The Wilson Journal of Ornithology 131(1):000–000, 2019

The behavior and diet of the Shining Sunbeam (*Aglaeactis cupripennis*): A territorial high-elevation hummingbird

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ABSTRACT—The Shining Sunbeam (*Aglaeactis cupripennis*) is a widespread and relatively common high-elevation hummingbird in the tropical Andes. Despite this, there is no comprehensive record of its natural history. In this study we present our findings on the diet and territorial behavior of Shining Sunbeam at sites in Peru and Ecuador. Using radio telemetry to track and observe individuals, we examined territory size and vegetation characteristics, activity budgets, diet composition, and territorial aggression. We found that average territory size was 0.13 ha (SD 0.05) with 100% minimum convex polygon estimation and 0.19 ha (SD 0.06) with 95% kernel density estimation. We found high variation in territory sizes, which was not explained by locality, year of data collection, or flower density. The diet of the Shining Sunbeam within our study sites was composed primarily of nectar from flowers of the tree *Oreocallis grandiflora* (Proteaceae), which comprised 93% (SD 9) of all nectar feeding events in Peru and 99% (SD 1) in Ecuador. Other flowering plant resources included *Brachyotum*, *Centropogon*, *Fuchsia*, *Gaultheria*, and *Macleania*. Insects made up 7% (SD 4) and 3% (SD 1) of observed foraging events of *A. cupripennis* in Ecuador and Peru, respectively. Mean activity budgets across individual birds were 68% (SD 16) perching, 28% (SD 15) foraging, 3% (SD 3) in aggressive behavior, and 2% (SD 1) in non-aggressive flight. Of the observed aggressive interactions, the majority were directed toward other hummingbirds (77% in Ecuador and 84% in Peru). When only considering interactions with hummingbirds, most aggression was intraspecific in Ecuador (71%) but interspecific in Peru (95%). We observed aggressive behavior directed toward other common, non-hummingbird nectarivores, such as *Diglossa* flowerpiercers, while aggression directed toward non-nectarivores was rare. Our results highlight the need for comparative studies to better understand hummingbird foraging and territorial behavior in the Andes, and the utility of radio telemetry for studying larger hummingbird species like the Shining Sunbeam. *Received 7 March 2018. Accepted 20 October 2018*.

Key words: Andes, cloud forest, foraging ecology, Neotropics, *Oreocallis*, telemetry, Trochilidae.

El comportamiento y la dieta de *Aglaeactis cupripennis*: Un colibrí territorial de alta montaña

RESÚMEN (Spanish)—*Aglaeactis cupripennis* es una especie de colibrí altoandino relativamente común y ampliamente distribuida. A pesar de esto, no existe información detallada sobre su historia natural. En este artículo presentamos nuestros hallazgos sobre la dieta y el comportamiento territorial de *A. cupripennis* en sitios en Perú y Ecuador. Usando radio-telemetría para rastrear y observar individuos, estudiamos el tamaño de sus territorios y las características de su vegetación, su actividad, la composición de su dieta y sus interacciones agresivas. Encontramos que, en promedio, usando una estimación basada en el polígono mínimo convexo, los territorios tienen un tamaño de 0.13 hectáreas (DE 0.05), y de 0.19 hectáreas (DE 0.06) usando una estimación basada en densidad de kernel al 95%. Encontramos gran variación entre individuos en el tamaño de los territorios, la cual no está explicada por la localidad, el año de toma de datos o la densidad de flores. La dieta de *A. cupripennis* en los sitios muestreados está compuesta principalmente por néctar de *Oreocallis grandiflora* (Proteaceae), que comprende el 93% (DE 9) y el 99% (DE 1) de todos los eventos de consumo de néctar en Perú y Ecuador, respectivamente. Otras flores visitadas por *A. cupripennis* pertenecen a los géneros *Brachyotum*, *Centropogon*, *Fuchsia*, *Gaultheria*, y *Macleania*. El consumo de insectos correspondió al 3% (DE 1) y 7% (DE 4) del total de eventos de alimentación en Perú y Ecuador, respectivamente. Las actividades diarias de los individuos observados correspondieron en un 68% (DE 16) a estar perchados, 28% (DE 15) a forrajear, 3% (DE 3) a participar en interacciones agresivas y 2% (DE 1) a vuelos no relacionados con comportamientos agresivos. Entre las interacciones agresivas observadas, la mayoría involucraron otros colibríes (77% en Ecuador y 84% en Peru). Sólo considerando interacciones con otros colibríes, la mayoría de las interacciones agresivas fueron intraespecíficas en Ecuador (71%) e interespecíficas en Perú (95%). Observamos frecuentes comportamientos agresivos dirigidos a otras aves nectarívoras, como pinchaflores del género *Diglossa*, mientras las interacciones agresivas involucrando no nectarívoros fueron inusuales. Nuestros resultados resaltan la necesidad de conducir estudios comparativos que permitan entender mejor el comportamiento territorial y de forrajeo de colibríes andinos, y la utilidad de la radio-telemetría para estudiar especies relativamente grandes como *A. cupripennis*.

Palabras clave: Andes, bosque de niebla, ecología de forrajeo, Neotrópico, *Oreocallis*, telemetría, Trochilidae.

Hummingbirds are highly specialized nectarivores (Wolf et al. 1976), and several species are characterized by aggressive territoriality (Stiles and Wolf 1970, Wolf and Hainsworth 1971). Their foraging patterns are shaped by a combination of foraging strategy, flower abundance and distribution (Kodric-Brown and Brown 1978, Justino et al. 2012), and by species-specific factors such as size (e.g., smaller species are often excluded by larger

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species from feeding patches; Stiles and Wolf 1970). While overall hummingbird territoriality and foraging behavior have been extensively studied, much of this work has been performed in temperate regions and from an energetics perspective (Stiles 1971, Ewald and Carpenter 1978, Ewald and Bransfield 1987). Vertebrate pollinators are critical to the maintenance of biodiversity in many systems globally, and their foraging ecology is directly related to pollen movement and the vitality of dependent plant populations (Ratto et al. 2018). Increasing the focus on behavioral observations in territorial hummingbirds could yield new insights into the ecology and management of these important pollinator species (Chapman et al. 2003). Information on the feeding and territorial behavior of hummingbirds in the tropical Andes is still lacking, despite this being a region with the highest levels of hummingbird diversity in the world (McGuire et al. 2014) and a global biodiversity hotspot (Brummit and Lughadha 2003). In this study we describe multiple aspects of the natural history of an Andean hummingbird, the Shining Sunbeam (*Aglaeactis cupripennis*), with a focus on territoriality and foraging behavior using radio telemetry to track individuals over a period of several days.

The Shining Sunbeam is a large Andean hummingbird (6.4–8.1 g; Schuchmann 2010) that occurs in cloud and elfin forest, disturbed habitats, and high-altitude grassland from central Colombia to southern Peru (Hilty and Brown 1986, Schuchmann 2010). As with many other species, this hummingbird is well known for being territorial, and often engages in aggressive interactions with other nectarivores (Woods et al. 1998). Previous observations of the diet of Shining Sunbeams included nectar from a variety of flowering plants such as *Barnadesia*, *Bomarea*, *Brachyotum*, *Centropogon*, *Embothrium*, *Fuchsia*, *Moninna*, *Mutisia*, *Passiflora*, and *Puya* (Parker and O'Neill 1980, Salinas et al. 2007, Schuchmann 2010, González and Loiselle 2016). Other studies note the role of flowers of the plant *Oreocallis grandiflora* in the diet of closely related species of hummingbirds such as *Aglaeactis aliciae* (Lambert and Angulo-Pratolongo 2007) and highlight Shining Sunbeams as one of its pollinators (Hazlehurst et al. 2016). *O. grandiflora* is a high-elevation shrub or small tree with large inflorescences of tubular white or pink flowers found throughout the Andes of Peru and Ecuador (Prance et al. 2007). Although descriptions of Shining Sunbeam dietary components exist, their relative importance remains undescribed.

We undertook observations on the behavior and diet preferences of Shining Sunbeams as part of a larger study to document the response of territorial hummingbirds to nectar robbing by *Diglossa* flowerpiercers (Hazlehurst and Karubian 2018). Using recent reductions in the size of radio telemetry transmitters, we aimed to characterize the diet of *A. cupripennis* and describe their territorial behavior in terms of agonistic interactions, territory size, and the composition of vegetation within their territories. Our study is one of the first to describe the territorial behavior of an Andean hummingbird in such detail (but see Tinoco et al. 2009) and provides critical groundwork for future studies on hummingbirds in this important biodiversity hotspot.

Methods

Study sites

The data for this study were derived from 2 field locations: the Wayqecha Biological Station on the border of Manu National Park, Peru (2,800 m a.s.l., 13°10′S, 71°35′W; Fig. 1) and the Bosque Comunal "El Carmen" in the Azuay province of Ecuador (2,900 m a.s.l., 2°59′S, 78°44′W; Fig. 1a). Each site was characterized by both montane evergreen forest and a successional grassland–forest matrix (Fig. 1b) following anthropomorphic fire (estimated at 30–40 years ago in both cases by area residents). Although the Peruvian site had fewer trees and less dense vegetation, the habitat characteristics of both locations were visually similar. Both sites had high densities of the tree *O. grandiflora* (Proteaceae; Fig. 1c). Data collection took place between August and October 2013 and 2014 in Peru, and from October to December 2015 in Ecuador.

Territory mapping

Hummingbirds were captured using 30 mm mist-nets, aged by bill corrugation, and then fixed with a 0.23 g radio telemetry tag (Blackburn Telemetry, Nacogdoches, TX, USA) ($n = 19$ birds). We also inspected the proportion of

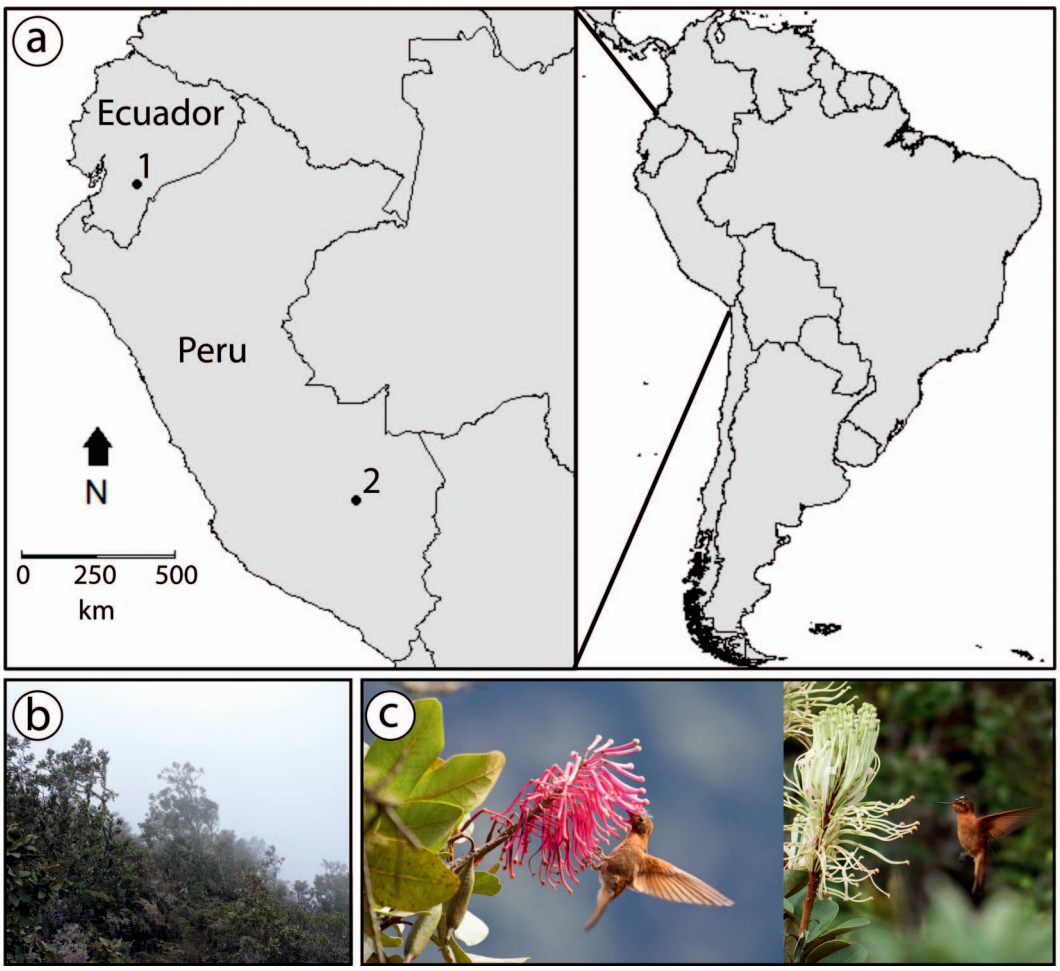

Figure 1. Location of field sites and habitat of *A. cupripennis*. (a) Filled circles indicate locations of field sites at 1: Bosque Comunal "El Carmen," Ecuador, and 2: Wayqecha Biological Station, Peru. (b) Photo representing habitat of *A. cupripennis* at Wayqecha Biological Station, taken within a tracked individual's territory. (c) Individuals of *A. cupripennis* feeding in *O. grandiflora*, one of the most common plants at both sites (Peru on the left, Ecuador on the right). Photo credits: Laura Céspedes (b), Nicole LaRoche (c left) and Alisa Muniz (c right).

iridescent plumage on the back to tentatively assign sex to individuals (Hilty and Brown 1986, Ridgely and Greenfield 2001, Schuchmann 2010). Assigning sex based on this criterion alone, however, was difficult and somewhat subjective, and the literature disagreed on this point (Schulenberg et al. 2010), therefore we present the results with putative females and males combined. Radio tags were only attached to individuals if the tag was $<3\%$ of the bird's body mass (Kenward et al. 2001). Sexual dimorphism in size is thought to be nonsignificant in this species (but see Schuchmann 2010), thus it is unlikely that the size requirement biased the tagging of males or females (Colwell 2000, Berns 2013). Tags were attached on the back between the lower scapulas using eyelash glue, and antennas were trimmed to prevent interference with hovering flight wing motion. Individuals were tracked using 3-element folding Yagi antennas and telemetry receivers (Wildlife Materials, Murphysboro, IL, USA) for 2–3 d in 2 h observation sessions performed twice daily between either 0630–0830 h and 1300–1500 h or 0900–1100 h and 1530–1730 h. Times were alternated between days to achieve full coverage of the day's activities. The bird's location was recorded every

5 min during a session, although for 5 out of 19 sessions location was only recorded every 15 min. These protocols varied by researcher and their broader project objectives, with the 15 min intervals used for 5 birds tracked in Peru in 2013 and the 5 min intervals used for 14 birds tracked in Peru in 2014 and in Ecuador in 2015. While different observers were involved in tracking the birds, the same team of 2 people remained consistent for each individual bird. The tags could be detected by the antennae up to 1 km away, although due to the steep and varied terrain the actual detection capacity was often less. Tags remained on the bird for 5 d to 2 weeks. Past studies using similar tags did not report adverse effects on hummingbird behavior (Hadley and Betts 2009), and we similarly did not observe any obvious negative effects of the tags.

Vegetation surveys

Vegetation surveys were performed immediately following the conclusion of tracking for 16 out of 19 individuals (Table S1); however, methods varied by researcher. In 5 territories surveyed in Peru in 2013, 10 circular sample plots 5 m in diameter were randomly positioned without overlap and within the boundaries of each sampled territory (established using tracking data). For the remaining 11 individuals surveyed in 2014 and 2015 in Peru and Ecuador, respectively, similar circular sample plots were spaced every 15 m along 2 transects running through the longest line of the territory and then along a transect perpendicular to the first. The following variables were measured in all sample plots: number and density of both *O. grandiflora* trees and inflorescences as well as any other potential floral resources (excluding flowers that were too minute for hummingbirds to use or that were clearly wind-pollinated), canopy height (tallest tree), and canopy cover. Non-*Oreocallis* flower species were not identified for the 5 territories studied in 2013 in Peru (Table S1). Canopy cover was visually estimated as the percentage of visible sky that was impeded by vegetative growth within the sample circle at a point 2 m above the ground. The height of the tallest tree was estimated by measuring the distance to the highest accessible point and then visually extrapolating and estimating to account for the entire tree. The density of *O. grandiflora* trees was calculated by dividing the number of trees in each territory by the area calculated by kernel density analysis for each individual. However, because the data compiled here were collected by different researchers across multiple years and projects, not all of these vegetative characteristics were calculated for all 19 birds (Table S1).

Behavior and diet observations

Throughout tracking sessions used to quantify territory size, 5 min scan samples were also conducted to record behaviors in the following categories: foraging, perching, preening, aggression (fights and directed vocalizing), and nonaggressive flight (flight not directed at a territory intruder). These data were not recorded for the 5 birds from Peru in 2013. Whenever foraging behavior was observed, the identity of the food item was also recorded to morphotype or, if known, to species level. Foraging behavior was also observed continuously between scan samples, so that a wider range of food resources was described, and these methods were consistent between observers. Plant morphotypes were photographed in the field and the photos were used to identify plants to genus by consulting the herbarium collections at the Universidad San Antonio Abad del Cusco and the Universidad de los Andes, and assistance from the Universidad del Azuay (B. Tinoco, pers. comm.).

Data analysis

Territory size was calculated using minimum convex polygon (MCP) and kernel density analysis (KDE) with h_{ref} as the smoothing parameter in the package 'adehabitatHR' (Calenge 2006) in R 3.2.3 (R Core Team 2015). The MCP is calculated by drawing the smallest possible convex polygon around the points, whereas the KDE method calculates a utilization distribution based on point locations. Areas were averaged over each day of observation per individual. The 95% isopleth (the contour line describing 95% of all the observed spatial variation in hummingbird movements) was selected to be the upper boundary. Comparisons between territory size estimation methods and mean territory sizes between the 2 study sites were all performed using *t*-tests. Differences between the mean territory size observed in individuals

each year, irrespective of location, were compared using a one-way ANOVA. A linear regression was conducted to test the relationship between territory area and resource density for the density of hummingbird-type inflorescences and the density of *O. grandiflora* inflorescences and the area of the 95% isopleth. All statistical analyses were conducted in R 3.2.3 (R Core Team 2015). Diet composition was analyzed based on continuous observations of tracked birds by averaging the percentage of observations an individual was observed at each food source per day, across all individuals. Similarly, activity budget was analyzed by averaging the percentage of scan observations observed in each type of activity per day, across all individuals. Scan samples were representative of the full coverage of the day's activities, as detailed in the territory mapping methods previously. Floral density was averaged across all points per transect per individual, across all individuals.

Results

Territories

The mean estimated territory size of observed individuals was influenced by the estimation method utilized: 95% kernel density estimations (95% KDE) or 100% minimum convex polygons (100% MCP) (Fig. 2). On average, estimated territory sizes were 20–67% larger when using the 95% KDE method, although comparisons between individuals were statistically similar when using either estimation method (paired t-test = 1.83, P = 0.09, n = 19). There were also no territory size differences between individuals that were observed in different years (100% MCP: $F_{3,18} = 1.20$, P = 0.29, n = 19; 95% KDE: $F_{3,18} = 1.36$, P = 0.33, n = 19).

We found a high variation in territory size among individuals, with the largest territory being 7.8–14.7 times larger than the smallest one using KDE and MCP estimation methods, respectively (Fig. 2a). The distribution of territory sizes estimated with both methods appears to be unimodal (Hartigan's Dip Test; 100% MCP: D = 0.085, P = 0.28, n = 19; 95% KDE: D = 0.051, P = 0.97, n = 19; Fig. 2a). This variation is not explained by site; there was no difference in mean estimated territory size of individuals observed at the 2 field sites either using 100% MCP (t-test = –0.74, P = 0.48, n = 19; Fig. 2b) or 95% KDE (t-test = –1.24, P = 0.23, n = 19; Fig. 2b). Although differences between sites were not significant, individuals at the Ecuador site had slightly larger territories than individuals in Peru using both estimation methods (95% KDE: Ecuador 0.23 ha [SD 0.11] vs. Peru 0.16 ha [SD 0.09]; 100% MCP: Ecuador 0.16 ha [SD 0.11] > Peru 0.12 ha [SD 0.06]). This represents a 44% and 33% difference when using 95% KDE and 100% MCP methods, respectively.

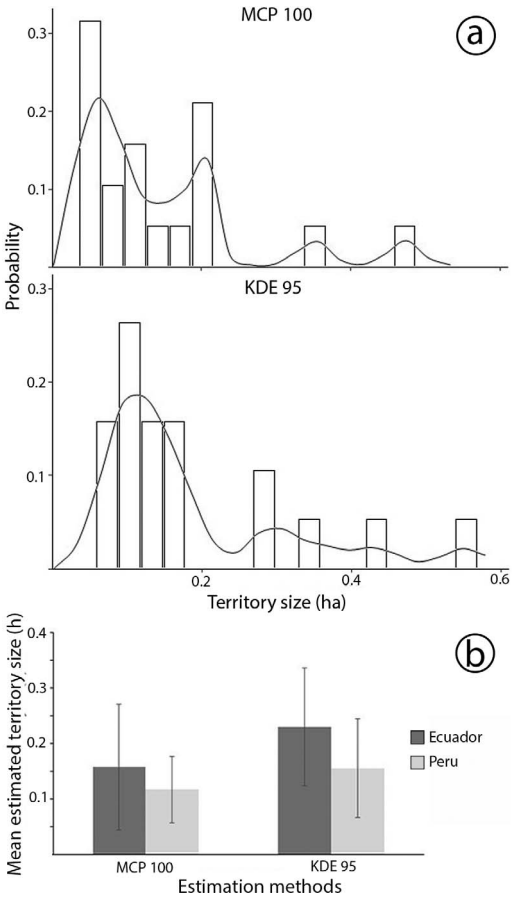

Figure 2. Variation in territory sizes of tracked individuals of *A. cupripennis*. (a) Distribution of observed territory sizes at both study sites using the MCP100 and the KDE95 methods. The line corresponds to the probability density and the y axis to the frequency probability. (b) Mean estimated territory size in Peru and Ecuador using 100% minimum convex polygon (MCP 100) and 95% kernel density estimation (KDE 95) methods. Error bars represent 95% confidence intervals. There was no difference in mean territory size at the 2 field sites (100% MCP: t-test = 0.74, P = 0.48, n = 19; 95% KDE: t-test = –1.24, P = 0.23, n = 19).

Vegetation characteristics

Territories had a mean canopy height of 4.7 m (SD 1.7; $n = 16$) and a canopy cover of 24.1% (SD 11.8; $n = 16$). *O. grandiflora* trees were present on all territories. Territories had a mean flowering plant species richness of 5.4 (SD 1.4; $n = 11$), and the mean density of flowering plants that could potentially serve as a resource for Shining Sunbeams was 2.4 inflorescences/m^2 (SD 2.1; $n = 16$). The mean density of *O. grandiflora* was 0.15 inflorescences/m^2 (SD 0.17; $n = 16$). Several genera of potential flowering plant resources occurred at field sites in Ecuador and Peru, including *Oreocallis* as well as *Gaultheria* (Ericaceae) at a mean density of 0.48 inflorescences/m^2 (SD 0.36; $n = 11$) and *Monnina* (Polygalaceae) at a mean density of 0.17 inflorescences/m^2 (SD 0.21; $n = 11$). The following flowering plant genera were found in *A. cupripennis* territories only at the Peruvian site: *Brachyotum*, *Bomarea*, and *Passiflora*, with *Brachyotum* being the most abundant at 0.05 inflorescences/m^2 (SD 0.06; $n = 5$). The following flowering plant genera were found in *A. cupripennis* territories (though not necessarily visited or pollinated by hummingbirds) only at the Ecuadorian site: *Macleania*, *Viola*, *Bejaria*, *Disterigma*, and *Salvia*, with *Bejaria* being the most abundant of the Ecuador-only flora at 0.04 inflorescences/m^2 (SD 0.09; $n = 6$). While sample sizes for territories where all floral resources were surveyed are too small to merit statistical comparison between sites ($n = 5$ in Peru, $n = 6$ in Ecuador), there is a trend toward mean density of floral resources being greater at the Ecuadorian site (4.46 inflorescences/m^2 [SD 0.87] $>$ 1.17 inflorescences/m^2 [SD 1.56]). Similarly, the canopy height at the Peruvian site was greater (5.7 m $>$ 3.1 m). There was no relationship between the density of *O. grandiflora* inflorescences and territory size, but there was a marginally significant positive relationship between the density of all potential hummingbird visited inflorescences and territory size (Linear Model: Estimate = 0.001, SE = 0.001, $t = 2.25$, $P = 0.040$, $F = 5.06$, df = 14, $r^2 = 0.27$).

Diet

The majority of observed foraging events by Shining Sunbeams involved nectar consumption (93% [SD 4] in Ecuador, $n = 1{,}935$ observations; 97% [SD 1] in Peru, $n = 1{,}453$ observations), but insects were also consumed (7% [SD 4] in Ecuador, $n = 1{,}935$ observations; 3% [SD 1] in Peru, $n = 1{,}453$ observations). Fly-catching behavior of small-bodied flying insects from elevated perches was relatively common. In Peru, we observed Shining Sunbeams feeding from flowers belonging to 7 different genera of plants, from the families *Ericaceae*, *Melastomataceae*, *Campanulaceae*, *Onagraceae*, and *Proteaceae* (Fig. 3; Table 1). In Ecuador we observed Shining Sunbeams using flowers from 3 families: *Ericaceae*, *Melastomataceae*, and *Proteaceae* (Fig. 3; Table 1). *O. grandiflora* was the dominant diet item at both sites (Fig. 3) with tracked individuals feeding almost exclusively on *O. grandiflora* flowers (99% [SD 1] in Ecuador, $n = 1{,}803$ observations; and 93% [SD 9] in Peru, $n = 1{,}412$ observations). Other visited plant species included *Gaultheria* and *Brachyotum* in Peru and *Macleania* in Ecuador (Fig. 3; Table 1).

Activity budgets and description of territorial behavior

Birds spent the most time perching (68% [16]) (mean [SD]) and foraging (28% [15]), with much less time spent engaging in aggressive territorial behavior (3% [3]) and in nonaggressive flight (2% [1]). Shining Sunbeams chased intruders while vocalizing, which typically resulted in the abscondence of the territory by the intruder. We also observed other nectarivores chasing territory holders; however, this was fairly uncommon. Chases initiated by territory-holding Shining Sunbeams were more often directed toward other hummingbirds (77% in Ecuador, $n = 85$ observations; 84% in Peru, $n = 90$ observations; Fig. 4a) or flower-piercers in the genus *Diglossa* (14% in Ecuador, $n = 85$ observations; 16% in Peru, $n = 90$ observations; Fig. 4a). Very few interactions with non-nectarivorous birds were observed during the tracking periods (9% only in Ecuador). Regarding chasing events with other hummingbirds, the proportion of conspecific and heterospecific interactions differed between sites (Fig. 4b; 2-proportions z-test: $P < 0.001$). In Peru most of the interactions involved other species of hummingbirds (95% with heterospecifics, 5% with conspecifics, $n = 90$ observations; Fig. 4b) while in Ecuador most of the agonistic interactions dis-

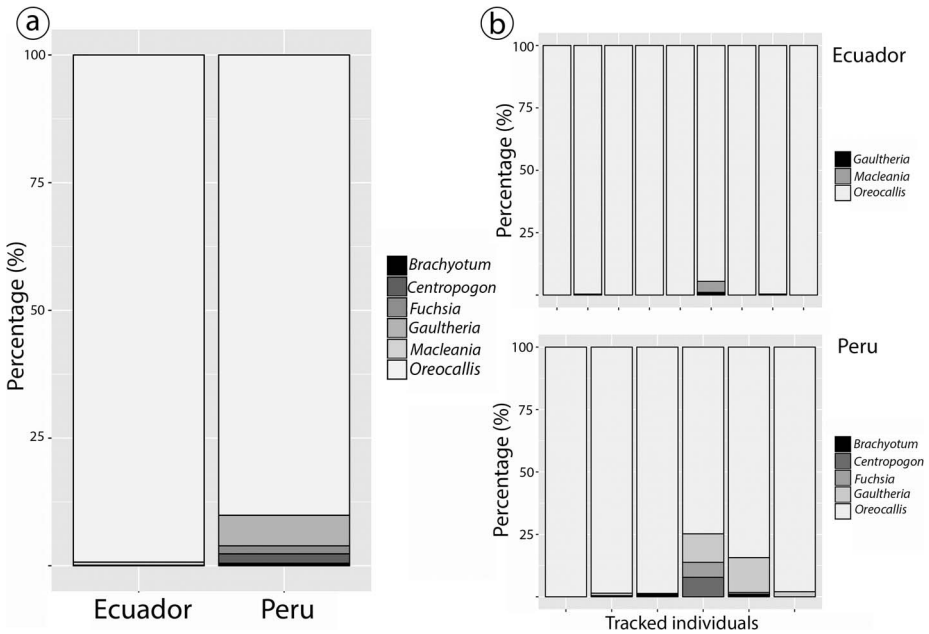

Figure 3. Percentage of flowering plant genera used by *A. cupripennis* at study sites in Ecuador and Peru. Bars are divided according to the proportion of time that individuals were observed feeding on different flowers during tracking periods. (a) The highest proportion of nectar feeding events in both localities involved nectar consumption from *O. grandiflora*. (b) Despite individual variation, *O. grandiflora* formed the principal diet component of all tracked Shining Sunbeam individuals (99.3% [SD 1.2] in Ecuador, $n = 1{,}803$ observations; 92.6% [SD 8.5] in Peru, $n = 1{,}412$ observations).

played by the tracked individuals involved conspecifics (29% with heterospecifics, 71% with conspecifics, $n = 85$ observations; Fig. 4b). The number of interactions observed per bird was variable and low in most cases, and therefore we only present the proportions by site. Taking into account both observations of the tracked individuals and additional opportunistic observations recorded as field notes by researchers in the studies detailed here, we identified several species of hummingbirds that elicited an apparent territorial response by Shining Sunbeams: *Boissoneaua matthewsii*, *Coeligena violifer*, *Colibri coruscans*, *Chalcostigma ruficeps*, *Ensifera ensifera*, *Heliangelus amethysticollis*, and *Metallura tyrianthina* in Peru; *C. coruscans*, *M. tyrianthina*, *Lesbia victoreae*, and *Lesbia nuna* in Ecuador. We also observed agonistic interactions between Sunbeams and individuals of every species in the genus *Diglossa* present in the localities (*Diglossa cyanea*, *Diglossa brunneiventris*, and *Diglossa mystacalis* in Peru; *D. cyanea* and *Diglossa*

Table 1. Flowers used as nectar resources by Shining Sunbeams at study sites in Ecuador and Peru.

Family	Genus	Species	Ecuador	Peru
Campanulaceae	*Centropogon*	—		X
Ericaceae	*Gaultheria*	—	X	X
Ericaceae	*Siphonandra*	—		X
Ericaceae	*Macleania*	—	X	
Melastomataceae	*Brachyotum*	—		X
Onagraceae	*Fuchsia*	—		X
Passifloraceae	*Passiflora*	*Passiflora mixta*		X
Proteaceae	*Oreocallis*	*Oreocallis grandiflora*	X	X

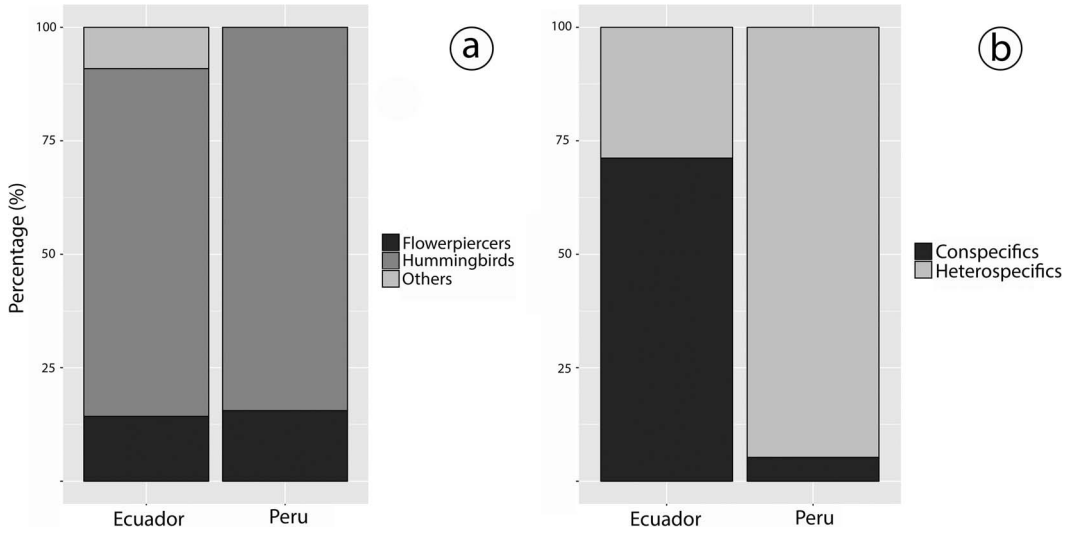

Figure 4. Participants in agonistic interactions with tracked individuals of *A. cupripennis*, shown as a percentage of encounters in Ecuador and Peru. (a) Most agonistic interactions involved other hummingbirds (77% in Ecuador, $n = 85$ observations and 84% in Peru, $n = 90$ observations). (b) In Ecuador most agonistic interactions with hummingbirds involved conspecifics (71% conspecific, 29% heterospecific, $n = 85$ observations), opposite to what was observed in Peru (5% conspecific, 95% heterospecific, $n = 90$ observations).

humeralis in Ecuador). Aggression against nectarivores, both hummingbirds and flower-piercers, was often preceded by the intruders feeding from flowers inside Shining Sunbeam territories. We registered aggressive behavior against non-nectarivores such as *Buthraupis montana* and *Cacicus chrysonotus* in Peru, as well as *Turdus fuscater*, *Pipreola* sp., *Asio flammeus*, and *Elaenia* sp. in Ecuador.

Discussion

In this study we document the first detailed description of the foraging and territorial behavior of the Shining Sunbeam. Through radio telemetry, we examined individual variation in territory size, activity budgets, diet composition, aggression patterns, and territory vegetation characteristics. We discuss these results in comparison to findings from previous studies of foraging behavior, aggression, and competition in other species of hummingbirds.

The territory sizes of tracked individuals ranged from 0.03 to 0.54 ha depending on the estimation method and revealed a positively skewed distribution. This variation, however, is not well explained by locality or year of data collection. We hypothesize that the variation could be driven partly by intersexual differences in territory sizes. Differences in territory sizes between females and males have been reported in other hummingbird species (Temeles et al. 2005). Because all territories were nonoverlapping and because no definitive courtship behavior or mating events were observed in putative males, it is difficult to discern whether breeding pressure contributed to territory size, despite some overlap with the breeding season. Given the difficulty to assign sex in the Shining Sunbeam based on described plumage differences (Hilty and Brown 1986, Ridgely and Greenfield 2001, Schuchmann 2010), this hypothesis of intersexual differences in territory sizes could be evaluated using molecular sexing (Hagadorn et al. 2016).

Previous work has shown a strong inverse relationship between resource density and territory size in hummingbirds (Kodric-Brown and Brown 1978, Hixon et al. 1983); however, our data show no relationship between the density of *O. grandiflora* and territory area, and only a marginally significant positive relationship between the density of all potential hummingbird flowers and area. This may be because patchy resource distribution rendered the transect method impractical for

calculating resource density, or because factors other than the density of floral resources, such as insect abundance, could be at play. Variation in territory sizes might also be explained by differences in physical condition, with some individuals being able to defend more resources than others despite increased costs of guarding a larger area (Temeles and Kress 2010). Comparisons between territorial behavior and underlying resource density also reveal interesting regional differences, despite the limitations described above. Even though within-territory flower diversity was lower in Ecuador (Table 1), and the mean density of *O. grandiflora* was similar at both sites, the total density of all potential floral resources was higher in Ecuador, signifying that the overall flowering community at that site is characterized by a higher proportion of species other than *O. grandiflora*.

According to our observations at both study sites, Shining Sunbeams rely heavily on the tree *O. grandiflora* for floral nectar and perching sites (Fig. 3), at least where the ranges of these species overlap. Although previous studies observed Shining Sunbeams visiting *O. grandiflora* flowers (Hazlehurst et al. 2016, Hazlehurst and Karubian 2018) and recorded *O. grandiflora* as a dietary element of closely related *Aglaeactis* species (Lambert and Angulo-Pratolongo 2007), this paper underscores its importance in the sunbeam diet. *O. grandiflora* was present within the territories of all tracked hummingbirds and was the dominant flowering species in many of them. *O. grandiflora* is characterized by production of large amounts of nectar (Hazlehurst et al. 2016, Tinoco et al. 2016) and, at our Peruvian site, this species presented higher levels of nectar sugar concentration compared to other flowers used by *A. cupripennis* (J.A.H., unpubl. data). Nectar sugar concentrations have been shown to be important for the determination of food choice by hummingbirds (Hainsworth and Wolf 1976, Tamm and Gass 1986), since foraging efficiency can be increased by visiting flowers with concentrated nectar (Wolf et al. 1976). The correlation between Shining Sunbeam foraging behavior and elevated nectar sugar concentrations suggests that sugar content may also influence flower selection in this species. Alternatively, given the overriding dominance of *O. grandiflora* in both localities, a higher proportion of visitation to *O. grandiflora* may be driven by its elevated availability (Wolf et al. 1976). Shining Sunbeam also visited other flowering species during feeding episodes, most of them with long tubular corollas (*Fuchsia*, *Centropogon*, *Siphonandra*, *Passiflora*), but some small and bell-shaped flowers (*Gaultheria*). We observed only one Shining Sunbeam feeding on the flowers of *Passiflora mixta*, which has an extremely long corolla. However, in this event, the bird acted as a nectar robber by extracting nectar from the base of the flower (likely as a secondary nectar robber using a hole cut by a *Diglossa* flowerpiercer).

Within each territory, all tracked hummingbirds showed strong territorial behavior directed toward both hummingbirds and flower-piercers (Fig. 4). Previous studies observed that Shining Sunbeams are aggressive toward larger nectarivores such as *Patagona gigas* (Woods et al. 1998), *Pterophanes cyanopterus* (Parker and O'Neill 1980), and *Diglossa cyanea* (Martin and Ghalambor 2014). In this study, we also documented aggression directed toward several smaller species, such as *M. tyrianthina*, *C. ruficeps*, and *H. amethysticollis*. This was expected and is consistent with previous knowledge of the negative correlation between territory aggression and intruder body mass (Dearborn 1998). Because all documented nectarivores, at least at the Peru site, have been observed to visit *O. grandiflora* (Hazlehurst and Karubian 2016), the elevated territorial aggression displayed by Shining Sunbeams toward other species, irrespective of size, may be due to direct competition for nectar resources. We also observed Shining Sunbeam aggression directed toward non-nectarivores (Fig. 4), consistent with reports from other hummingbird species (Williamson 2000, Boal 2008). Shining Sunbeams displayed considerable regional variation in the target of territorial aggression, with 71% of aggressive interactions with other hummingbirds directed toward conspecifics in Ecuador, compared to just 5% in Peru (Fig. 4). Although the prevalence of conspecific aggression is consistent with previous reports from the northern extent of its range, near the Colombia–Ecuador border (Woods and Ramsay 2001), the apparent prevalence of heterospecific aggression in Peru has not been described. These differences may be explained, for example, by the density of *A. cupripennis* territories in the landscape or differences in the timing of breeding, when increased aggression toward conspecifics can be expected (Pitelka 1942). Future work

should focus on understanding the mechanism underlying this variation.

Our study provides an overview of *A. cupripennis* diet and behavior across 2 high-Andean forest sites, yet it opens the door to many other research avenues. Comparisons of territory size between male and female hummingbirds, and further investigation of the role of ecological factors such as resource density in determining territory size, are needed to further our knowledge of the foraging ecology of this Andean species. By using radio-telemetry and focal observations of individuals, we were able to identify potential geographic variation in agonistic behavior across the Shining Sunbeam distribution. Additional research is needed to understand how nectarivore communities, including hummingbirds and flower-piercers, interact with available flowering plant resources to influence regional patterns of interspecific aggression. Our study underscores the utility of radio-tracking to gather detailed information on behavior and diet that is largely unknown for tropical species, and this technology shows promise in its application for large species of hummingbirds, such as the Shining Sunbeam. Overall, these results highlight both the need and potential for future studies that focus on behavioral observation in territorial hummingbirds, which could yield new insights into the ecology and conservation of these important pollinator species.

Acknowledgments

We are thankful to V Londoño, A Jara, and B Tinoco for help with plant identification, to JO Karubian and J Avendaño for their advice in preparing this manuscript, to the many field assistants who have helped over the years, and to GA Londoño, B Tinoco, and PO Chambi Porroa for their help in establishing field sites.

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