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Differential Use of Nectar Feeders Among Migrant and Resident Hummingbirds

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Abstract

The use of artificial nectar feeders has increased in the past decades. Feeders represent extra food resource at a low cost that can cause an increment of hummingbird populations in urban and rural areas. Assuming that migrant hummingbirds have had contact with feeders in breeding areas, we propose that when feeders are held for the first time in an area, migrant hummingbirds will be visiting the novel resource faster than the resident species. Second, assuming that the finding of new resources is correlated with habitat structure, hummingbirds will visit earlier the feeders in places with less environmental complexity as a rural area. This study was done at the southern coast of the Mexican state of Jalisco in a rural area and in a protected natural area. Three twin feeders were placed in each area and visitation was recorded in periods of 50 minutes during morning and afternoon. We found that (a) migrant hummingbird began visiting the feeders in less time than residents at all the feeders, (b) once migrants used the feeder's residents began visiting, and (c) in the rural site visitation occurred earlier than in the natural forest. These findings support that hummingbirds learn to use novel food sources and remember used resources recognizing them at the landscape level, and that residents never exposed to an artificial food source learn to use them faster in more open areas and after migrants used them.

Keywords

feeders, resident hummingbird, migrant hummingbird, hummingbird learning, Mexico

Introduction

Hummingbirds are the most specialized birds adapted to nectar feeding (Feinsinger & Colwell, 1978). In the past decade, nectar feeders are commonly used to attract hummingbirds, principally in the United States and Canada (Arizmendi, Monterubio-Solis, Juárez, Flores-Moreno, & López-Saut, 2007; Sonne et al., 2016; True, 1993). The nectar feeders produce an artificial resource that can provide the energy hummingbirds would find when visiting between 2,000 and 5,000 flowers. This can cause significant increments in hummingbird populations due to increased food availability in rural and urban habitats (Arizmendi et al., 2007; French et al., 2005; Sonne et al., 2016; True, 1993; Wethington & Russell, 2003).

In addition, learning is the mechanism by which animals modify their behavior to respond efficiently to environmental conditions and to other interactions resulting from the relationship of animals and their environment (Cole, Hainsworth, Kamil, Mercier, & Wolf, 1982). Several studies have shown that nectarivorous birds can remember the spatiotemporal location of the resources, and for hummingbirds, there is evidence on the use

of spatial memory; for example, in laboratory experiments, they can return to artificial flowers that have been enriched with nectar (González-Gómez & Vasquez, 2006; Healy & Hurly, 1995; Hurly, 1996; Hurly & Healy, 1996; Henderson, Hurly, & Healy, 2001). Hummingbirds learn quickly to use new resources (see Altshuler & Nunn, 2001; Lara, González, & Hudson, 2009). They have two different ways to learn: First, when fledging, they follow their mother for several

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weeks learning by observing their tutor (Hainsworth, 1977); and second, during all their lives, they can do the same with conspecifics or heterospecifics while using different floral patches during migration or breeding season (Altshuler & Nunn, 2001). In addition, they can learn without the tutor, but this learning is slower (Healy & Hurly, 2013).

Nectar feeders are a new resource for hummingbirds in the neotropics where its use is very recent. During winter, Mexican tropical areas have two kinds of hummingbirds regarding feeders: migrants who have learned to use feeders in their breeding areas and then migrate into the tropical grounds, and the residents that are not used to feeders as a food resource. In this situation, we tested whether, when feeders are first introduced, migrants are the first to use them, followed by residents. Moreover, as vegetation structure can cause differences in visual recognition of a resource (Healy & Hurly, 1995; Hurly, 1996; Hurly & Healy, 1996; Sutherland & Gass, 1995; Tamm, 1987), we tested this prediction in two different situations, in an open rural area and an adjacent natural tropical deciduous forest.

Methods

Study Sites

The Biological Station Chamela (protected area) is located inside the Biosphere reserve Chamela-Cuitzmalá and has 3,319 ha of well-preserved tropical dry forest (Arizmendi, Márquez-Valdelamar, & Ornelas, 2002), located in the Mexican Pacific slope in Jalisco ($19^{\circ}29'–19^{\circ}34'$ N and $104^{\circ}58'–104^{\circ}04'$ W), 65 km north of Barra de Navidad, and has an elevation gradient between 50 and 500 m above sea level (Bullock, 1985; Macías-Rodríguez & Pérez-Jiménez, 1994). Medium annual temperature is 24.6°C , and yearly medium rainfall is 788 mm, with rains concentrated in 5 summer months (June–October; Noguera, Vega-Rivera, García-Aldrete, & Quesada-Avendaño, 2002). The dominant vegetation is a tropical deciduous forest with trees of 15 m in height that lose their leaves for between 5 and 8 months a year. (Macías-Rodríguez & Pérez-Jiménez, 1994; Noguera et al., 2002).

The rural site is called Juan Gil Preciado and is located 12 km northwest of the biological station ($19^{\circ}36'00''–19^{\circ}43'37''$ N and $105^{\circ}00'25''–105^{\circ}06'50''$ W; Figure 1). It has 7,067 ha, of which natural vegetation covers 2,495 and has an elevation gradient between 75 and 600 m asl. It has a population of 300 inhabitants that make their living from agriculture and ranching. Sites used were the backyards of three houses measuring approximately 600 m^2 and covered by introduced ornamental plants, fruiting trees, and medicinal plants.

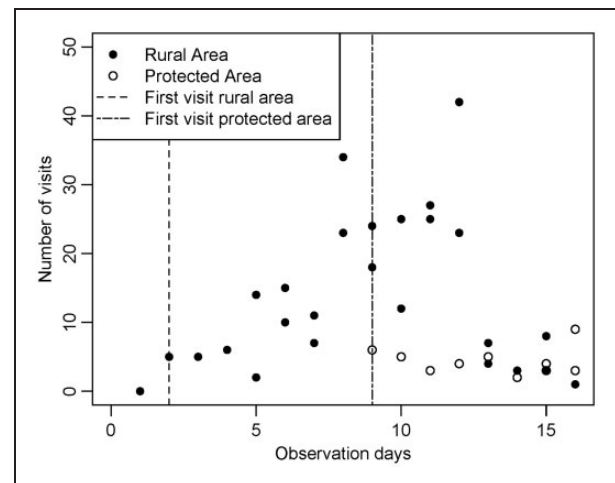


Figure 1. First visit by site for rural area and protected area.

Nectar feeders had never been used before in this study area.

Experiment With Artificial Feeders

We used three twin feeders (at a height of 1.5 m) and separated between them by 6 m and located at three sites between 300 and 450 apart. In the protected area, feeders were hanging from trees. The distance between paired feeders was between 300 and 450 m. In the rural area, feeders were placed in the backyards of houses covered by introduced fruiting plants such as *Manguifera indica*, *Psidium guajava*, *Citrus limon*, *Tamarindus indica*, *Annona muricata*, *Passiflora sp.*, *Prunus domestica*, and *Carica papaya*, among others. The distance between paired feeders was between 350 and 400 m. All observations are made by same observer.

Feeders were filled with a 20% sucrose solution that is the mean reported concentration of preferred nectar by hummingbirds (Baker, 1975; Blem, Blem, Felix, & Van Gelder, 2000), measured with a pocket refractometer (ATAGO model 300848).

In both areas, feeders were observed for 16 days in a row (beginning January 22, 2009, in the rural area and February 21, 2009, in the natural area). All observation days each feeder was filled with 250 ml of nectar. Nectar was changed each day. In each pair of feeders, observations were done in four periods of 50 minutes beginning from 7:30 to 11:20 a.m., and two in the afternoon from 4:30 to 6:20 p.m., changing each day the sequence of feeder observation to have two observation periods each day per twin feeders, one during the morning and the other in the afternoon. In each observation period, we annotated the time and hour, visitor species and sex where possible, time of the visit (using continuous time from 0 to 9,600 total observation minutes) and entire

time of the foraging bout. For agonistic interactions, we recorded the minute when the fight was observed, species that initiated the fight, winner, and loser.

Statistical Analysis

Each visit to nectar feeder was converted to number of visits per day for each site, resident status, and species. In addition, we used number of visits per day as response variable, and resident status (migrant vs resident), species, sex, and site as independent variables. For statistical analysis, we used Generalized Linear Model and Poisson distribution; we used the lme4 package (Bates, Maechler, Bolker, & Walker, 2015). All analysis and figures are carried in R v.3.6.1 (R Core Team 2019).

Results

Three species visited the nectar feeders during the experiment, one migrant, Black-chinned Hummingbird, and two residents, Broad-billed hummingbird and Cinnamon Hummingbird. We observed nectar feeders for 16 days in each area with a total observation time of 320 hours (160 hours in each site); in the rural area, the visitants were Black-chinned and Broad-billed hummingbirds, and at the protected area, Black-chinned and Cinnamon Hummingbirds. We found that nectar feeders in rural areas were visited earlier than in protected areas ($Z = 3.402$, $p < .001$, $df = 35$); the visit in rural area occurred at the second day, and in the protected area until ninth day (see Figure 1). The nectar feeders were visited by migrant hummingbirds earlier than resident species in both sites ($Z = 2.198$, $p = .027$, $df = 35$; Figure 2). In the rural area, the first visit occurred at 730th minute (2nd day) by Black-chinned Hummingbird female and Broad-billed hummingbird female at 1,680th

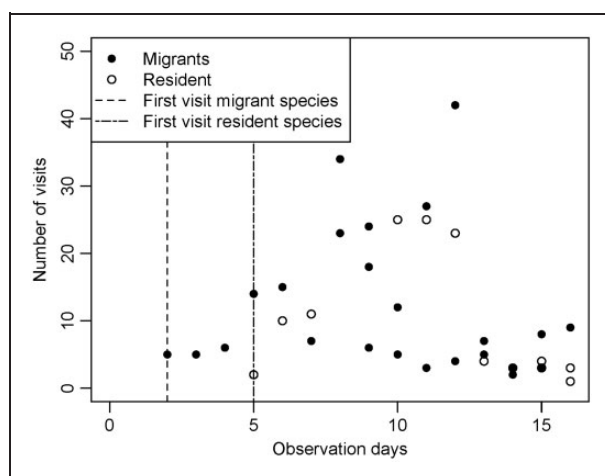


Figure 2. Feeder visitation by migrants and residents species in rural area and protected area.

minute (5th day), while in protected area, the visit of migrant species occurred at 4,930th minute (9th day), and Cinnamon Hummingbird at 8,512th minute (15th day).

Cinnamon Hummingbird did not defend feeders but defended sites where the nectar feeders were located. Females of Black-chinned Hummingbird won more encounters than males (proportion of contacts won for females 0.68, while males 0.33), whereas Broad-billed hummingbird females won 39% of the fights, while males won only one fight of the two recorded.

Discussion

Feeders use has increased in the United States and Canada during the past decades; in 2011, more than 52 million American feed wild birds (Horn & Johansen, 2013; Horn, Johansen, & Wilcoxon, 2014; U.S. Fish and Wildlife Service, 2012). Nectar feeders represent an extra food resource for hummingbirds while breeding is taking place during summer months (Baicich, Barker, & Henderson, 2015). The increase in the available resources can cause changes in the foraging strategies and territorial behavior, for example, can increase territorial behavior (Robb, McDonald, Chamberlain, & Bearhop, 2008). Several authors suggest that nectar feeders have an effect on hummingbird abundances (Arizmendi et al., 2007; Sonne et al., 2016).

Hummingbirds can learn the spatial position and the temporal variation in resource abundances in the environment (Healy & Hurly, 2003; Sutherland & Gass, 1995). Learning result in a behavioral change due to experience and birds can retain those learnings as spatial memory and use those data when arriving to a novel area (Cole et al., 1982; Lara et al., 2009; Martínez-García, 2009). The quick recognition of the nectar feeders by migrant species may be the result of having learned to use this resource in their breeding areas and remembering when using a tropical site during migration. Once the migrants used the feeders, residents began using them, probably utilizing a tutorial learning system described elsewhere (Altshuler & Nunn, 2001; Lara et al., 2009). Experimental work is needed to expose clearly this relation.

Habitat complexity is another factor that apparently affects the ability to learn how to use new resources (Altshuler & Nunn, 2001). In natural habitats where many possible food resources are used, the finding of a novel resource can be harder than in an open area as stated here. There were seven plant species used by hummingbirds (Arizmendi & Ornelas, 1990) flowering during our experiments (*Tillandsia pauciflora*, *Ipomoea bracteata*, *Ipomoea wolcottiana*, *Erythrina lanata*, *Nopalea karwinskiana*, *Vitex mollis*, and *Combretum farinosum*). However, in the open area, we found only very few

flowers of *I. bracteata* and *I. wolcottiana*, and *C. farinosum* was the most used plant species during this time in the house's backyards. The simplicity of habitat structure and the low availability of food resources can account for differences in the time elapsed until feeder visitation (Altshuler & Nunn, 2001; Lara et al., 2009).

These findings support that hummingbirds can learn from the habitat as can be shown by the soon use of feeders by residents when other hummingbirds first used the feeders and may retain this knowledge as it can be shown by repeated visits after the first one (Altshuler & Nunn, 2001; González-Gómez & Vasquez, 2006; McCaffrey & Wethington, 2008). They also support the idea of tutorial learning and its value for these nectar-feeding birds (Altshuler & Nunn, 2001; Lara et al., 2009). The use of a novel, human-made resource can be essential for hummingbird conservation, especially in this time where spatiotemporal changes in plant phenology and habitat quality can be responsible for failures in migration phenological coupling between hummingbirds and their food sources.

Implications for Conservation

The pollination by hummingbirds is common in wild plants; Nicolson and Fleming (2003) mentioned that 8,000 plant species (>60 families) have evolved flowers whose principal pollinators are hummingbirds, and they are the principal avian pollinators in America (Temeles & Kress, 2003). The nectar feeders for hummingbirds can be considered as an alternative food resource and can increase the density and diversity of hummingbird populations (Arizmendi et al., 2007). Several authors have documented changes in diversity and abundance in hummingbirds associated with the presence of nectar feeders (Arizmendi et al., 2007; Sonne et al., 2016); in sites where the green areas decrease, the artificial feeder's presence represents an extra food for hummingbirds. The artificial feeders can have a positive effect on hummingbirds, but on plants, the results can be negative, principally in visitation rates and in turn in seed production (Arizmendi et al., 2007). In natural areas or sites with original vegetation, the presence of artificial feeders can reduce the visitation rate on plants and have a negative effect on pollen transfer and seed production. Although the feeders can have positive effects in hummingbird populations, their use must be considered carefully, because of their effect on plant pollination, that can cause a decrement in seed production of the native plants (Arizmendi et al., 2007; Avalos, Soto, & Alfaro, 2012; Sonne et al., 2016). However, the use of a novel, human-made resource can be essential for hummingbird conservation, especially in this time where spatiotemporal changes in plant phenology and habitat quality can be responsible for

failures in migration phenological coupling between hummingbirds and their food sources.

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Author Contributions

L. E. Nuñez-Rosas collected and analyzed the data and also wrote the article. M. C. Arizmendi wrote, reviewed, and corrected the article.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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