

Article

Factors affecting the dominance hierarchy dynamics in a hummingbird assemblage

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Abstract

Intra and interspecific competition for nectar play an important role in hummingbird communities. Larger sized species usually exclude smaller species from the rich floral resources. However, it has been recently postulated that the competitive advantages of a large body size decline as the evolutionary distance between the contending species increases. In this study, we analyzed dominance hierarchy dynamics in a hummingbird assemblage in central Mexico. By monitoring hummingbird territories established in three plant species through 1 year, we assessed the effects of energy within territories and the territory owners identity in the frequency of inter and intraspecific encounters. We also evaluated if these factors affect the dominance of larger species when they compete against smaller distantly related contenders. Our results show that their frequency of intraspecific encounters was related with the identity of the territory's owner. On the contrary, the frequency of interspecific encounters was related with both the territory and the identity of the territory's owner. We did not find a significant difference between the number of encounters dominated by larger and smaller species and their contenders. However, the increase in genetic distance between contenders was positively associated with a higher frequency of encounters dominated by small hummingbirds. Our results showed that the ecological factors and evolutionary relationships among contenders play important roles in the dominance hierarchy dynamics.

Key words: agonistic behavior, competition, hummingbirds, resource quality, territoriality

Dominance hierarchy is defined as the social position of one individual relative to one or more competitors (Ewald 1985). In hummingbirds, competition for the access to floral nectar plays an important role in shaping the species composition of local communities (Wolf et al. 1976; Graham et al. 2009). This close relationship drives many species of hummingbirds to follow flowering plants through altitudinal and latitudinal migrations in order to ensure nectar availability (Montgomerie and Gass 1981). This behavioral response to plant phenology promotes seasonal changes in the species composition of the hummingbird community at a given site (Stiles 1980).

Consequently, these changes can affect the levels of intraspecific and interspecific competition resulting in spatial and temporal patterns or resource sharing (Cotton 1998; Lara et al. 2011).

The hummingbird species can perform different foraging strategies to compete for access to nectar. Feinsinger and Colwell (1978) define 6 foraging roles that hummingbirds could fill in a community: territorialists monopolize access to nectar by establishing and defending foraging territories against other hummingbirds; trapliners (high and low reward) realize sequential visits to different feeding locations (trapline); territory parasites (marauders and filchers) consume the

nectar of flowers within a foraging territory in absence (filchers) or even in the presence of the territory owner (marauders); and generalists, which either act opportunistically or their role within the community is not clearly defined. These roles are based on the behavioral and morphological traits (e.g., body size and bill length) associated with the hummingbird foraging strategies. These authors emphasize on the ability of hummingbirds to change their role within the community based on the resources available and the identity of the rest of hummingbird species competing for access to resources.

Body size has been shown to explain the dominance hierarchy of hummingbirds in different assemblages (Stiles and Wolf 1970; Dearborn 1998; López-Segoviano et al. 2017). Overall, larger hummingbird species tend to dominate, excluding smaller species from high quality energy resources (Hainsworth and Wolf 1972; Dearborn 1998; Araújo-Silva and Bessa 2010; Justino et al. 2012; Mendiola-Islas et al. 2016). However, in some cases, smaller species also establish and defend foraging territories against larger contenders (Wolf et al. 1976; Chaves 1997; Antunes 2003).

Martin and Ghalambor (2014) provided an explanation for this pattern and suggested that small species may accumulate characteristics that allow them to overcome the competitive disadvantages associated with smaller body size in interspecific encounters (e.g., greater muscle development, increased acceleration and maneuverability during flight, and increased production of testosterone) through evolutionary time. Recently, Dakin et al. (2018) provide information on how this pattern might work. They demonstrated that the changes in morphological or physiological traits generate behavioral divergence between species. For example, the maneuverability (i.e., the ability to change the speed and direction of the flight) is an important factor that can determine the success in competitive interactions (Dudley 2002). In this sense, Dakin et al. (2018) demonstrated that the enhanced maneuverability in hummingbirds is directly related to an increase in muscular capacity (measured as the maximum mass of beads that the bird can lift in vertical flight) rather than body mass, and to a lower wing loading (i.e., larger wing area relative to body mass) that also is associated with the use of complex turns as yaw or downward rotations. That is, the morphological traits and maneuver abilities of distantly related species could generate different competitive advantages. Thus, the small species can capitalize such differences to win encounters against larger distantly related contenders. This highlights the importance of phylogenetic relationships between contenders because they could be a determinant factor in the outcome of aggressive encounters.

In addition to harboring resident populations, the highlands of Mexico (>1550 m a.s.l.) are used as stopover or wintering sites by migratory hummingbird species (Russell et al. 1994). Such communities are suitable to study the mechanisms that modify the dominance hierarchies. In this article, we analyzed the dominance hierarchy dynamics of a hummingbird assemblage in a temperate montane forest in central Mexico. Our study aimed to specifically address the following two questions: 1) whether the identity of the defended plant species,

the energy contained within territories and the identity of the territory owner affected the frequency of interspecific and intraspecific encounters and 2) whether the frequency of encounters won was affected by the body size and the genetic distance of the contending species.

Materials and Methods

Fieldwork was carried out from October 2015 to October 2016 at the La Malinche National Park (LMNP), Tlaxcala (98°58' W, 19°14' N). We used climate data collected at Zitlaltepec weather station (97°54'27" W, 19°11'59" N) from 1981 to 2010 (SMN 2018). Mean annual temperature over this period was 13.9°C, and annual precipitation was 788.8 mm. The vegetation in the study area is mainly a mosaic of pine and oak forests and secondary vegetation. The ornithophilous plants have sequential flowering periods that generate a variation of abundance and availability of different flowering plant species throughout the year (Lara et al. 2009). The most abundant ornithophilous plants in LMNP are *Penstemon roseus* (Plantaginaceae), *Salvia elegans* (Lamiaceae), and *Bouvardia ternifolia* (Rubiaceae). The 3 species are perennial herbs that grow in patches (Lara 2006). We focused on the agonistic hummingbird interactions occurring around floral territories of these plant species over a 1-year period. Additional information about the plant species is given in Table 1. *Bouvardia ternifolia* (1–1.5 m high) flowers last 4–5 days and each plant have 2–50 flowers, and 1–15 flowers on average opens per day (Lara and Ornelas 2002). *Penstemon roseus* (0.4–1.2 m high) bear 10–20 paniculate inflorescences, each opening 2–4 pendant flowers per day and the flowers last 2–4 days (Lara and Ornelas 2008). *Salvia elegans* (0.8–2 m high) display 22–52 flowers per plant and flowers last an average of 4 days (Espino-Espino et al. 2014).

In this study, we focused in the 5 most abundant hummingbird species in the LMNP: *Colibri thalassinus* (migratory), *Lampornis clemenciae* (migratory), *Eugenes fulgens* (resident), *Hylocharis leucotis* (resident), and *Selasphorus platycercus* (altitudinal and latitudinal migratory populations) (Lara et al. 2009). Additional information about the studied hummingbird species is given in Table 2. Other 7 more hummingbird species have been recorded in the study area (*Lampornis amethystinus*, *Amazilia beryllina*, *Atthis*

Table 2. Body size and clade of each hummingbird species studied

Hummingbird species	Body size (g)	Hummingbird clade
<i>Lampornis clemenciae</i>	8.39 ± 0.12 (n = 61)	Mountain Gems
<i>Eugenes fulgens</i>	7.65 ± 0.11 (n = 49)	Mountain Gems
<i>Colibri thalassinus</i>	6.00 ± 0.06 (n = 128)	Mangoes
<i>Hylocharis leucotis</i>	3.95 ± 0.06 (n = 80)	Emeralds
<i>Selasphorus platycercus</i>	3.74 ± 0.07 (n = 61)	Bees

The body size was estimated of individuals captured in the LMNP from September 2009 to September 2011. The hummingbird clade was defined according to McGuire et al. (2014).

Table 1. Characteristics of the most abundant ornithophilous plant species in the LMPN

Plant species	Flowering season	Plant grow area	Flowers/plant	Nectar volume/flower (μL)	Energy/flower (Kj)
<i>Salvia elegans</i>	October–April	Forested	22–52	4.18 ± 0.34	1.56
<i>Bouvardia ternifolia</i>	May–August	Unforested	2–50	4.38 ± 0.2	1.66
<i>Penstemon roseus</i>	July–November	Forested	10–20	5.74 ± 0.56	3.18

Floral display data were taken from Espino-Espino et al. (2014), Lara and Ornelas (2002, 2008), respectively. Mean nectar volume (± SE) and energy produced per flower (n = 20 flowers in both cases).

heloisa, *Archilochus colubris*, *Calothorax lucifer*, *Selasphorus sasin*, and *S. rufus* albeit in very low numbers (Lara 2006).

Foraging territories were searched and monitored from 29 October 2015 to 23 October 2016. A floral patch was considered a foraging territory if a hummingbird foraged and perched inside and defended it against intruders (Camfield 2006; Márquez-Luna et al. 2015; Mendiola-Islas et al. 2016). We looked for foraging territories following the hummingbird vocalizations (territorial and feeding calls). The individuals that establish and defend a foraging territory (territory owners) often perform vocalizations to advertise their presence to potential competitors (Goldberg and Ewald 1991). In addition to these cues, we randomly selected floral patches to observe if these were foraging territories.

The number of flowers in each of the monitored territories was counted around the time that each owner was observed. The territory boundaries were defined visually by the foraging and aggressive behavior of the territory owner. In addition, we chose 20 flowers from 20 plants (outside the boundaries of the territories) in the same condition as the plant species inside the territories to measure nectar volume (standing crop) in a nondestructive way by using calibrated micropipettes (5 μ L) (Corbet 2003). Sugar concentration (percentage sucrose) was measured with a hand-held pocket refractometer (Atago, Master Refractometer 50H, range concentration 0°–50° Brix). Subsequently, the nectar volume and the sugar concentration (Degrees Brix) of each plant species were used to calculate the mean energy per flower (Kilojoules; Bolten et al. 1979). Finally, the number of flowers in each territory was multiplied by the estimated energy per flower (Kj/flower). We assessed the energy within the territories at the moment of the observations with these approximations. The number of flowers could also represent a surrogate measure of the energy within the territories but the number of flowers and the energy within each territory was highly correlated ($r=0.975$, $n=85$, $P<0.001$). For this reason, we only use the estimate of the energy in each territory for the statistical analyzes.

In each of the territories, we recorded the behavior of the territory owner and the intruders, from 07:00 h to 13:00 h, the period of highest hummingbird activity (Lara 2006). The territory owners were identified by their constant vocal behavior and because they often perched in high branches over or near the defended floral patch. We visually followed the owner within its territory to identify its preferred perches. All territory owners only used few perches on their own territories over the observation period. This helped us determine that we were looking at the same individual before and after the agonistic encounters (Márquez-Luna et al. 2015). During each of the field work days we searched for foraging territories in different locations to prevent repeated records of the same territorial individuals. The searching and observation locations were defined depending on the floral abundance and the flowering season.

In each territory, we recorded 1) the identity of the territory owner and the intruders, 2) the frequency of inter and intraspecific agonistic interactions, and 3) the winning species of each agonistic interaction for 90 continuous minutes. A winning species was recognized when it returned to perch or forage in or near the territory after the encounter.

Dominance hierarchy

Hummingbird dominance hierarchy was established for each of the floral resources we studied. Dominance hierarchy was calculated using David's score (DS; David 1987). DS has been previously used to determinate the dominance hierarchy in a hummingbird

assemblage (López-Segoviano et al. 2017). This method considers the proportion of encounters won and lost by each species' pair as well as the total interactions between both contending species (Gammell et al. 2003) through the following equation: $DS = w + w_2 - l - l_2$, where w represents the sum of the encounters won by species i against species j divided by the total of agonistic interactions between i and j (i.e., P_{ij}), w_2 represents the sum of values w (already weighted by the P_{ij} values of the species with which species i interacted), l represents the sum of the encounters won by species j against species i (i.e., P_{ji}) and l_2 represents the sum of the values l (already weighted by the P_{ji} values of the species with which the species j interacted). Species with high DS index values have a higher rank in the dominance hierarchy than the species with lower values.

Genetic distance of contenders

The genetic distance between the contending species was estimated using genetic mitochondrial sequences available from GenBank (Clark et al. 2015). The sequences were aligned using the ClustalW alignment algorithm (Thompson et al. 1994). Once aligned, the genetic distance between the sequences belonging to the contending species was estimated with the Tamura–Nei model (Tamura and Nei 1993) in the MEGA software version 7.0 (Kumar et al. 2016). The genetic distance is expressed as the number of nucleotide substitutions between two DNA sequences (Piñero et al. 2008); that is, a high genetic distance value indicates a greater degree of divergence between two species. Cytochrome b is the most widely used mitochondrial gene to estimate the genetic distance between species. However, since very few cytochrome b sequences are available for hummingbird species, we used the following sequences of the mitochondrial gene nicotinamide dehydrogenase subunit 2 (*sensu* Martin and Ghalambor 2014): *S. platycercus* AY830522; *L. clemenciae* KJ602257; *H. leucotis* KJ602252; *E. fulgens* AY830481 and *C. thalassinus* EU042544.

Statistical analysis

We used two generalized linear models (GLM) with a quasi-Poisson error distribution due to overdispersion of the data and the log link function to determine the effect of the identity of the territory owner species, the plant species and the energy (log transformed, to prevent outliers influence) within territories (fixed factors) on the number of inter and intraspecific agonistic interactions (response variables). Likewise, we used a GLM with a binomial distribution and the logit link function to determinate the factors associated with the dominance of larger hummingbirds over the small contenders. In this model we codified the encounters as a dummy response variable, using “1” for encounters won by the larger hummingbird and “0” for those won by the smallest hummingbird. We also included in the model the plant species, the energy (log transformed) within territories and the genetic distance between contenders with three levels: close (0.15–0.17), medium (0.18–0.21) and wide (0.22 or more) as fixed factors. These separation categories were based on the frequency distribution of the genetic distance between bird genera for the same family reported by Johns and Avise (1998). We confirmed that the variables did not have collinearity by means of the variance inflation factor (< 10 for all variables; Neter et al. 1990). All statistical analyzes were performed using the package “base” (R Development Core Team 2017) of the R software version 3.3.3 (R Development Core Team 2017).

Table 3. Genetic distance between the hummingbird species at the LMNP

Hummingbird species	<i>S. platycercus</i>	<i>L. clemenciae</i>	<i>H. leucotis</i>	<i>E. fulgens</i>	<i>C. thalassinus</i>
<i>Selasphorus platycercus</i>	*				
<i>Lampornis clemenciae</i>	0.15	*			
<i>Hylocharis leucotis</i>	0.16	0.18	*		
<i>Eugenes fulgens</i>	0.16	0.17	0.18	*	
<i>Colibri thalassinus</i>	0.23	0.24	0.21	0.23	*

The genetic distance was calculated using the Tamura–Nei model. *Represents the comparison between intraspecific genetic sequences.

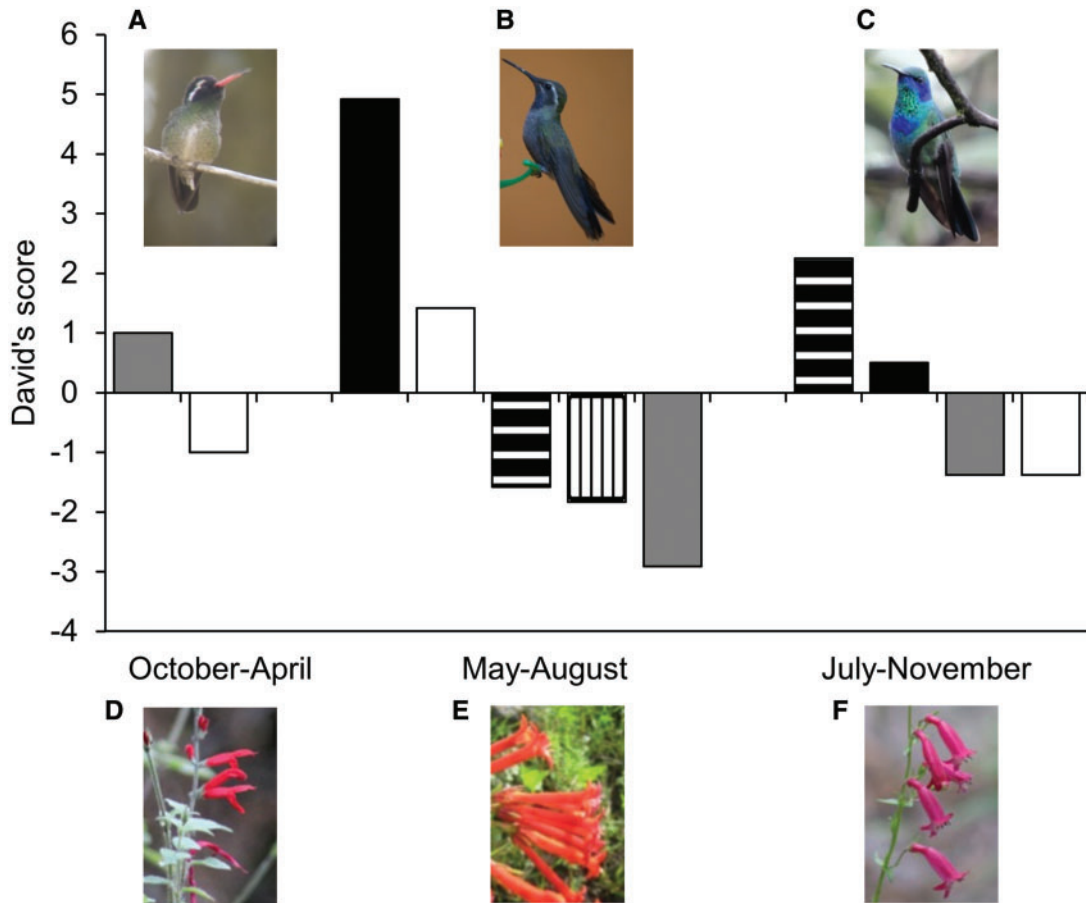


Figure 1. DS for the hummingbird assemblage at LMNP, Mexico, showing the hummingbird species with the higher dominance rank (A) *H. leucotis*, (B) *L. clemenciae* and (C) *C. thalassinus*, through the flowering period of (D) *B. ternifolia*, (E) *S. elegans*, and (F) *P. roseus*. Bars are code-colored as grey (*H. leucotis*), white (*S. platycercus*), black (*L. clemenciae*), horizontal lines (*C. thalassinus*), and vertical lines (*E. fulgens*). Photos by Gustavo Hernández-Orta, Carlos Lara, and Ubaldo Márquez.

Results

We found and monitored a total of 85 hummingbird territories (*S. elegans*, $n = 47$; *B. ternifolia*, $n = 28$ and *P. roseus*, $n = 10$), that represent 127.5 observation hours. *Penstemon roseus* had the highest nectar volume and energy produced per flower (Table 1). During our study only *E. fulgens* did not establish territories, instead acting as a marauder or trapliner in the three flowering seasons throughout the year.

The genetic distance between hummingbird species ranged from 0.15 to 0.24 (Table 3). The widest genetic distance was found between *L. clemenciae* and *C. thalassinus* (0.24) and the closest between *L. clemenciae* and *S. platycercus* (0.15).

Different hummingbird species were dominant in each of the three flowering seasons (Figure 1). We recorded 122 agonistic

encounters, 75% of which were intraspecific (92 encounters) and the remainder occurred among hummingbirds of different species (30 encounters; 25%). The GLM indicated that the frequency of intraspecific encounters was related with the territory owner species identity ($\chi^2 = 9.69$, $df = 4$, $P = 0.045$; Figure 2). However, the plant species identity and the energy contained in a territory had no significant effect on the frequency of intraspecific encounters ($\chi^2 = 5.05$, $df = 2$, $P = 0.063$ and $\chi^2 = 0.55$, $df = 1$, $P = 0.454$, respectively).

The frequency of interspecific encounters was significantly related with the energy within the territories ($\chi^2 = 2.57$, $df = 1$, $P = 0.003$; Figure 3) and the territory owner identity ($\chi^2 = 7.32$, $df = 4$, $P < 0.001$; Figure 2). However, the plant species identity had

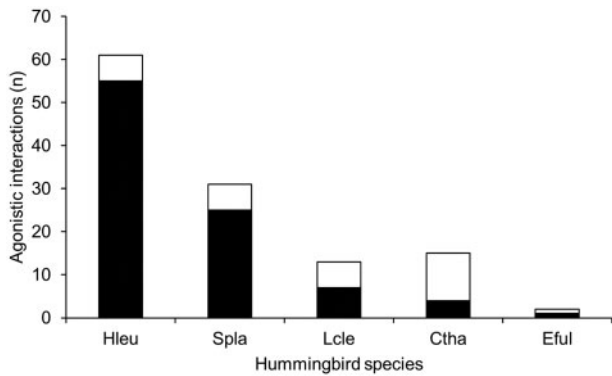


Figure 2. Intraspecific (black bars) and interspecific encounters (white bars) won by territory owners. The horizontal axis represents the territory owner's identity: Hleu = *Hylocharis leucotis*, Spla = *Selasphorus platycercus*, Lcle = *Lampornis clemenciae*, Ctha = *Colibri thalassinus*, and Eful = *Eugenes fulgens*.

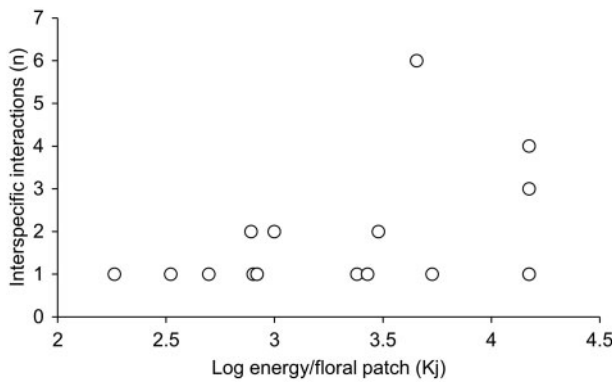


Figure 3. Frequency of encounters between the studied hummingbird species, and the energy contained within their territories.

no significant effect on the frequency of interspecific interactions ($\chi^2 = 0.840$, $df = 2$, $P = 0.252$).

Larger hummingbird species dominated 53% of the interspecific encounters ($n = 16$), while 47% ($n = 14$) were dominated by species smaller than their contender. There was no significant difference between the number of encounters dominated by larger and smaller species than their competitors ($\chi^2 = 30$, $g.l. = 29$, $P = 0.41$). The genetic distance was positively associated with a higher frequency of encounters dominated by small hummingbirds ($\chi^2 = 7.31$, $df = 2$, $P = 0.025$; Figure 4). That is, the small hummingbirds dominated more encounters against larger contenders when the genetic distance between contenders was wider (Figure 4). On the contrary, the plant species identity ($\chi^2 = 2.78$, $df = 2$, $P = 0.247$) and the energy within the territory ($\chi^2 = 0.82$, $df = 1$, $P = 0.362$) did not have a significant effect on the frequency with which large hummingbirds dominated encounters against smaller contenders.

Discussion

The dominance hierarchy of the hummingbird assemblage in the study site was highly dynamic. The frequency of intraspecific agonistic encounters was associated with identity of the territory owner. Interspecific encounters were related to the energy within the territories and with the identity of the territory owner. There was no

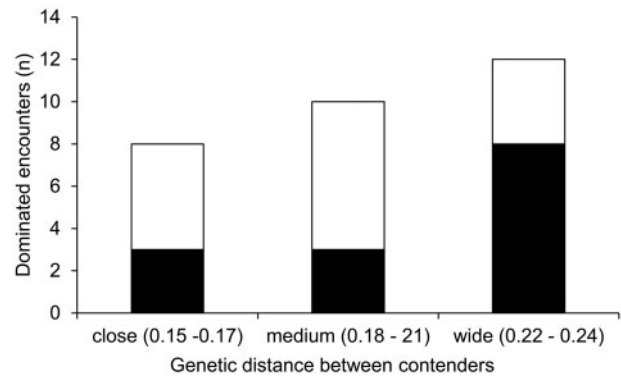


Figure 4. Encounters dominated by larger (white bars) and smaller (black bars) hummingbirds than their contender and the genetic distance between the contenders.

significant difference between the number of encounters dominated by larger and smaller species and their contenders. However, the increase in genetic distance between contenders was positively associated with a higher frequency of encounters dominated by small hummingbirds.

Dominance hierarchy

Dominance hierarchy in the hummingbird assemblage changed during the flowering seasons of the three plant species we studied. The dominant species were *H. leucotis*, *L. clemenciae* and *C. thalassinus* during the sequential flowering periods of *S. elegans*, *B. ternifolia*, and *P. roseus*, respectively. Two of these species (*L. clemenciae* and *C. thalassinus*) weigh more than 6 g, representing the largest hummingbird species in the assemblage. That is, the higher rank within the dominance hierarchy was associated with large body size species, which coincides with that reported by different authors (Hainsworth and Wolf 1972; Dearborn 1998; Justino et al. 2012). However, these same species were dominated in turn by other hummingbird species when the available floral resource changed. For example, when *P. roseus* was flowering, the dominant species was *C. thalassinus* and not *L. clemenciae* the species with the highest body size at that time. These changes in dominance hierarchy could be explained by different factors such as: 1) temporal variability of the hummingbird feeding roles in the assemblage and 2) preference of hummingbird species to defend a specific floral resource.

Temporal variability of hummingbird feeding roles

In our study, *H. leucotis* fits the role of territorialist (sensu Feinsinger and Colwell 1978) in patches of *S. elegans*. However, its foraging strategy changed from territorial to marauder in the presence of migratory hummingbird species that arrived in the study area at the beginning of the flowering season of *B. ternifolia*. The change in the hummingbirds foraging role associated to the abundance of competitors has been corroborated experimentally by using feeders and controlling the density and identity of the competitors (Pimm et al. 1985). Even the abundance of competitors could promote a spatial segregation among hummingbird species to maximize energy consumption, and avoid energy and time expenditure in chasing away competitors (Vizentin-Bugoni et al. 2017).

Resource preferences

The hummingbirds preference for exploiting a particular floral resource may be related to traits such as the floral display (number of

flowers per plant and inflorescence number), the shape and color of the corollas, and the nectar volume and sugar concentration (Meléndez-Ackerman et al. 1997). The floral displays of *S. elegans* and *B. ternifolia* are greater than *P. roseus*. Hummingbirds can visually assess the quality of floral patches by the flower displays; this can drive the foraging preference of both territorial and non-territorial hummingbirds (Trombulak 1990). In our study, the flowering season of *B. ternifolia* was the only one in which five hummingbird species were present as territorial or territory parasites. Also, in this same flowering season the largest hummingbird in the assemblage (*L. clemenciae*) had the highest rank in the dominance hierarchy. Another factor to consider is the structural characteristics of the vegetation in which the plant species grow. For example, in the forested areas the detection of intruders should be more difficult than in open areas, which could drive the intrusion pressure over the territories. Contrarily, territory parasites could prefer the territory owner to detect more easily the intruders in territories of open areas (*B. ternifolia*), because it would imply that the territory owner spent more time chasing intruders outside the territory boundaries and this period could be used for the filchers to forage in the territory. However, further research is needed to corroborate these hypotheses.

The 3 plant species included in our study share similar morphological traits. They have tubular corollas ranging from 23 to 30 mm in length. Since the bill length of the hummingbird species was 16–26 mm (Morales et al. 2012), all the hummingbird species can exploit the floral resources in the study area. Color variation in the corollas was wider, since *S. elegans* and *B. ternifolia* have colors ranging from red to reddish salmon, respectively, whereas *P. roseus* has magenta flowers (Pérez et al. 2011). However, it has been reported that hummingbirds learn to associate the color of the corollas with the reward offered by a flower. This association is based on the previous experience of a hummingbird exploiting that same floral resource (Meléndez-Ackerman et al. 1997). Therefore, the preference for a particular floral resource depends on the reward quality and previous experience of hummingbirds and not just on corolla color. Finally, the energy per flower was higher in *P. roseus* and this could drive the preference of hummingbirds for this floral species.

Agonistic interactions

The frequency of inter and intraspecific encounters was associated with the territory owner's identity. Most of the recorded agonistic encounters (75%) occurred between individuals of the same species. The species with more intraspecific interactions was *H. leucotis*. This hummingbird species was the only one that used advertisement calls as part of their territorial defense in *S. elegans* floral patches. The advertisement calls might not only deter intruders from stealing resources but also could inform competitors of the presence of a high quality area and encourage their presence (Goldberg and Ewald 1991). This cost-benefit of vocal behavior could explain the higher intraspecific competition between *H. leucotis* individuals. Arguably, agonistic encounters among conspecifics would be frequent because they compete for the same preferred resources (Lyon 1976; Carpenter et al. 1993) and they also share morphological traits that confer to them similar competition abilities (Dearborn 1998). Furthermore, the intraspecific encounters could be motivated by social factors such as the competition and dominance between sexes or age classes (Carpenter et al. 1993), or even may be regulated by their hormone levels (González-Gómez et al. 2014).

In contrast, the occurrence of interspecific interactions was low. *Colibri thalassinus* was the species that won more interspecific

encounters. This hummingbird was dominant during the flowering season of *P. roseus* and expelled larger intruders as *L. clemenciae*. This can be explained through a cost-benefit balance of establishing and defending a foraging territory. The cost of defending *P. roseus* territories could exceed the benefits of exclusive access to nectar from the territory for larger species such as *L. clemenciae* (Kodric-Brown and Brown 1978). This reinforces the existence of energy thresholds within which territorial behavior is performed in hummingbirds (Justino et al. 2012; Márquez-Luna et al. 2015). In LMNP, flowering season of *B. ternifolia* and *P. roseus* coincides with the arrival and permanence of migratory hummingbird species, which suggests that in this period the interspecific interactions would have to increase. However, in our study these encounters were scarce (only the 25%), suggesting a probable resource segregation which is evidenced in the changes of the species ranks in the dominance hierarchy.

Body size and genetic distance

There was no a clear dominance of the larger species over the small contenders, which contrasts with findings in other hummingbird communities (Hainsworth and Wolf 1972; Dearborn 1998; Araújo-Silva and Bessa 2010; Justino et al. 2012). However, the frequency of encounters won by smaller species was positively associated with a wider genetic distance between contenders. This pattern could be explained through the differences in the maneuverability, which is associated to the variation in flight-muscle size (Altshuler et al. 2010). In hummingbirds, the flight muscles (pectoralis—supracoracoideus) amount to 21–30% of their total weight (Hartman 1961; Greenewalt 1962). However, the muscle capacity is not always related to body mass; for example, *C. thalassinus* has a greater muscle capacity than larger species (e.g., *E. fulgens*; Dakin et al. 2018). In this study, *C. thalassinus* was the species that dominated more competitive interactions versus larger species (e.g., *L. clemenciae*).

In our study, we did not evaluate the wing loading of the hummingbirds due the lack of data on species' wing area. However, as a surrogate measure, we used span loading (body mass/wing span²) which has been used as an estimator of induced power requirements in hovering (Greenewalt 1975). The two hummingbird species with the lowest wing span (Figure 5) were involved in the majority of intraspecific and interspecific encounters (*H. leucotis* and

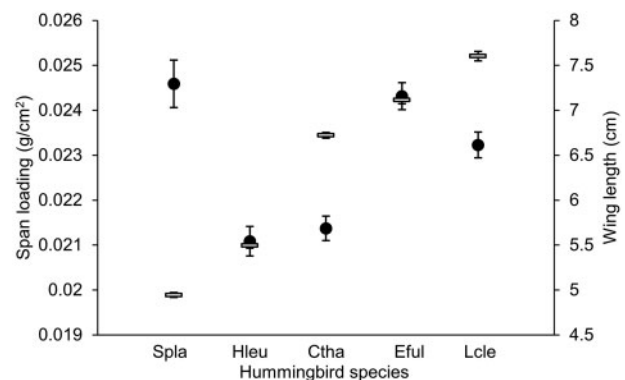


Figure 5. Differences in span loading (black dots) and wing length (white hyphens) between hummingbird species. Vertical lines indicate the standard error and the horizontal axis represents hummingbird species. Species were ordered according to their body mass. Sample sizes are the same as those reported in Table 2 to estimate body size of the hummingbird species.

C. thalassinus, respectively). These two species also won encounters against larger competitors (*H. leucotis* won encounters against *E. fulgens* and *C. thalassinus*; *C. thalassinus* won encounters against *L. clemenciae*). However, *S. platycercus*, which had the higher span loading (Figure 5), also dominated larger competitors with lower span loading (*H. leucotis* and *C. thalassinus*). Dakin et al. (2018) report that smaller species or those with a higher wing loading could use another kind of maneuvers (arcing turns) as a tactical or competitive advantage over competitors. The morphological traits associated with the maneuverability (wing area, muscle capacity, and wing loading) are, on average, conservative within the hummingbird clades, namely closely related species have similar morphologies and maneuvering styles (Skandalis et al. 2017; Dakin et al. 2018). These can explain why some hummingbird clades (e.g., Emeralds) frequently take part in encounters for resources (Márquez-Luna et al. 2018). However, in hummingbirds, the body mass and wing surface may change depending on molting period and food availability (Carpenter et al. 1983; Chai 1997). These changes modify the species maneuverability (Dakin et al. 2018) and, therefore, the competitive skills between species.

The variability in those factors associated to the maneuverability and aggression could promote temporal changes in the dominance hierarchy of hummingbird assemblages. Such temporal dynamic of dominance hierarchy could generate partition of resources, allowing the coexistence of different hummingbird species as a consequence of low levels of interspecific competition (Ornelas et al. 2002). Even at a macroecological scale, resource partitioning and interspecific competition among closely related hummingbirds might also play an important role in structuring interactions in hummingbird–plant networks (Martín González et al. 2015). This highlights the role of the species evolutionary relationships and the possible effects on the way hummingbird species exploit and compete for resource access. Teasing out the varied morphological, physiological, and evolutionary effects on hierarchies is evidently not straightforward, and due to the limited number of encounters observed in this study, we are unable to properly evaluate the role of evolutionary relationships between contender species on the dynamics of dominance hierarchy. This avenue of future research is likely to generate important insights into this field.

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