


The role of size and dominance in the feeding behaviour of coexisting hummingbirds

GABRIEL LÓPEZ-SEGOVIANO,¹  RAFAEL BRIBIESCA¹ & MARÍA DEL CORO ARIZMENDI^{2*}

¹*Posgrado en Ciencias Biológicas, Unidad de Posgrado, Coordinación del Posgrado en Ciencias Biológicas, UNAM, Edificio D 1^{er} piso, Cd. Universitaria, Coyoacán, 04510 D.F., Mexico*

²*Laboratorio de Ecología, UBIPRO Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios 1, Los Reyes Iztacala, Tlalnepantla, Edo. México, CP 54090, Mexico*

Interspecific competition can strongly influence community structure and limit the distribution and abundance of species. One of the main factors that determine hummingbird community structure is competition for food. The temporal and spatial distribution of nectar has a strong impact on hummingbird assemblages, shaping foraging niches according to hummingbird dominance and foraging strategy. We investigated whether body size and the degree of aggressive dominance influence feeding behaviour of hummingbirds in a temperate forest in northwestern Mexico (El Palmito, Mexico) when winter migrant hummingbirds are present in the community. First, we determined the dominance status of hummingbirds and evaluated the relationship between dominance and body mass, wing disc loading and migratory status. Secondly, we determined how hummingbird species used plant species differently. Thirdly, we examined whether the most dominant hummingbird species defended floral patches with more energy and/or with a larger number of flowers. At each flower patch, hummingbird species, number of hummingbird interactions, feeding time and number of flowers present were recorded. The total number of calories available within each floral patch was also determined. Our results demonstrate that the dominance hierarchy of 13 hummingbird species (migratory and resident) was correlated with body size but not wing disc loading, and that members of the hummingbird community showed a clear separation in resource use (by plant species). Hummingbirds at the top of the dominance hierarchy defended and fed on the best flower patches, defined by the quantity of calories available. Hence, the feeding behaviour of hummingbirds at El Palmito depends on the abundance of plant species used by hummingbirds and on the amount of energy available from each flower patch. Thus, hummingbird body size, aggressive dominance and defence of quality flower patches determines niche partitioning among species.

Keywords: competition, David's score, hierarchy, preferences, resources, Sierra Madre Occidental.

Competition for food resources is thought to be one of the primary drivers determining community organization in hummingbirds (Feinsinger 1976, Wolf *et al.* 1976, Ornelas *et al.* 2002). Competition for resources has promoted morphological and behavioural divergence in hummingbird assemblages (Brown & Bowers 1985, Maglianesi *et al.*

2015a,b) as well as in other species assemblages, for example among desert rodent and lizard communities (Pianka 1973, 1975, Kelt & Brown 1999). Hummingbirds have developed a wide range of morphological and behavioural adaptations to fill individual feeding niches (Abrahamczyk & Kessler 2015). Such adaptations are often correlated with the availability of food resources, enabling morphological matching with particular flowers and niche separation among members of a

*Corresponding author.
Email: coro@unam.mx

community (Stiles & Wolf 1970, Maruyama *et al.* 2014, Abrahamczyk & Kessler 2015, Maglianesi *et al.* 2015b, Rodríguez-Flores & Arizmendi 2016).

Niche segregation among floral resources is particularly important among members of a hummingbird community as they derive ~85–90% of their dietary requirements from floral nectar (Gass & Montgomerie 1981), have high metabolic rates (Schuchmann 1999), visit hundreds of flowers each day (Hurly & Healy 1996) and transfer pollen among flowers during visits (Healy & Hurly 2001). Abrahamczyk and Kessler (2015) found that the temporal and spatial distribution of nectar has a strong impact on hummingbird assemblages, shaping foraging niches according to hummingbird dominance and foraging strategy. Therefore, the co-evolutionary relationship between hummingbird species and floral resources is capable of explaining many of the principles of community organization (Feinsinger & Colwell 1978, Martín-González *et al.* 2015).

Morphological complexity of hummingbird assemblages within the temperate forests of North America is lower (medium-sized birds with short-medium straight bills) relative to those of the tropical forests of Central and South America (small to large hummingbirds with short to long, straight to curved bills; Kodric-Brown *et al.* 1984, Brown & Bowers 1985). Hummingbird species richness is also reduced in North America (Brown & Bowers 1985) when compared with the Central or South American tropics. These patterns could indicate that hummingbirds in North America have wider, more generalized and overlapping feeding niches than do hummingbird species occurring around the equator (Abrahamczyk & Kessler 2015). For species pairs with high niche overlap, competition intensity between species is expected to be high (Pianka 1973, Ricklefs & Miller 1999). However, the morphological similarity among North American hummingbird species may indicate that niche separation occurs through variation in feeding behaviour. In Mexico, several studies have established different feeding behaviours among coexisting hummingbird species (Lyon 1976, Martínez del Río & Eguiarte 1986, Ornelas *et al.* 2002, Lara *et al.* 2011).

Feinsinger (1976) found evidence for two types of feeding behaviour in hummingbirds: holding a territory and trap-lining. Territorial hummingbirds defend an area where food sources, usually the best available and most abundant, are found (Wolf

1970). Trap-lining hummingbirds travel among clumps of flowers, presumably following a regular route and visiting these clumps of flowers in a particular sequence (Stiles 1975). However, aggressive hummingbirds can gain access to the best food resources without the cost of establishing and defending a territory, feeding on high-quality resources even when they are not clumped (Stiles & Wolf 1970). The dominance of aggressive hummingbirds facilitates priority access to the best floral resources (Feinsinger 1976, Wolf *et al.* 1976, Wolf 1978) while decreasing available options for smaller subordinates (Morse 1982). Hence, behaviourally dominant hummingbirds can play a central role in determining the spatial and temporal distribution of the hummingbird assemblage using floral resources (Stiles & Wolf 1970, Ornelas *et al.* 2002). Dominant hummingbirds may influence the feeding behaviour of subordinate hummingbirds (Sandlin 2000b, Muchhala *et al.* 2014), but the dominant behaviour is subject to the quality of the resources defended to compensate for the cost of this behaviour (Cotton 1998, Justino *et al.* 2012). Thus, floral abundance and nectar resource availability can directly influence the aggressive behaviour of hummingbirds (Justino *et al.* 2012, Rodríguez-Flores & Arizmendi 2016).

In other nectarivorous birds (honeycreepers), the interspecific dominance hierarchy is correlated with body size and the degree of dependence of each species on nectar for food (Carpenter 1978). In general, dominant species are larger than subordinate ones and often access the best food resources (Wolf *et al.* 1976, Morse 1982). Likewise, some authors have proposed that aggressive dominance in hummingbirds is related to body size (Lyon 1976, Las-Casas *et al.* 2012), higher wing disc loading (Feinsinger & Chaplin 1975, Kodric-Brown & Brown 1978, Carpenter *et al.* 1993) and migratory status (Des Granges 1979, Rodríguez-Flores & Arizmendi 2016). Des Granges (1979) defined the dominance hierarchy of the hummingbird community as the species at the top of the hierarchy that wins most of their interspecific chases while the species at the bottom lose most chases.

Complex hummingbird assemblages composed of species with different body size and migratory status occur during winter in western Mexico (Arizmendi 2001). Hummingbird communities in western Mexico have greater species diversity and morphological variation (Des Granges 1979, Arizmendi 2001) compared with other North

American communities (Kodric-Brown *et al.* 1984, Brown & Bowers 1985). In our study, we investigated whether body size and aggressive dominance influence feeding behaviour of hummingbirds in a temperate forest in northwestern Mexico. First, we quantified the dominance status of hummingbird species and determined whether dominance is related to body size, wing disc loading and migratory status. Secondly, we evaluated whether the hummingbird assemblage was organized by feeding preferences for different plant species. Finally, we examined whether the most dominant hummingbird species defended floral patches with more energy and/or with larger number of flowers. We predicted that the body size of a hummingbird is directly related to their level of dominance, which in turn determines feeding preferences and the quality of the flower patch defended.

METHODS

Study area

The study took place at El Palmito-Concordia, located in the Sierra Madre Occidental (23°35' 20"N, 105°52'0"W), Mexico. The study area is between 1800 and 2133 m above sea level (asl). The climate is temperate sub-humid with an average annual precipitation of 1247 mm (SMN 2000). Fourteen hummingbird species have been documented at the study site, including five migratory species that breed in the USA and Canada (López Segoviano 2012). The flower patches were located in an area of 300 ha within different types of vegetation (oak-pine forest, cloud forest, forest edges and clear-cut vegetation; Díaz 2005). Observations and data collection were carried out from 10 November 2010 to 24 February 2011 and from 1 November 2015 to 28 February 2016, during the autumn and winter seasons, when migratory and resident hummingbirds coexist. The largest numbers of hummingbird species are present in the Sierra Madre Occidental region during the winter season, mainly due to the arrival of migratory hummingbirds and the increased abundance of food (Arizmendi 2001).

Body size

Body mass and wing disc loading were measured as estimates of body size for hummingbird species (Feinsinger & Chaplin 1975, Fleming & Muchhala

2008). Three standard mist-nets (12 × 3 m) were placed near flowering sites for hummingbirds. The mist-nets were operated for 2 days (from 07:00 to 17:00 h) at each site, representing a single sampling period. There were 10 sampling periods between late autumn and winter (12 November 2010 to 26 February 2011). Sporadic mist-net sampling was later performed to augment the data for particular species (60 mist-net hours from 1 November 2015 to 28 February 2016). A total of 260 mist-net hours were dedicated to catching hummingbirds over the course of the study. Wing-chord length (mm) of each captured individual was measured using a wing-ruler and body mass was recorded using a digital scale to the nearest 0.10 g (Table S1). To calculate wing disc loading, the formula $L_{WD} = W/\pi(b/2)^2$ was used, where W is bodyweight (g) and b is 2.5 times wing-chord (cm) (Feinsinger & Chaplin 1975).

Hummingbird behaviour

We documented the interactions among hummingbirds by conducting behavioural observations at a distance of ~8 m from flower patches (following Cotton 1998). A flower patch was considered to be a defined set of flowers. Each flower patch was made up of one species of flowering plant. We observed 324 flower patches belonging to seven plant species (the most abundant ornithophilic species in the area); each flower patch was delimited from other flower patches by more than ~20 m. The observed flower patches had an average of 714 flowers per patch (a minimum of 29 and a maximum of 7134 flowers). The seven plant species (*Salvia elegans*, *Salvia iodonantha*, *Salvia mexicana*, *Cuphea* sp., *Loeselia mexicana*, *Cestrum thyrsoideum* and *Agave inaequidens barrancensis*) represented five families (Lamiaceae, Lythraceae, Polemoniaceae, Solanaceae and Asparagaceae). The number of observed flower patches of each species was proportional to their abundance in the study area. Each behavioural observation was made at a different floral patch at 1-h intervals between 07:00 and 15:00 h. Five hours of observations were performed per day by two observers (324 in total); for each observation, we recorded the hummingbird species, the time and duration of each visit, the number of flowers probed and the outcome of aggressive interactions. The aggressive interactions were characterized by a hummingbird chasing, vocalizing and attacking other hummingbirds (Kodric-Brown & Brown 1978, Cotton 1998, Camfield 2006). The winner of an

aggressive interaction was identified as the hummingbird that returned to feed or perch nearby (usually within 3 min) after it had successfully defended and/or chased off another hummingbird from a floral patch (following Justino *et al.* 2012).

We recorded 13 hummingbird species of the 14 species known to occur in the region (Table S1). Rufous Hummingbird *Selasphorus rufus* and Allen's Hummingbird *S. sasin* are not always distinguishable in the field, as only adult male *S. rufus* can be identified in the field by their entirely rufous back (Healy & Calder 2006). In the study site 24 adult male Rufous Hummingbird and only one Allen's Hummingbird were captured. Hence we considered all individuals recorded during the focal observations as Rufous Hummingbird.

Resource quality

Nectar concentration and volume was measured from the most abundant flower species (*S. iodantha*, *S. elegans*, *C. thyrsoides* and *A. inaequidens* subsp. *barrancensis*). Flowers were bagged before they opened, nectar was extracted in the evening and morning (*S. iodantha* $n = 16$ plants, 179 flowers; *S. elegans*, $n = 5$ plants, 50 flowers; *C. thyrsoides*, $n = 17$ plants, 191 flowers; and *A. inaequidens* subsp. *barrancensis*, $n = 10$ plants, 111 flowers). In the case of the *Agave*, flowers were not bagged and nectar was extracted at dawn because these flowers feed bats and hawkmoths at night and all their nectar will not necessarily be used by hummingbirds (Rocha *et al.* 2005). The nectar was extracted using microcapillary tubes, and the nectar concentrations were calculated using a portable refractometer (Atago N-brand IEBX with a range of 0–32 Brix). To take into account the quality and quantity of nectar produced by a flower, the calories produced per flower were calculated by multiplying the volume of nectar (μL) by the sugar concentration (mol) by 1.34, as proposed by Stiles (1975). With this method, we can infer the amount of energy available in the floral patch for hummingbirds to use and associate this with their behaviour.

Statistical analysis

We determined the dominance hierarchy of the 13 captured hummingbird species at El Palmito using David's score ($D_i = w + w^{(2)} - l - l^{(2)}$). This score equally reflects the proportion of wins by species i in its interactions with another species j , where w is the

number of i wins, l is i losses, $w^{(2)}$ is the wins of species defeated by i , and $l^{(2)}$ is the losses of species to whom i lost (David 1987, De Vries 1998). This index for ranking dominance was designed for an incomplete data matrix, with paired comparisons in which not all species compete against each other (David 1987). The resulting David's scores indicate the range of dominance of each species within the interspecific interaction matrix (Chen *et al.* 2011). In this case we considered an interspecific interaction matrix of 13 hummingbird species from which a David's score was calculated. A linear regression was then performed in the GRAPHPAD PRISM software package (2007) to determine whether body mass and wing disc loading of hummingbird species were related to their resulting dominance score. We used generalized linear models (GLMs; Gaussian distribution and identity link) to determine whether the migratory status of hummingbird species was related to their resulting dominance score. Normality and homogeneity of variance of the data were tested by a Shapiro–Wilk normality test (Crawley 2007). We evaluated the nectar quantity of the most abundant flower species to determine whether there is a difference in the number of calories available among the flower patches constituted by different plant species: *A. inaequidens* subsp. *barrancensis* (22 patches observed), *C. thyrsoides* (54 patches observed) and *S. iodantha* (240 patches observed). The flower patches of these species represented 97.5% of all observed patches. The differences in energy available among plant species (*S. iodantha*, *C. thyrsoides* and *A. inaequidens*) was determined by a non-parametric Kruskal–Wallis test and a *post-hoc* Dunn's multiple comparison test, after detecting a lack of normality and homogeneity of variance of the data.

In addition, to determine whether the most dominant hummingbird species dominate the best floral patches (by the number of flowers and quantity of calories), we used David's scores from each hummingbird species as the response variable and the quality of flower patches as the predictor variable. The response variable was David's score for interactions won. The relationship of the David's scores for hummingbird species to the number of flowers (log-transformed) and calories (log-transformed) in each flower patch was determined using generalized linear mixed models (penalized quasi-likelihood; Faraway 2005, Crawley 2007). We assume that interactions are not spatially independent and used the identity of each flower patch and interactions recorded during the same

session and site as a random effect (Patch nested within Site). Because the response variable is categorical, we used the penalized quasi-likelihood approximation to maximum likelihood (quasi-distribution and identity link) and a Wald test based on a chi-squared distribution was used to obtain *P*-values to assess the model (Faraway 2005, Crawley 2007). Analyses were performed within the R software (2017) using the MASS (Ripley *et al.* 2016) and ado (Lesnoff & Lancelot 2015) packages.

RESULTS

We observed 654 hummingbird interactions (intra- and interspecific), including 477 interspecific interactions in which one of the hummingbirds defended a floral patch (Table S2). David's score (Ds) showed that larger hummingbird species (Rivoli's Hummingbird *Eugenes fulgens* and Blue-throated Hummingbird *Lampornis clemenciae*) occupied the top positions of the dominance hierarchy, whereas smaller hummingbird species (Costa's Hummingbird *Calypte costae* and Bumblebee Hummingbird *Atthis heloisa*) were less dominant (Fig. 1). Dominance (Ds) was positively related to body mass (Fig. 2a; $R^2 = 0.88$, $F_{1,12} = 72.0$, $P < 0.0001$), and wing disc loading (Fig. 2b; $R^2 = 0.33$, $F_{1,12} = 4.79$,

$P < 0.0511$) but was only significant for body mass. Migratory status was not significantly associated (either positively or negatively) with dominance ($\chi^2_2 = 898.93$, $P < 0.0742$).

The top dominant hummingbird species visited more flower patches of plant species with higher energetic rewards than did species at the bottom of the dominance hierarchy (Fig. 3). Patches of *A. inaequidens* and *C. thyrsoides* had significantly more calories than patches of *S. iodonantha* (Kruskal–Wallis = 50.06, $P < 0.0001$; Dunn's multiple comparisons test, $P < 0.05$; Fig. 4).

Generalized linear mixed models indicated that hummingbird species with the higher David's score (Ds) defended floral patches with more available calories; however, David's score for a species decreased with the number of flowers in a patch (Table 1).

DISCUSSION

Dominant hummingbird species

Our results demonstrated that the most dominant hummingbird species was Rivoli's Hummingbird followed by Blue-throated Hummingbird (see also Lyon 1976, Martínez del Río & Eguiarte 1986,

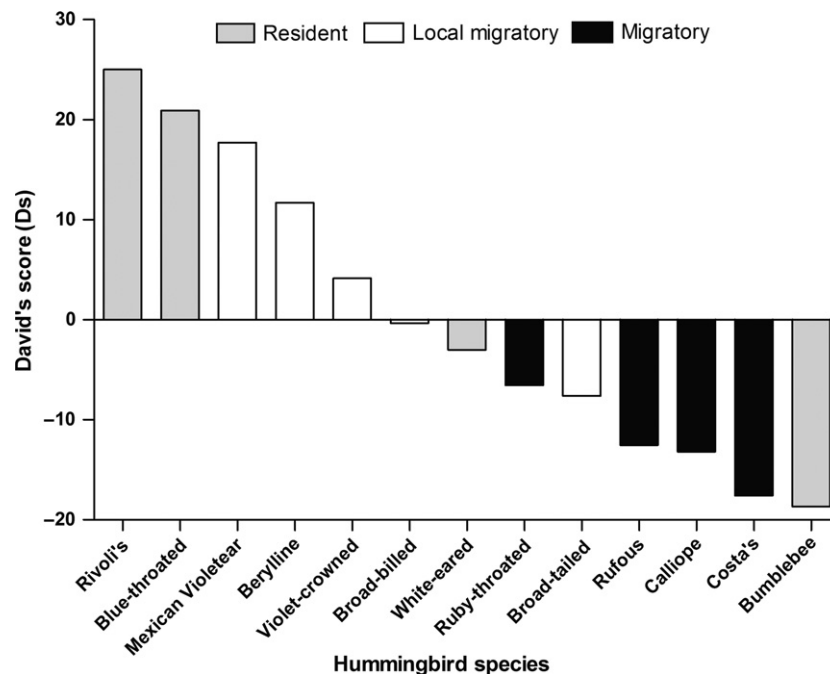


Figure 1. David's score for the 13 hummingbird species at El Palmito, Mexico. The resident Blue-throated Hummingbird and Rivoli's Hummingbird have the highest dominance index (Ds) score.

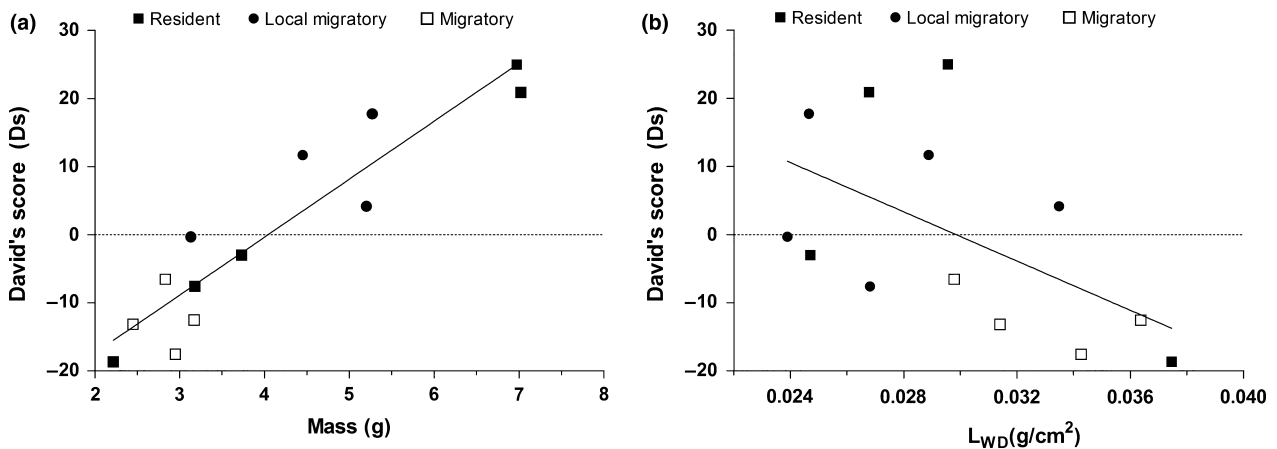


Figure 2. Relationship of the David's score index (Ds) with (a) body mass (g) and (b) wing disc loading L_{WD} (g/cm²) of 13 species of hummingbirds (Resident hummingbird solid square, Local migratory solid circle, and Migratory clear square). David's score (Ds) was positively related to body mass ($R^2 = 0.88$, $F_{1,12} = 72.0$, $P < 0.0001$) but not to wing disc loading ($R^2 = 0.30$, $F_{1,12} = 4.79$, $P < 0.0511$).

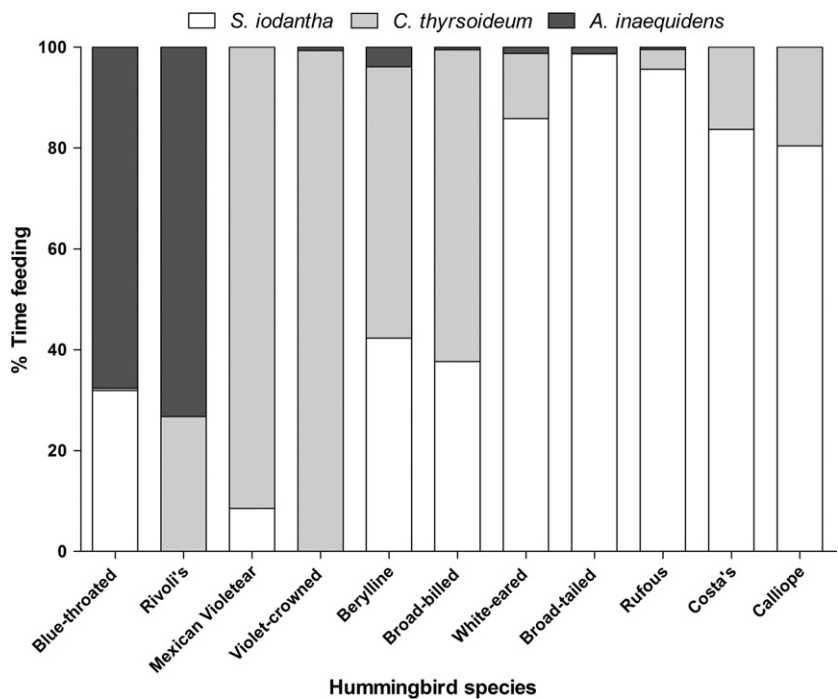


Figure 3. Percentage of time that each hummingbird species spent feeding in each type of flower patch (Bumblebee Hummingbird and Ruby-throated Hummingbird *Archilochus colubris* were excluded because of the small number of observations).

Lara *et al.* 2011). However, Blue-throated Hummingbirds dominate Rivoli's Hummingbirds in 79% of their encounters (Table S2), a result similar to what was reported for a southern Arizona hummingbird community (Sandlin 2000b). This apparent contradiction with David's scores,

showing Rivoli's Hummingbird to be the most dominant species within the community, occurs because this species only loses interactions for access to floral resources to Blue-throated Hummingbirds. In contrast, Blue-throated Hummingbirds occasionally lose interactions with Rivoli's

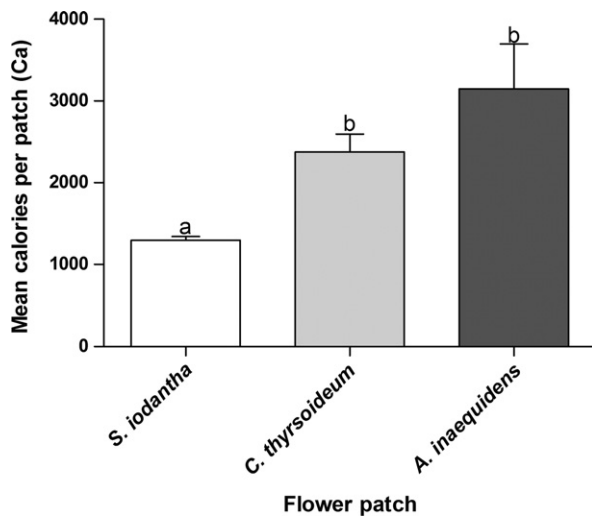


Figure 4. Mean (\pm se) calories produced by flowers in patches consisting of *Agave inaequidens*, *Cestrum thyrsoidium* and *Salvia iodonantha* at El Palmito, Mexico. The Kruskal–Wallis test showed that flower patches of *S. iodonantha* differed in the quantity of calories offered. Dunn's multiple *a posteriori* comparison test confirmed the differences among types of flower patches (Kruskal–Wallis = 61.94, $P < 0.0001$; Dunn's multiple comparisons test, $P < 0.05$).

Table 1. Generalized linear mixed model showing the relationship between the David's score index (of the interactions won by each hummingbird species), the number of flowers and total calories in each flower patch ($\chi^2_3 = 11.0$; $P < 0.01$).

	β	<i>t</i> -Value	<i>P</i>
Intercept	−14.608	−2.416	0.01
Log (number flowers per patch)	−4.246	−2.405	0.01
Log (calories per flower patch)	5.905	3.013	0.003

The results demonstrate a significant positive relationship between dominance index and the number of calories in each flower patch and a negative relationship with number of flowers. Bold values indicate $P < 0.05$.

Hummingbird as well as with less dominant hummingbird species (Berylline Hummingbird *Amazilia beryllina* and Rufous Hummingbird). In this sense, David's score reflects the strength of the dominance of a species vs. the entire local species assemblage (David 1987, De Vries 1998). It should be noted that the flower patches where Blue-throated Hummingbird lost to Berylline Hummingbird and Rufous Hummingbird had few calories, far below those of the flower patches of *A. inaequidens*, the plant species preferred by Blue-throated Hummingbirds.

Relationships between dominance hierarchy and body size

We found a positive relationship between body size and the dominance status of hummingbird species at El Palmito, Mexico. In a hummingbird community in western Mexico, Des Granges (1979) also proposed that the size of hummingbird species determines their interspecific dominance. Although dominance by larger species appears clearly to occur in many hummingbird communities (Lyon 1976, Des Granges 1979, Las-Casas *et al.* 2012), this could differ for more complex and diverse communities. Martin and Ghalambor (2014), for instance, found that larger bird species were dominant over smaller species during aggressive interactions for shared resources in three guilds (vultures, hummingbirds and antbirds/woodcreepers), but the advantage of a larger body size declined with increasing evolutionary distance among the species. These authors indicated that the dominance of larger species over small ones was not an absolute rule, even though this rule was evident in our study.

We did not find a relationship between wing disc loading and dominance status of hummingbird species, unlike in previous studies where high wing disc loadings were related to high dominance and the degree of aggression displayed by different hummingbird species (Feinsinger & Chaplin 1975, Kodric-Brown & Brown 1978, Feinsinger *et al.* 1979, Carpenter *et al.* 1993). Because higher wing disc loading confers the ability to maximize acceleration and high manoeuvrability, it could provide a competitive advantage (Feinsinger & Colwell 1978, Feinsinger *et al.* 1979) but it may be influenced by multiple interacting features (Altshuler 2006). In addition, some hummingbird species studied here have high wing disc loading and low dominance indexes but are considered to be territorial and dominant in other places (e.g. Rufous Hummingbird, Kodric-Brown & Brown 1978, Calliope Hummingbird *Selasphorus calliope*, Armstrong 1987). Hence, wing disc loading alone does not appear to be a reliable predictor of the interspecific dominance of hummingbirds.

Finally, we did not find a relationship between migratory status and the dominance of hummingbird species, unlike previous studies (Des Granges 1979, Rodríguez-Flores & Arizmendi 2016). Migratory hummingbird species in North America are small and tend to be subordinate to resident

and local migratory hummingbirds (Des Ganges 1979). However, migrants can also be dominant depending on local abundance of other hummingbirds and resource availability and this can change even on a daily basis (Rodríguez-Flores & Arizmendi 2016).

Feeding behaviour

Species at the top of the dominance hierarchy (Rivoli's Hummingbird and Blue-throated Hummingbird) foraged in the best resources that offered higher amounts of energy in fewer flowers, as in *A. inaequidens* in our study (for other species of *Agave* see Martínez del Río & Eguiarte 1986, Ornelas *et al.* 2002). Although there was no significant difference in the average number of calories between flower patches of *C. thyrsoides* and *A. inaequidens*, *C. thyrsoides* patches had 400–7134 flowers (mean = 1814.46) and *A. inaequidens* patches had 70–920 (mean = 291.13). However, the *A. inaequidens* flowers had the greatest amount of calories per flower (mean = 10.81 calories), unlike the flowers of *C. thyrsoides* (mean = 1.30 calories). The characteristic of having a large amount of calories in a small number of flowers makes the *A. inaequidens* patches the best floral resources at our study site.

In our study, less dominant hummingbird species were detected feeding on the poorer resources (patches of *S. iodantha*; Fig. 4), which could be due to larger dominant hummingbird species feeding on floral patches with more calories (Figs 3 and 4). Hummingbird species that occupy lower positions of the hierarchy may appear to prefer areas of poorer resource quality (Stiles 1976, Sandlin 2000a, Muchala *et al.* 2014). This may be due to the relationship between size and the number of calories needed. Hence, because of the smaller size of subordinate hummingbirds, smaller quantities of nectar are needed, rendering small species more efficient in the exploitation of less calorie-rich resources (Wolf 1978). Smaller species can also exploit more dispersed floral resources (Wolf 1978, Des Ganges 1979, Cotton 1998). In this sense, food resources of lower quantity or quality may not contain sufficient rewards for larger hummingbirds, but they can be exploited by small hummingbirds (Cotton 1998). This segregation strategy may also allow small hummingbirds to reduce risks of injury during encounters with more aggressive territorial hummingbirds (Ornelas *et al.* 2002, Lara *et al.* 2011).

Dominance hierarchy and feeding behaviour

Our results showed that the most dominant hummingbird species defended flower patches that offered more energy, a result consistent with that of other studies (i.e. Stiles & Wolf 1970, Sandlin 2000a). However, dominance level decreased with increasing number of flowers per patch (Table 1). Calories per flower seems to be the most important feature, unlike other studies where the most dominant hummingbird species defend the patches with the greatest number of flowers (Feinsinger 1976, Cotton 1998, Justino *et al.* 2012), up to a patch size where the energetic threshold makes defending it too costly (Justino *et al.* 2012). In our case patches with flowers of *A. inaequidens* provided a large amount of calories per flower and generally a reduced number of flowers than the patches with flowers of *S. iodantha* and *C. thyrsoides*. Even a patch with few flowers, by providing more calories per flower, is more profitable to defend for a hummingbird (Kodric-Brown & Brown 1978, Gass 1979, Montgomerie *et al.* 1984, Carpenter 1987).

CONCLUSIONS

We found that the dominance hierarchies of hummingbird species at El Palmito, Mexico, were determined by body size, similar to previous work on hummingbird assemblages and for other feeding guilds (Martin & Ghalambor 2014). The flower patches of different plant species provide different energetic rewards. Feeding behaviour of hummingbirds in this region may depend on the distribution of plant species visited and on the amount of energy available from each flower patch. Distinct types of resources and the positioning of hummingbird species along the dominance hierarchy reduce overlap in resource exploitation. In the same way, less aggressive species may coexist by using less calorie-rich resources that are not profitable for aggressive species. Therefore, the relationship between hummingbird size, their level of aggressive dominance and the quality of flower patches defended was seen to determine hummingbird community assemblages.

We are grateful for the comments and suggestions provided by Roy Teo and Maribel Arenas. We especially thank Ejido Forestal El Palmito for access to facilities and the study site. This work was supported by

Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México who hosted G.L.S. during his Ph.D. studies. We thank PAPIIT-UNAM-IN216514, PAEP-UNAM and the US Fish and Wildlife Service's Neotropical Migratory Bird Conservation Act (Grant 5087) for financial support. We thank Consejo Nacional de Ciencia y Tecnología (CONACYT) for the fellowship (239903) awarded to G.L.S. Pietro K. Maruyama, Colleen Downs and Rauri Bowie provided helpful comments and suggestions on an earlier version of the manuscript. We obtained permits from the Mexican government from the Subsecretaría de Gestión para la Protección Ambiental: Dirección General de Vida Silvestre (permit numbers SGPA/DGVS/01833/11 and SGPA/DGGFS/712/1289/16).

REFERENCES

- Abrahamczyk, S. & Kessler, M. 2015. Morphological and behavioural adaptations to feed on nectar: how feeding ecology determines the diversity and composition of hummingbird assemblages. *J. Ornithol.* **156**: 333–347.
- Altshuler, D.L. 2006. Flight performance and competitive displacement of hummingbirds across elevational gradients. *Am. Nat.* **167**: 216–229.
- Arizmendi, M.C. 2001. Multiple ecological interactions: nectar robbers and hummingbirds in a highland forest in Mexico. *Can. J. Zool.* **76**: 997–1006.
- Armstrong, D.P. 1987. Economics of breeding territoriality in male Calliope Hummingbirds. *Auk* **104**: 242–253.
- Brown, J.H. & Bowers, M.A. 1985. Community organization in hummingbirds: relationships between morphology and ecology. *Auk* **102**: 251–269.
- Camfield, A.F. 2006. Resource value affects territorial defense by Broad-tailed and Rufous Hummingbirds. *J. Field Ornithol.* **77**: 120–125.
- Carpenter, F.L. 1978. A spectrum of nectar-eater communities. *Am. Zool.* **18**: 809–819.
- Carpenter, F.L. 1987. Food abundance and territoriality: to defend or not to defend? *Am. Zool.* **27**: 387–399.
- Carpenter, F.L., Hixon, M.A., Russell, R.W., Paton, D.C. & Temeles, E.J. 1993. Interference asymmetries among age-sex classes of Rufous Hummingbirds during migratory stopovers. *Behav. Ecol. Sociobiol.* **33**: 297–304.
- Chen, C., Wu, H., Liu, T. & Shieh, B. 2011. Dominance rank and interference competition in foraging among six species of birds in a park in Kaohsiung City, Taiwan. *Taiwan J. For. Sci.* **26**: 255–266.
- Cotton, P.A. 1998. Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis* **140**: 647–653.
- Crawley, M.J. 2007. *The R Book*. Chichester: John Wiley & Sons Ltd.
- David, H.A. 1987. Ranking from unbalanced paired-comparison data. *Biometrika* **74**: 432–436.
- De Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Anim. Behav.* **55**: 827–843.
- Des Granges, J.L. 1979. Organization of a tropical nectar feeding bird guild in a variable environment. *Living Bird* **17**: 199–236.
- Díaz, J.S. 2005. *Tipos de Vegetación y Flora del Ejido el Palmito, Concordia Sinaloa*. Culiacan: PRONATURA.
- Available at: <http://www.conabio.gob.mx/institucion/proyectos/resultados/VegetacionCQ01.pdf> (accessed 30 March 2017).
- Faraway, J.J. 2005. *Extending the Linear Model With R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Boca Raton, FL: Chapman and Hall/CRC.
- Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. *Ecol. Monogr.* **46**: 257–291.
- Feinsinger, P. & Chaplin, S.B. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. *Am. Nat.* **109**: 217–224.
- Feinsinger, P. & Colwell, R.K. 1978. Community organization among neotropical nectar-feeding birds. *Am. Zool.* **18**: 779–795.
- Feinsinger, P., Colwell, R.K., Terborgh, J. & Chaplin, S.B. 1979. Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. *Am. Nat.* **113**: 481–497.
- Fleming, T.H. & Muchhala, N. 2008. Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. *J. Biogeogr.* **35**: 764–780.
- Gass, C.L. 1979. Territory regulation, tenure and migration in Rufous Hummingbirds. *Can. J. Zool.* **57**: 914–923.
- Gass, C.L. & Montgomerie, R.D. 1981. Hummingbird foraging behaviour: decision-making and energy regulation. In Kamil, A. & Sargent, T. (eds) *Foraging Behaviour: Ecological, Ethological and Physiological Approaches*: 159–196. New York, NY: Garland STPM Press.
- GraphPad Prism 2007. GraphPad Software. San Diego, CA, USA, www.graphpad.com.
- Healy, S. & Calder, W.A. 2006. Rufous Hummingbird (*Selasphorus rufus*). In Poole, A. (ed.) *The Birds of North America*. Ithaca, NY: Cornell Lab of Ornithology. Available at: <http://bna.birds.cornell.edu/bnaproxy.birds.cornell.edu/bna/species/053>
- Healy, S.D. & Hurly, T.A. 2001. Foraging and spatial learning in hummingbirds. In Chittka, L. & Thomson, J. (eds) *Pollination Biology*: 127–147. Cambridge: Cambridge University Press.
- Hurly, T.A. & Healy, S.D. 1996. Memory for flowers in Rufous Hummingbirds: location or local visual cues? *Anim. Behav.* **51**: 1149–1157.
- Justino, D.G., Maruyama, P.K. & Oliveira, P.E. 2012. Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *J. Ornithol.* **153**: 189–197.
- Kelt, D.A. & Brown, J.H. 1999. Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. In Weiher, E. & Keddy, P. (eds) *Ecological Assembly Rules*: 75–106. Cambridge: Cambridge University Press.
- Kodric-Brown, A. & Brown, J.H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* **59**: 285–296.
- Kodric-Brown, A., Brown, J.H., Byers, G.S. & Gori, D.F. 1984. Organization of a tropical island community of hummingbirds and flowers. *Ecology* **65**: 1358–1368.
- Lara, C., Martínez-García, V., Ortiz-Pulido, R., Bravo-Cadena, J., Loranca, S. & Córdoba-Aguilar, A. 2011. Temporal-spatial segregation among hummingbirds foraging on honeydew in a temperate forest in Mexico. *Curr. Zool.* **57**: 56–62.
- Las-Casas, F.M., Azevedo Junior, S.M. & Dias Filho, M.M. 2012. The community of hummingbirds (Aves: Trochilidae)

- and the assemblage of flowers in a Caatinga vegetation. *Braz. J. Biol.* **72**: 51–58.
- Lesnoff, M. & Lancelot, R.** 2015. Package 'aod'. Available at: <http://cran.r-project.org/package=aod> (accessed 30 March 2017).
- López Segoviano, G.** 2012. *Comportamiento territorial y preferencias de forrajeo del Colibrí migratorio Selasphorus rufus dentro de un sitio invernal*. M.Sc thesis, Universidad Nacional Autónoma de México.
- Lyon, D.L.** 1976. A montane hummingbird territorial system in Oaxaca, Mexico. *Wilson Bull.* **88**: 280–298.
- Maglianesi, M.A., Blüthgen, N., Böhning-Gaese, K. & Schleuning, M.** 2015a. Functional structure and specialization in three tropical plant-hummingbird interaction networks across an elevational gradient in Costa Rica. *Ecography* **38**: 1119–1128.
- Maglianesi, M.A., Böhning-Gaese, K. & Schleuning, M.** 2015b. Different foraging preferences of hummingbirds on artificial and natural flowers reveal mechanisms structuring plant-pollinator interactions. *J. Anim. Ecol.* **84**: 655–664.
- Martin, P.R. & Ghalambor, C.K.** 2014. When David beats Goliath: the advantage of large size in interspecific aggressive contests declines over evolutionary time. *PLoS One* **9**: e108741.
- Martínez del Río, C. & Eguiarte, L.E.** 1986. Bird visitation to *Agave salmiana*: comparisons among hummingbirds and perching birds. *Condor* **89**: 351–363.
- Martín-González, A.M., Dalsgaard, B., Nogués-Bravo, D., Graham, C.H., Schleuning, M., Maruyama, P.K., Abrahamczyk, S., Alarcón, R., Araujo, A.C., Araújo, F.P., de Azevedo, S.M., Baquero, A.C., Cotton, P.A., Ingversen, T.T., Kohler, G., Lara, C., Las-Casas, F.M.G., Machado, A.O., Machado, C.G., Maglianesi, M.A., McGuire, J.A., Moura, A.C., Oliveira, G.M., Oliveira, P.E., Ornelas, J.F., Rodrigues, L.d.C., Rosero-Lasprilla, L., Rui, A.M., Sazima, M., Timmermann, A., Varassin, I.G., Vizentin-Bugoni, J., Wang, Z., Watts, S., Rahbek, C. & Martinez, N.D.** 2015. The macroecology of phylogenetically structured hummingbird–plant networks. *Global Ecol. Biogeogr.* **24**: 1212–1224.
- Maruyama, P.K., Vizentin-Bugoni, J., Oliveira, G.M., Oliveira, P.E. & Dalsgaard, B.** 2014. Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network. *Biotropica* **46**: 740–747.
- Montgomerie, R.D., Eadie, J.M. & Harder, L.D.** 1984. What do foraging hummingbirds maximize? *Oecologia* **63**: 357–363.
- Morse, D.H.** 1982. *Behavioral Mechanisms in Ecology*. Cambridge, MA: Harvard University Press.
- Muchhala, N., Johnsen, S. & Smith, S.D.** 2014. Competition for hummingbird pollination shapes flower color variation in *Andean solanaceae*. *Evolution* **68**: 2275–2286.
- Ornelas, F.J., Ordano, M., Hernández, A., López, C.J., Mendoza, L. & Perroni, Y.** 2002. Nectar oasis produced by *Agave marmorata* Roezl. (Agavaceae) lead to spatial and temporal segregation among nectarivores in the Tehuacán Valley, México. *J. Arid Environ.* **52**: 37–51.
- Pianka, E.R.** 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**: 53–74.
- Pianka, E.R.** 1975. Niche relations of desert lizards. In Diamond, J.M. & Cody, M.L. (eds) *Ecology and Evolution of Communities*: 292–314. Cambridge: Belknap Press of Harvard University Press.
- R Core Team** 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ricklefs, R.E. & Miller, G.L.** 1999. *Ecology*, 4th edn. New York, NY: W. H. Freeman and Company.
- Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A. & Firth, D.** 2016. MASS: Support Functions and Datasets for Venables and Ripley's MASS. R package version 7.3-45. Available at: <https://cran.r-project.org/web/packages/MASS/> (accessed 10 October 2016).
- Rocha, M., Valera, A. & Eguiarte, L.E.** 2005. Reproductive ecology of five sympatric *Agave Littaea* (Agavaceae) species in central Mexico. *Am. J. Bot.* **92**: 1330–1341.
- Rodríguez-Flores, C.I. & Arizmendi, M.C.** 2016. The dynamics of hummingbird dominance and foraging strategies during the winter season in a highland community in Western Mexico. *J. Zool.* **299**: 262–274.
- Sandlin, E.A.** 2000a. Cue use affects resource subdivision among three coexisting hummingbird species. *Behav. Ecol.* **11**: 550–559.
- Sandlin, E.A.** 2000b. Foraging information affects the nature of competitive interactions. *Oikos* **91**: 18–28.
- Schuchmann, K.L.** 1999. Familia Trochilidae (Hummingbirds). In Del Hoyo, J., Elliot, A. & Sargatal, J. (eds) *Handbook of the Birds of the World: Volume 5: Barn-owls to Hummingbirds*: 468–680. Barcelona: Lynx Edicions.
- SMN** 2000. *Servicio Meteorológico Nacional*. Available at: <http://smn.cna.gob.mx/> (accessed 20 September 2016).
- Stiles, F.G.** 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* **56**: 285–301.
- Stiles, F.G.** 1976. Taste preferences, color preferences, and flower choice in hummingbirds. *Condor* **78**: 10–26.
- Stiles, F.G. & Wolf, L.L.** 1970. Hummingbird territoriality at a tropical flowering tree. *Auk* **87**: 467–491.
- Wolf, L.L.** 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. *Condor* **72**: 1–14.
- Wolf, L.L.** 1978. Aggressive social organization in nectarivorous birds. *Am. Zool.* **18**: 765–778.
- Wolf, L.L., Stiles, F.G. & Hainsworth, F.R.** 1976. Ecological organization of a tropical, highland hummingbird community. *J. Anim. Ecol.* **45**: 349–379.

Received 19 January 2017;
revision accepted 24 September 2017.
Associate Editor: Colleen Downs.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Migratory status, mean body mass, wing chord and wing disc loading of the hummingbirds at El Palmito.

Table S2. Interspecific interaction matrix of 13 hummingbird species from El Palmito, Sinaloa state, Mexico, during 324 h of focal observations.