics predicted to be important in microhabitat use. The habitat characteristic most strongly associated with core areas was canopy height, but this regression also had a low fit to the observed data ($R^2 = 0.27$, $t_{110} = -2.6$, $P = 0.09$, $N = 112$).

Patterns of microhabitat use outside of core areas were also poorly explained by habitat characteristics (Table 2). Use of peripheral

territory habitat was not related to *Oreocallis* abundance ($R^2 = 0.11$, $t_{31} = -1.3$, $P = 0.21$, $N = 33$), canopy cover ($R^2 = 0.07$, $t_{31} = -0.3$, $P = 0.78$, $N = 33$), or canopy height ($R^2 = 0.08$, $t_{31} = -1.5$, $P = 0.16$, $N = 33$; Fig. 4).

DISCUSSION

Based on the concepts of space use by birds (Barg et al. 2006, Tomasevic and Marzluff 2018), we expected that Shining Sunbeam territories would be characterized by central core areas with high overall use, but low foraging activity, and that core areas would be associated with particular habitat structural features. We also expected that territory use outside core areas would be associated with foraging behavior and related environmental variables. We found that Shining Sunbeam territories were characterized by highly utilized central core areas, where foraging effort was disproportionately low. Core areas were not, however, associated with particular structural habitat features, except for a weak association with canopy height, and habitat use outside of core areas was not related to resource density.

By examining the distribution of non-feeding and feeding observations relative to territory centroids, we show that Shining Sunbeam territories were centered on core areas with lower proportional foraging effort. The mean density of non-feeding observations of Shining Sunbeams was significantly higher within the 15% isopleth than at any other distance from territory centers. In contrast, the mean density of feeding observations did not show any differences until the 75% isopleth. If the likelihood of a foraging event occurring were equivalent for all points in a territory, the distribution of feeding observations would resemble the distribution of overall observations (i.e., feeding plus non-feeding observations), with foraging activity being determined solely by the density of general activity. Instead, uniformity in the density of feeding observations suggests that relative foraging effort was independent of the distribution of overall observations and skewed toward territory boundaries. This provides evidence for a territory structure defined by activity clustered around a central point with proportionally less foraging effort.

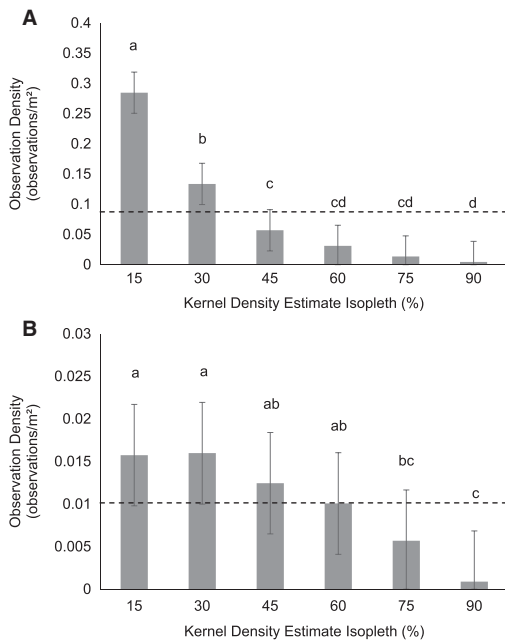


Fig. 2. Mean density of (A) non-feeding and (B) feeding observations that occurred at different distances (KDE isopleths) from each territory centroid. There was a significant difference between non-feeding groups ($F_{5, 747} = 38.8$, $P = 0.0001$) and also between feeding groups ($F_{5, 120} = 3.9$, $P = 0.0027$). Games-Howell post-hoc analysis indicates significant pairwise comparisons at the 15% isopleth for non-feeding observations and for the 75% isopleth for feeding observations. Significant pairwise comparisons are indicated by unique letters. Error bars are 95% confidence intervals, and each dashed line represents the overall mean between groups for each observation type.

Table 1. Summary of the linear regression analyses performed on the relationship between four measured habitat variables and the distance from the territory center.

Habitat variable	Linear regression	P	t	N	R^2
Canopy height	$y = -0.016x + 4.77$	0.09	-2.6	112	0.27
Abundance of <i>Oreocallis</i> inflorescences	$y = -0.13x + 12.60$	0.33	-1.0	112	0.16
Canopy cover	$y = 0.068x + 18.67$	0.52	0.7	112	0.04
Abundance of total inflorescences	$y = -0.0033x + 1.92$	0.82	-0.2	112	0.43

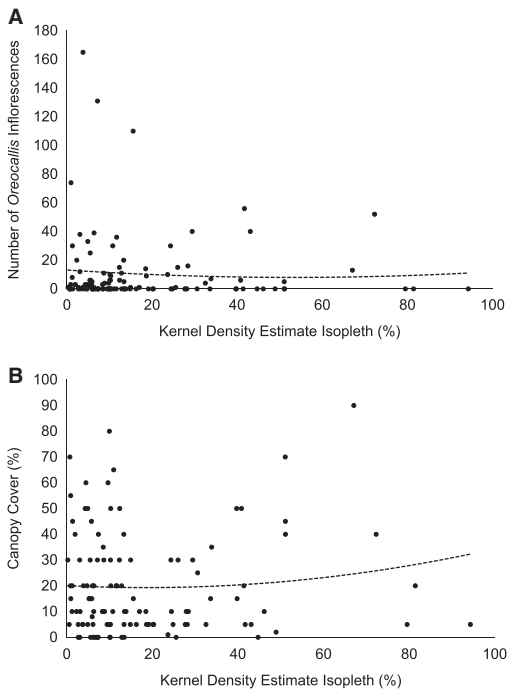


Fig. 3. Linear regression of (A) number of *Oreocallis* inflorescences and (B) canopy cover compared to the distance from the territory center (KDE Isopleth). Neither environmental variable was significantly related to the distance from the territory center (number of *Oreocallis* inflorescences: $R^2 = 0.16$, $t = -1.0$, $P = 0.33$; canopy cover: $R^2 = 0.04$, $t = 0.7$, $P = 0.52$). Of the four measured environmental variables, canopy height showed the strongest relationship, although the estimated fit of the regression was low (canopy height: $R^2 = 0.27$, $t = -2.6$, $P = 0.09$). A complete summary of results is provided in Table 1. Lines represent estimated lines of best fit.

Many studies of habitat use by birds have revealed core areas of concentrated use in territories (e.g., Samuel et al. 1985, Barg et al. 2006, Anich et al. 2012, Tomasevic and Marzluff 2018) and, in some cases, the location

of core areas has been found to be related to either habitat characteristics associated with structural complexity, such as canopy cover and vegetation density (Walsberg 1993, Anich et al. 2012), or the location of nesting and roosting sites (Tomasevic and Marzluff 2018). In our study, however, most observations within the 15% isopleth involved perching/movement rather than other territorial or feeding behaviors. In addition, core areas in the territories of Shining Sunbeam were not associated with any variables reflecting either structural complexity or resource acquisition. This suggests that the location of core areas in Shining Sunbeam territories may be influenced by factors unrelated to vegetation structural components associated with mitigation of environmental stressors such as predator avoidance and territory defense (Lima 1998, Rousseu et al. 2014).

The only environmental characteristic that varied relative to the position of core areas was canopy height, although this relationship was weak (Table 1). In some species, space use in territories can be influenced by the need to transmit auditory and visual signals (Krams 2001, Barg et al. 2006). In these cases, core areas with more exposed, elevated perches may be favored (Hunter 1980, Barg et al. 2006). Although not explicitly tested in our study, use of auditory and visual signals for territory advertisement by hummingbirds could influence the relationship between location of core areas and canopy height (Ewald and Bransfield 1987, Ornelas et al. 2002). In addition, use of exposed perches by hummingbirds is often associated with detection of intruders, leading to a correlation between territorial movements and visibility (Rousseu et al. 2014, Lanna et al. 2016). Further direct comparisons between the density of exposed perches and space-use patterns in territorial hummingbirds are needed to test these relationships.

Table 2. The summary of the analyses performed on the relationship between four measured habitat variables and the proportion of hummingbird observations overlapping vegetation plots inside (< 20% KDE; $N = 80$) and outside (> 20% KDE; $N = 33$) territory core areas.

	Linear regression	P	t	R^2
Habitat variable				
Canopy height	$y = 0.0016x + 0.0068$	0.06	1.9	0.07
Canopy cover	$y = 0.000078x + 0.015$	0.38	0.9	0.06
Abundance of total inflorescences	$y = 0.0000057x + 0.016$	0.51	0.7	0.06
Abundance of <i>Oreocallis</i> inflorescences	$y = -0.0000059x + 0.016$	0.93	-0.1	0.04
Habitat variable				
Canopy height	$y = -0.0064x + 0.043$	0.16	-1.5	0.08
Abundance of <i>Oreocallis</i> inflorescences	$y = -0.00051x + 0.015$	0.21	-1.3	0.11
Abundance of total inflorescences	$y = -0.000016x + 0.0090$	0.62	-0.5	0.08
Canopy cover	$y = -0.000089x + 0.011$	0.78	-0.3	0.07

We predicted, based on models of micro-habitat use in territories by songbirds, that the density of floral resources would be most correlated with points of high hummingbird use outside of core areas (Anich et al. 2012, Jimenez et al. 2012), but no measured environmental variable varied significantly with use of areas on the periphery of territories. Although we found that, proportionally, foraging effort was skewed toward territory boundaries, habitat characteristics associated with foraging may not be sufficient to describe use of peripheral territory space. The observed patterns of microhabitat use outside of territory core areas may represent a trade-off between resource acquisition and minimizing risk associated with environmental stressors such as predation pressure (Lima 1998). This may result in a pattern of peripheral habitat use where environmental variables associated with foraging or pressures like predation risk or aggressive interactions may not be the sole determinants of habitat use. More detailed information about the flowers and insects used as food resources may better inform these territorial patterns. Alternatively, peripheral space use may be influenced by interactions with neighboring hummingbirds. Intrusion pressure influences the size and shape of hummingbird territories and can lead to the periphery of territories being used for territory defense and vigilance (Norton et al. 1982, Paton and Carpenter 1984, Rousseu et al. 2014). We are unable to say whether this is the case for Shining Sunbeam territories because this would require direct comparisons between peripheral territory

space-use patterns observed under different conditions of territory intrusion.

Few investigators have attempted to use radio telemetry with hummingbirds. Transmitters have been successfully employed to track movements of Green Hermits (*Phaethornis guy*) in fragmented lower montane forest areas of Costa Rica, and no differences were noted in flight or other behaviors of tagged and untagged individuals (Hadley and Betts 2009, Volpe et al. 2016; also see Zenzal et al. 2014). Thus, for larger-bodied hummingbirds (e.g., where tags are < 3–5% of body mass), telemetry is a highly tractable method for monitoring movements of individuals, quantifying space use in territories, and assessing foraging behavior. Our results suggest that this technique could be employed for a number of other tropical hummingbird species across a diversity of habitats and elevations to understand variation in territorial and traplining behaviors.

Our results have important implications not only for hummingbird behavioral studies, but for broader plant–pollinator interactions and the role that territorial behavior may play in shaping the movement of plant genes. Resource monopolization by territorial hummingbirds can limit overall pollen movement, leading to inbreeding and reduced reproductive output of defended plants (Waddington 1983, García-Meneses and Ramsay 2012, Rousseu et al. 2014). Territorial intrusions by competing hummingbirds is one way these barriers are overcome. Because territory intrusion is most likely to be successful in areas less frequented by territory owners, the

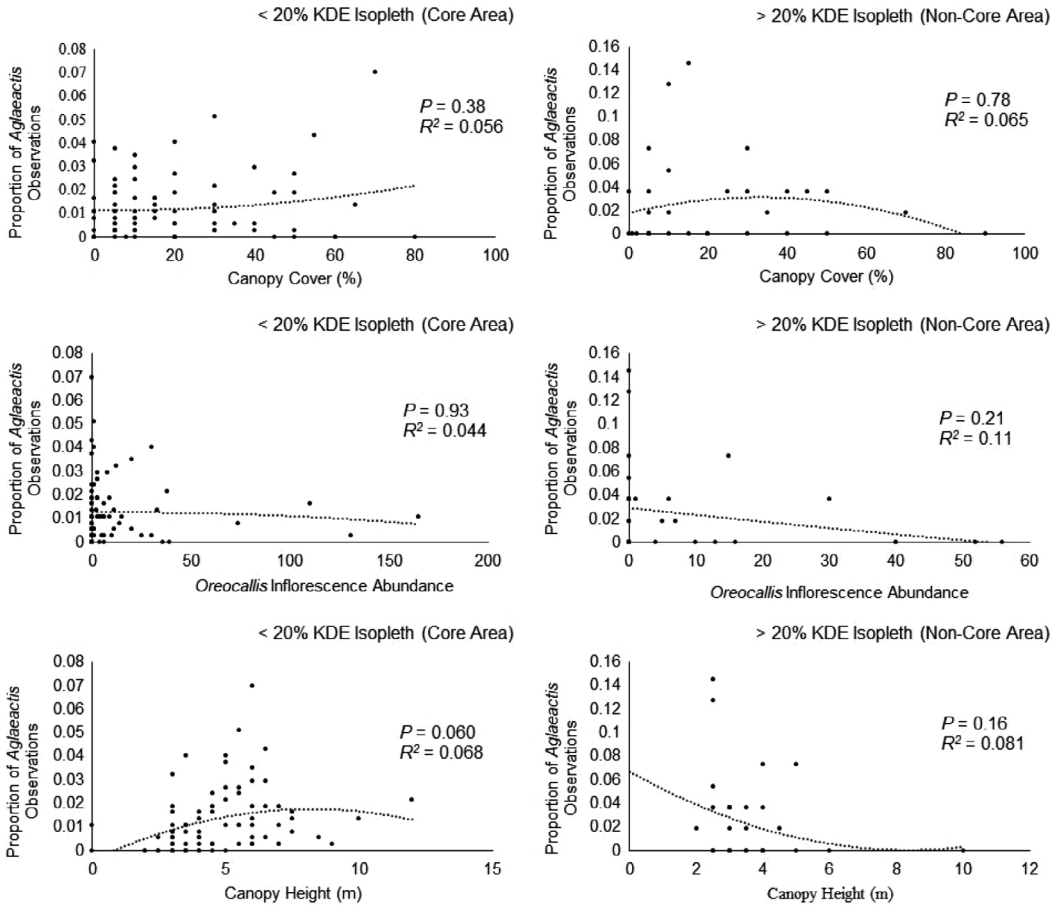


Fig. 4. Proportion of total Shining Sunbeam observations inside (< 20% KDE isopleth) and outside (> 20% KDE isopleth) the core areas of each territory compared to three different environmental variables: canopy cover, *Oreocallis* abundance, and canopy height ($N = 80$ inside core area, $N = 33$ outside core area). Proportion of Shining Sunbeam observations outside of the 20% KDE isopleth was not correlated with *Oreocallis* abundance following linear regression analysis ($R^2 = 0.11$, $t = -1.3$, $P = 0.21$), a factor predicted to be a major driver of use of peripheral habitat. None of the four measured environmental variables was significantly correlated with patterns of habitat use by Shining Sunbeams in non-core areas (Table 2). Lines represent estimated lines of best fit.

probability of intrusion is often reciprocal to territorial space-use patterns (Paton and Carpenter 1984, Franceshinelli and Kesseli 1999, García-Meneses and Ramsay 2012). Additional studies employing radio telemetry will, therefore, be key to understanding the structure of hummingbird territories and possible implications for both the movement of plant genes and the maintenance of genetic diversity in high-elevation Andean plant communities (Hazlehurst et al. 2016).

Overall, we found that space use by Shining Sunbeams was similar to that described

for some species of songbirds, especially with the presence of core areas in territories, but we also found reduced foraging effort in these core areas. We found no evidence that this core area pattern was due to differential habitat use based on either maximizing resource acquisition or other non-foraging behaviors. Although somewhat unexpected, these results may be broadly applicable to hummingbird foraging biology, especially when considering pollination interactions and the effects of pollinator behavior on pollen movement.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Summary of kernel density estimated areas, parameters, and the position of the core area for hummingbird territories 1-19.