



# Impacts of nectar robbing on the foraging ecology of a territorial hummingbird

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## ABSTRACT

While the effects of nectar robbing on plants are relatively well-studied, its impacts from the perspective of the pollinators of robbed plants is not. Numerous studies do consider the impacts of robbing on pollinator visitation to robbed plants, but rarely do they focus on its scaled-up impacts on individual pollinator behavior. We used radio telemetry to track the spatial and behavioral responses of the territorial hummingbird *Aglaeactis cupripennis* to experimental nectar robbing over a period of several days. Simulated nectar robbing impacted foraging behavior by increasing territory area, distance flown, and reliance on novel food resources, especially small-bodied flying insects. We did not observe any impact on the amount of time individuals spent foraging, nor did we observe territory abandonment. These findings indicate that nectar robbing may impose a significant energetic cost on pollinators via increased flight distances and shifts towards potentially less profitable food resources, and demonstrate the importance of quantifying the indirect effects of nectar robbing on pollinators in addition to plants.

## 1. Introduction

Plant-animal mutualisms can impact the population structure (Abe et al., 2011; Pérez-Méndez et al., 2016), gene flow and reproduction (Carlo and Morales 2016; Sork et al., 2015), and community assembly and evolution (Bartomeus et al., 2016; Carstensen, 2016; Song and Feldman, 2014) of the plants and animals involved. Mutualisms can be impacted indirectly in critical ways by the effects of ecological interactions with species outside of the mutualism. Nectar robbing is a common and widespread cause of indirect effects in plant-pollinator mutualisms (Irwin et al., 2010). Nectar robbing occurs when an animal extracts nectar from a flower but bypasses the reproductive structures, usually by means of a small incision in the flower corolla (Inouye, 1980; Maloof and Inouye, 2000).

Nectar robbing has been shown to have a range of direct and indirect effects on plant reproduction, ranging from positive (Navarro, 2000; Singh et al., 2014; Waser, 1979) to neutral (Arizmendi et al., 1996; Hazlehurst and Karubian, 2016; Zimmerman and Cook, 1985) to negative (González-Gómez and Valdivia, 2015; Irwin and Brody, 1999; Roubik, 1982). Several factors determine what the strength and direction of robbing will be on plant fitness, including pollen limitation and plant mating system (Burkle et al., 2007; Irwin et al., 2010) and whether robbers destroy floral reproductive structures during foraging

(McDade and Kinsman, 1980).

In contrast to the rich body of literature that exists for plants, the effects of nectar robbing on pollinators is sparse (Irwin et al., 2010). From the animal's perspective, changes to a plant-animal mutualism often involve changes in resource availability, such as decreases in fruit or nectar associated with selective harvesting of food sources. In some plants, nectar robbing can lead to continued nectar production but evaporation of nectar through the robbing incision in the side of the flower. This evaporation can lead to chronically lower nectar volumes and also concentrates the remaining nectar, which substantially increases its viscosity and can make it difficult for pollinators to consume (Pleasants, 1983; Zimmerman, 1988). Pollinators may respond to the decrease in nectar availability and increased difficulty of nectar extraction by avoiding robbed flowers (González-Gómez and Valdivia, 2015), with consequences for plant fitness (Irwin and Brody, 1998; Pyke, 1982). To our knowledge, no previous studies have observed if these one-time avoidance responses by pollinators to robbed flowers scale up to impact the overall foraging ecology of individual pollinators.

There exists an extensive literature on animal responses to changes in resource distribution in other contexts (Gray et al., 2002; Simon, 1975), which suggests that animals exhibit flexible behavioural responses to changes in resource availability. In the case of territorial species, both optimal foraging theory and empirical studies suggest that

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territoriality can only be maintained if the benefits of exclusive access to a resource patch outweigh the costs (Gill and Wolf 1975; González-Gómez et al., 2011; Trombulak, 1990), and animals adapt to resource depletion to mediate this interchange. For example, during times of resource depletion individuals may continue to defend territories but expand their home ranges, presumably to gain access to sufficient resources to maintain their energy intake (Carpenter, 1983; Edwards et al., 2013; Hixon et al., 1983; Ruby et al., 1994). However, larger home ranges are more energetically expensive to forage in, and animals may need to compensate by spending less time and energy in territory defence (Powers and McKee, 1994). Territorial individuals may also respond to resource depletion by expanding their diet niches to include secondary food resources (Jedlicka et al., 2006; Pimm et al., 1985) or by devoting more time to foraging (Garrison and Gass, 1999; Temeles et al., 2005). Alternatively, if resources are depleted below a critical level on the territory, this may lead to territory abandonment and adoption of a “floater” foraging strategy (Brown and Sherry, 2008). Justino et al. (2012) observed territory abandonment by hummingbirds in response to experimental reductions in floral resources.

The degree to which animals match their foraging strategy to changes in resource reduction is likely to have important effects on net energy gain and fitness (Suarez and Gass, 2002). In the case of pollinators, different foraging strategies may have significant effects on pollination services to plants (Maruyama et al., 2016). However, the ways in which pollinators may shift their foraging strategy in response to nectar robbing, and what the ramifications for animal energetics and demographics may be, is currently unclear. This is especially true when one considers the range of mutualism strengths exhibited in pollination networks, from highly specialized 1:1 interactions to more generalized interactions.

In systems where nectar robbing causes chronic nectar depletion it is possible that territorial pollinator species may abandon their territories (Justino et al., 2012) or switch to non-territorial foraging strategies. Shifts in foraging behaviour by pollinators may in turn have important consequences both for the energetics of the pollinator (Shackleton, 2016) as well as for gene flow in the plant (Maruyama et al., 2016). To fill this knowledge gap, we exposed the territorial hummingbird species *Aglaeactis cupripennis* to nectar robbing of its preferred food source, the Andean tree *Oreocallis grandiflora* (Family: Proteaceae) in the wild, and monitored their behavioural response in terms of territory area, distance flown, activity budgets, and diet. Hazlehurst and Karubian (2016) found that after simulated nectar robbing in *O. grandiflora* flowers were still able to produce nectar, however robbed flowers contained less nectar than unrobbed flowers. Nectar in robbed flowers also had a higher sucrose concentration than in unrobbed flowers, suggesting that evaporation of nectar occurs through the robbing incision and causes nectar sugars to become more concentrated. We therefore inferred that these responses would scale up to the territory level and have significant impacts on the foraging ecology of individual hummingbirds. Specifically, we hypothesized that focal *A. cupripennis* individuals would exhibit both territory expansion and an associated increase the time spent foraging. We did not expect to see diet shifts, due to the apparent tight mutualism between *A. cupripennis* and *O. grandiflora* and the relatively low nectar volume and sucrose content of other flowers within *A. cupripennis* territories as compared to *O. grandiflora*, and we did not expect to see territory abandonment due to the apparent limited availability of open territories at our study sites.

## 2. Materials and methods

### 2.1. Study site

This study took place from 2014 to 2015 in montane evergreen forests of Peru and Ecuador. Data were collected in 2014 in Peru between 2900–3100 m asl at the Wayqecha Biological Station in Manu

National Park, Cuzco Province (13°10′29″S, 71°35′14″W) and in 2015 in Ecuador between 2850–3100 m asl at the Bosque Comunal El Merced, Azuay Province (2°59′39″S, 78°44′01″W). The change in field site was precipitated by a lack of birds in Peru in 2015, perhaps due to El Niño conditions altering the poorly understood altitudinal migration patterns of *A. cupripennis*. Fieldwork in both sites corresponded to the transition from dry to rainy season and the start of the breeding season.

### 2.2. Study system

The shining sunbeam (*Aglaeactis cupripennis*) is a mid-sized hummingbird with a mean mass of 7.5 g that occurs in Andean cloud and montane forest and high-altitude grasslands from Southern Peru to Colombia at elevations from 2300–4300 m asl. Males are distinguishable from females by the extent of purple plumage on the back. Both sexes defend stands of Andean firebush (*Oreocallis grandiflora*; Family: Proteaceae), a shrub or small tree which produces terminal flowered raceme inflorescences of 10–50 tubular paired flowers that open sequentially from the base of the inflorescence towards the top. Hazlehurst et al. (2016) reported the standing crop and sucrose concentrations of *O. grandiflora* to be  $13.8 \pm 1.2 \mu\text{L}$  ( $n = 123$ ) and  $28.5 \pm 1.6\%$  Brix ( $n = 123$ ). Nectar robbing at both sites is caused by birds of the genus *Diglossa* (family: Thraupidae), including *D. cyanea*, *D. brunneiventris*, *D. mystacalis*, and *D. humeralis*. Mean natural robbing rates were measured by Hazlehurst and Karubian (2016) at  $21.0 \pm 0.3\%$  of flowers per inflorescence ( $n = 110$ ), but robbing intensity was observed as high as 100% of flowers per inflorescence in some parts of the field sites, especially along roads (J. Hazlehurst, personal observation).

### 2.3. Territory mapping

Hummingbirds were captured in stands of *O. grandiflora* using 30-mm mesh mist nets. Once a bird was captured, a 0.25 g radio telemetry tag (Blackburn Telemetry, Inc.) was attached to the back 1 cm below the intra-scapular region with eyelash glue (Fig. 1) (Hadley and Betts 2009). Antennas were trimmed dramatically to reduce any effects on flight and to further reduce the weight of the tag. Only adult birds for whom the weight of the tag was less than 3% were tagged (Kenward 2001), and no gravid females or obviously unhealthy or injured birds were tagged. Tags generally fell off naturally after 1–2 weeks – and on some occasions earlier. Additional data including mass, age, sex, and breeding status were also recorded. We placed tags on a total of 32 hummingbirds. Of these, 17 individuals were not used in the analyses below because they were either never located again after the initial tagging or had territories in areas where we could not track them due to dangerously steep terrain.

To map initial hummingbird territories, individuals were tracked for 8 h over a 2-day period, in alternating 2-h observation sessions in the morning and afternoon. Scan samples were conducted every 5 min to record coordinates and behaviour of the focal bird (See Supplementary information Table S1), and feeding observations were continuously recorded.

Kernel density analysis was conducted using the package ‘adehabitatHR’ (Calenge, 2006) in R version 3.2.3 (R Core Team, 2015) to map the 95th kernel of the territory. We used a rule-based method to minimize kernel area while restricting polygon fragmentation to calculate the smoothing parameter  $h$  (Kie 2013) using  $h_{ref}$  as a starting point. If the bird was known to have a distinctly segmented home range, we adjusted  $h$  to minimize both the number of biologically reasonable territory segments and the area of each segment.

### 2.4. Nectar robbing simulations

Each replicate of our experiment took place over five consecutive days beginning on the day after tag placement, unless weather

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