

The dynamics of hummingbird dominance and foraging strategies during the winter season in a highland community in Western Mexico

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Abstract

Coexistence between ecologically similar species can promote competition for resources. Hummingbirds (Aves: *Trochilidae*) are nectarivorous birds that usually coexist in sympatry, and visit flowers using different foraging behaviors and levels of aggressiveness as a strategy to diminish resource competition. Here, we describe the dynamics in territorial and dominance behaviors in a hummingbird community inhabiting a highland during winter in Western Mexico. We explored in natural conditions how foraging strategies and dominance status of the hummingbirds was influenced by community species composition, sex, age and size of the individuals, floral abundance, and nectar resource availability. The community studied was composed of 11 species (four residents, three altitudinal migrants, three latitudinal migrants), and all possible combinations of dominance and territoriality were found. Differences in the dominance status and foraging behavior were related to the species, sex, age and body size of the individuals, as well as the number of flowers in the patches, and the abundance of the migratory species over time. The aggressive and territorial species preferred the places with more flowers, and started the majority of the interactions attacking even birds that did not visited the flowers. The subordinate non-territorial hummingbirds visited floral patches of different sizes, did not start aggressive interactions and when they were involved in one, this occurred during their visits to the territorial hummingbird's flowers. Hummingbird dominance changed during the winter and at the end of the season, when the latitudinal migrant species left our study site, the resident species were more abundant, dominant and territorial. Dominance status and foraging behavior, together with floral preferences and the spatial distribution of nectar resources, acted as mechanisms organizing this hummingbird community.

Introduction

Resource dynamics is a key process that can model animal distributions (Bennett *et al.*, 2014), and some models, as the 'ideal free distribution', predicts that consumer densities will match with resource availability (Fretwell & Lucas, 1969). One example of this occurs in nectarivorous birds where the variation in resource abundance regulates the abundance of birds (Bennett *et al.*, 2014; Schmid *et al.*, 2015). However, this distribution in nature may be affected by other factors that can change resource use. One of these factors is biotic interactions, and in scenarios where the species have competitive differences, the dominant species (usually larger) will modify the habitat choices of subordinate species (Fretwell, 1972).

Hummingbirds (Aves: *Trochilidae*) are physiologically specialized nectarivorous birds (Schuchmann, 1999; Lotz & Martínez del Río, 2004), considered generalists from an

ecological perspective because they visit many different plant species to cover their energetic demands (Calder, 2004). In hummingbird communities, it is frequent to find several species living in sympatry, and a temporal and spatial overlap of the nectar resources that they use (Stiles, 1985; Collins, Grey & McNee, 1990; Arizmendi, 2001; Gutiérrez-Zamora & Rojas, 2001; Lara, 2006). The overlap in feeding niches of ecologically similar species increases the potential for competition for resources (Morin, 1999). The partition of resources among hummingbird species has been explained by different mechanisms related to: differences in nectar resource use (Lyon, 1976; Justino, Maruyama & Oliveira, 2012), variations in foraging behavior (Feinsinger & Colwell, 1978; Stiles, 1985; Sandlin, 2000a; Lara, Lumbreras & González, 2009), population movements at the landscape scale following plant blooming (Des Granges, 1979; Gutiérrez-Zamora & Rojas, 2001), microhabitat differences (Gutiérrez-Zamora & Rojas, 2001; Ritchie,

2002), interspecific morphological variations in traits such as weight, beak length and curvature (Stiles, 1975; Lyon, 1976; Snow & Snow, 1980; Rodríguez-Flores & Stiles, 2005; Maglianesi, Böhning-Gaese & Schleuning, 2015), spatial and temporal segregation in floral use patterns (Ornelas *et al.*, 2002; Lara, 2006; Lara *et al.*, 2009) and phylogenetic relationships among species (Martin & Ghalambor, 2014). Several of these mechanisms are based on the hummingbird's abilities and movement capabilities, all of which allow them to use a heterogeneous distribution of nectar resources at a given time, and take appropriate decisions on the basis of their morphological and physiological characteristics (Ritchie, 2002; Bacon, Hurly & Healy, 2011).

Hummingbirds visit flowers using two main behavior types: (1) territorial and (2) non-territorial or trapliners (Feinsinger & Chaplin, 1975). Territorial hummingbirds select a group of flowers and establish their feeding territory there (Wolf, 1969; Des Granges & Grant, 1980). Non-territorial hummingbirds use different groups of blooming plants that can be isolated and/or undefended by a territorial hummingbird, and usually visit these flowers by following circuits or foraging routes in specific sequences (Feinsinger & Colwell, 1978; Temeles *et al.*, 2006; Ohashi & Thomson, 2009). In addition to foraging strategies, the dominance among individuals affects the way they interact and visit their nectar resources, and can be related to sex, age and morphology (Wolf, 1969; Feinsinger & Chaplin, 1975; Carpenter *et al.*, 1993). However, although these classifications describe properly the types of behaviors observed, these are too simplistic because the foraging and dominance patterns within individuals of a species are not static, but rather constitute a gradient where individuals can use all behaviors throughout their life (Feinsinger, 1976; Des Granges, 1979; Collins *et al.*, 1990; Cotton, 1998).

The purpose of this study was to investigate the relationship between dominance and territoriality in a dynamic hummingbird community located at Western Mexico and composed by latitudinal migrants (same species studied at many sites in USA and Canada), residents (as other communities studied in Central America) and altitudinal migrants sharing a complex array of nectar sources (Arizmendi, 2001). In this community, we studied a gradient from small to large species, resident to altitudinal to latitudinal migrant to see behavioral responses used to coexist. To this end, we tested three hypotheses: (1) If sex, age and size of the individuals affect hummingbird dominance and foraging strategies (Feinsinger & Colwell, 1978; Des Granges, 1979; Snow & Snow, 1980; Calder & Calder, 1994; Russell, 1996; Stiles *et al.*, 2005; Justino *et al.*, 2012), we hypothesized that the large- and medium-sized resident species (>5 g following Stiles & Wolf, 1979; Schuchmann, 1999) would be territorial and dominant over the other hummingbird species (Lyon, 1976). In the case of age and sex, we expected that males would be dominant over females in the species with plumage sexual dimorphism (Wolf, 1969; Kodric-Brown & Brown, 1978; Snow & Snow, 1980), and adults would be dominant over the juveniles in the monomorphic species (Feinsinger & Chaplin, 1975). (2) If hummingbird foraging and dominance strategies change as a function of community composition (Feinsinger & Chaplin, 1975; Feinsinger & Colwell,

1978; Des Granges & Grant, 1980; Lara, 2006), then we expected that when hummingbird species composition changed in our study site, the hierarchy between the species would change as well. (3) If floral abundance and nectar resource availability modify the level of territoriality (Lyon, 1976; Ewald & Carpenter, 1978; Kodric-Brown & Brown, 1978; Snow & Snow, 1980; Dearborn, 1998; Baltosser & Russell, 2000; Lara *et al.*, 2009; Justino *et al.*, 2012) and the foraging strategy of hummingbirds (Feinsinger & Colwell, 1978; Carpenter, 1987a; Ohashi & Thomson, 2009), then we expected a positive relationship between nectar availability and aggressiveness and territoriality.

Materials and methods

Study area

The Sierra de Manantlán Biosphere Reserve is located in the Sierra Madre Occidental, between Jalisco and Colima States. In the central-western part of the Reserve is Las Joyas Scientific Station (LJSS), which encompasses an area of 1245 hectares (19°35'–19°37'N, 103°15'–104°37'W) (Lara & Ornelas, 2001). The LJSS has altitudinal gradient changes ranging from 1500 to 2242 m.a.s.l., a mean annual temperature of 15.5°C, mean annual precipitation of 1826 mm and a vegetation mosaic of different types of forest and perturbation levels including secondary vegetation, pine and cloud forest (Jardel *et al.*, 1990). This area is submitted to controlled and uncontrolled fires, a mechanism to maintain forest biodiversity and vegetation mosaic. The data used in our research were collected from 14th January to 22nd March 2008. We focused on the winter season because this is the time of the year with the highest hummingbird diversity and flower abundance. Latitudinal migrants arrive to this area on November and leave on March, while the altitudinal migrants stay in LJSS from November to June (Arizmendi, 2001).

Hummingbird species composition

To establish whether the composition of the hummingbird community changed during the winter season, we performed six capture sessions using 5 mist nets (6 × 3 m, 25 mm) for 8 hours beginning at sunrise (See Appendix S1 for capture session dates). Each individual captured was identified, aged, weighted, banded and classified as resident, latitudinal migrant and altitudinal migrant following Arizmendi (2001). We used the mass of each hummingbird as a direct indicative of size (Snow & Snow, 1972; Stiles, 1995), and we supplemented our weight data with observations from Contreras-Martínez (2014) (Appendix S2).

Dominance and foraging strategies

To characterize the dominance and foraging strategies used by the hummingbirds, we conducted 118 focal observation sessions, 68 in secondary vegetation, 27 in cloud forest and 23 in pine forest. During each monitoring session (minimum 2 hours, maximum 4 hours, in the morning and in the afternoon, 2 days

per week, with two to three observers), we recorded the number of aggressive interactions, the identity (species, sex and age) and migratory status of the interacting hummingbirds, which individual initiated each aggressive interaction and the result of this (winner vs. loser). As well, we recorded the number of flowers visited for each hummingbird during the foraging bout, and counted the number of open flowers of each plant species in the patch at the end of the observation period.

Selasphorus rufus and *S. sasin* are nearly indistinguishable species that have been reported at our study site (Arizmendi, 2001). Because *S. sasin* is a scarce species at Central-western Mexico and was rarely caught during the Manantlán Bird Monitoring and Banding Program (Contreras-Martínez, 2014), we called all the individuals of these species recorded during the focal observations '*S. rufus*'.

Dominance categories

In order to understand the hierarchy of the hummingbirds in this community, we evaluated the proportion of interactions won by each hummingbird species discriminating these records at the intraspecific level. Based on the species, sex and/or age, we grouped the hummingbirds (see Statistical methodology section) and assigned to each group a specific dominance category, from highly aggressive (dominant), through intermediate dominance (subdominant), to lower dominance (subordinate) (Des Granges, 1979).

Foraging strategies

Based on the foraging behavior recorded during the focal observations, we explored differences between hummingbirds at the interspecific and intraspecific levels. Each hummingbird was sorted into one of two foraging behaviors. We classified as territorial hummingbirds those birds that permanently visited the same group of flowers, staying at the same place at least 60 minutes without long-distance movements. Those hummingbirds that did not stay in the same floral patch and showed evasive or inconspicuous behavior were considered non-territorial hummingbirds.

Floral abundance and nectar resource availability

We classified all the floral patches observed according to the abundance and number of species found blooming together. The three classifications were as follows: **large monospecific** patches, **small monospecific** patches and **mixed** patches. In addition, we recorded the type of vegetation (cloud forest, pine forest or secondary vegetation) and the number of open flowers in the patch during the observation sessions.

To establish the relationship between energy availability (calories) and hummingbird foraging behavior, we characterized the nectar production for six plant species (*Lobelia laxiflora*, *Ipomoea orizabensis*, *Moussonia depeana*, *Salvia iodantha*, *S. mexicana*, and *Fuchsia encliandra*). These plants species were the most abundant and most intensively used by

hummingbirds in the area during the fieldwork. Specifically, between nine and 40 floral buds were bagged at night. To avoid nectar consumption by mites, we applied wax at floral pedicels and peduncles (Lara & Ornelas, 2001). At sunset of the next day, we used microcapillary tubes and a hand refractometer (ERMA, 0–32% Brix) to establish nectar volume (accumulated) and sugar concentration. Also, we used the recompilation of Ornelas *et al.* (2007) to obtain information about the nectar volume and concentration of other plant species visited by hummingbirds in our community. We calculated the number of calories per flower using the formula proposed by Stiles (1975), and established the calories produced in all floral patches studied. When possible, we characterized floral territories, identifying the territory holder, the size of the territory and the number of open flowers of each plant species.

Statistical methodology

Previous to model selection process, we followed the protocol for data exploration proposed by Zuur, Ieno & Elphick (2010). During the model selection process, we ran the saturated model with different random slopes and intercepts, corrected for heteroscedasticity and correlation, and used Akaike information criterion and χ^2 distributed likelihood ratio test for model comparisons and estimating model parameters (Johnson & Omland, 2004; Zuur *et al.*, 2009).

Effect of hummingbird size, age and sex on dominance and territoriality

To analyze whether the proportion of aggressive encounters won by the hummingbirds was related to species, age, sex and migratory status, we fitted a generalized linear mixed model (GLMM) with binomial distribution and logit link (Zuur *et al.*, 2009). To control pseudoreplication between pairs of interactions, we used the variable 'number of interaction' (identity for the winner and loser of the same interaction) as a random effect. To avoid problems with model estimation, in these analyses, we concatenated the aggressive interactions of *Amazilia violiceps*, *Tilmatura dupontii* (altitudinal migrants) and *Selasphorus calliope* (latitudinal migrant) under a single group. Each one of these species had less than 11 interactions during all the fieldwork and lost between 91 and 100% of all the aggressive encounters where they participated. The statistically significant differences between hummingbird species, sex, age and/or migratory status were used to classify hummingbird species into different dominance groups.

For each dominance group, we applied Spearman correlation test (r_s) to assess the strength of the relationship between the proportion of interaction won, the proportion of interactions that it initiated and the proportion of interactions that occurred when the hummingbirds were visiting flowers. Also, we used post hoc multiple comparison test to evaluate the relationship between aggressiveness (dominance categories), territoriality (foraging categories) and body size (Appendix S2).

In order to establish whether the aggressiveness of the hummingbirds changed over time and type of vegetation, we fitted

a Zero-altered negative binomial (ZANB) model to solve the problem of overdispersion and the excessive number of zeros in our data. In this model, the response variable was the number of aggressive interactions, and we tested the effect of sampling day (Julian day), type of vegetation, flower number in the patch (log 10 transformed) and time of observation (minutes since the beginning of the session) as explanatory variables in the binomial and negative binomial part of the ZANB model.

In order to establish whether hummingbird dominance and territoriality changed through time, we fitted GLMM's with binomial distribution and logit link. The response variable was the proportion of interactions won. Time was the explanatory variable and we included this as a factor dividing the sample period in 2-week intervals. Because the aggressive interactions recorded during the same monitoring session are correlated with each other, we included session as a random intercept. We ran individual analyses for each dominance group (16 levels), dominance categories (three levels), foraging strategy (two levels) and migratory status (three levels).

Hummingbird community composition

We analyzed differences in hummingbird abundance between mist-net sessions using generalized linear models (GLM). We fitted a GLM with Poisson distribution and log link (Zuur *et al.*, 2009), where the number of hummingbird captured each season was the response variable, and session identity (included as a factor) and the hummingbird species were the explanatory variables. Because previous results at the same area found that changes in abundance of nectarivorous birds through the year was explained by the arrival of latitudinal and altitudinal migrants (Arizmendi, 2001), we also fitted a similar model but using migratory status as the independent factor.

Floral abundance and nectar resource availability

In order to establish whether the number of flowers available for the hummingbirds was different depending on vegetation and patch type, we fitted a generalized least squares model with an exponential variance function structure. In this model, the response variable was the number of flowers, and type of vegetation and type of patch were the explanatory variables.

To analyze the effect of the abundance of nectar resources on the aggressive interactions between hummingbirds, we constructed a two-by-two contingency analysis for hummingbird's dominance groups (defined previously with the GLMM models) and the type of floral patch (large monospecific patches, small monospecific patches and mixed patches). We conducted this analysis to compare the number of aggressive interactions observed against the number of interactions expected from the number of floral patches of each type sampled.

We used the Spearman correlation test (r_s) to assess the association between number of calories produced at floral patch and number of visits and aggressive encounters. We used a Mann–Whitney U test to test differences in the number of calories produced in floral territories defended by dominant and subdominant territorial hummingbirds.

All analyses were done using R software version 3.1.2 (R Development Core Team, 2014). Model selection process were performed using packages 'base' (R Development Core Team, 2014), 'pscl' (Wickham, 2009), 'blme' (Dorie, 2014), 'MCMCglmm' (Hadfield, 2010) and 'lme4' (Bates *et al.*, 2014). Post hoc multiple comparison tests were carried out with the general linear hypothesis function (glht) in the package 'multcomp' to the different fitted models (Hothorn, Bretz & Westfall, 2008). We used the Bonferroni correction for multiple testing, and an alpha of 0.05 or less to determine significance. All figures were done with the package 'ggplot2' (Wickham, 2009).

Results

Effect of hummingbird size, age and sex on dominance and territoriality

Dominance and foraging strategies

The focal observation sessions totaled 312 hours and 27 minutes, during which we recorded 1196 aggressive interactions that involved 11 hummingbird species (Table 1). During the focal observations, we identified 90 territories defended by five hummingbird species (Table 1).

We found variability in dominance between hummingbirds as a function of species ($X^2 = 460.490$, d.f. = 8, $P < 0.001$), sex ($X^2 = 90.125$, d.f. = 1, $P < 0.001$), age ($X^2 = 6.621$, d.f. = 1, $P = 0.010$) and migratory status of the birds ($X^2 = 62.000$; d.f. = 2; $P < 0.001$).

Large- and medium-sized resident species (*Lampornis amethystinus* and *Eugenes fulgens*) were dominant over the other hummingbird species (Table 1). In dimorphic species, males were generally dominant over females independently of age (i.e. *Lampornis amethystinus* and *Hylocharis leucotis*, Fig. S1, Tables 1 and 2). In the monomorphic *Amazilia beryllina* and *Colibri thalassinus*, adults won a higher percentage of aggressive interactions compared with the juveniles, but these differences were not statistically significant (Fig. S1, Table 2). This pattern did not hold in species such as *E. fulgens*, *Atthis heloisa*, *Selasphorus calliope* and *S. platycercus*, where dominance did not change with sex and/or age (Tables 1 and 2). Respect to migratory status, altitudinal migrant species won the majority of the aggressive encounters where they participated, whereas latitudinal migrant species lost most of these interactions, and resident species had an intermediate level of dominance (Table 1).

The analyses including the proportion of interactions won by the whole species, or parts of these regarding sexes or ages, defined 16 dominance groups (Table 1). Each one was assigned to one of the three dominance categories (dominant, subdominant and subordinate) and one of the two foraging behavior (territorial and non-territorial). Dominant and subdominant species were territorial, and non-territorial hummingbirds were subordinated (Table 1). The exceptions were males of *H. leucotis* and individuals of *E. fulgens*. Males of *H. leucotis* were classified as subordinate following our dominance criteria, but we observed three individuals holding feeding territories at

Table 1 Dominance categories and foraging strategies used for the 11 hummingbird species recorded at Las Joyas Scientific Station during winter

Species	Age	Sex	Total	WON %	BEG %	FLO %	COD	STR	Terr	Migratory status
<i>Amazilia beryllina</i> ^a			546	61.36	60.81	54.58	SubD	Territorial		Altitudinal migrant
	Juvenile		77	55.84	55.84	64.94	SubD	Territorial	2	
	Adult		369	61.79	60.98	52.12	SubD	Territorial	31	
<i>Amazilia violiceps</i> ^a			2	0.00	0.00	100.00	SubO	Non-territorial	0	Altitudinal migrant
<i>Atthis heloisa</i> ^b			35	28.57	31.43	65.71	SubO	Non-territorial		Resident
	Adult	Female	17	17.68	17.65	82.35	SubO	Non-territorial	0	
	Adult	Male	13	38.46	46.15	61.54	SubO	Non-territorial	0	
<i>Colibri thalassinus</i> ^a			56	83.93	89.29	51.79	Dom	Territorial		Altitudinal migrant
	Juvenile		1	0.00	0.00	0.00	Dom	Territorial	1	
	Adult		43	90.70	93.02	48.84	Dom	Territorial	5	
<i>Eugenes fulgens</i> ^b			29	34.48	17.24	62.07	SubD	Non-territorial		Resident
		Female	11	45.46	18.18	63.64	SubD	Non-territorial	0	
		Male	9	44.44	33.33	66.67	SubD	Non-territorial	0	
<i>Hylocharis leucotis</i> ^b			400	17.00	15.25	67.25	SubO			Resident
	Juvenile	Female	7	0.00	0.00	71.43	SubO	Non-territorial	0	
	Juvenile	Male	32	18.75	9.38	71.88	SubO	Territorial	1	
	Adult	Female	86	6.98	5.81	67.44	SubO	Non-territorial	0	
	Adult	Male	216	22.22	17.59	67.59	SubO	Territorial	2	
<i>Lampornis amethystinus</i> ^b			399	75.44	76.44	62.16		Territorial		Resident
		Female	27	44.44	44.44	62.96	SubD	Territorial	2	
		Male	341	82.70	83.87	63.93	Dom	Territorial	33	
<i>Selasphorus calliope</i> ^b			16	0.00	0.00	75.00	SubO	Non-territorial		Latitudinal migrant
		Female	4	0.00	0.00	100.00	SubO	Non-territorial	0	
		Male	5	0.00	0.00	100.00	SubO	Non-territorial	0	
<i>Selasphorus platycercus</i> ^b			47	4.25	6.38	74.47	SubO	Non-territorial		Latitudinal migrant
	Juvenile	Male	11	0.00	0.00	72.73	SubO	Non-territorial	0	
	Adult	Female	14	7.14	7.14	64.29	SubO	Non-territorial	0	
	Adult	Male	1	0.00	0.00	100.00	SubO	Non-territorial	0	
<i>Selasphorus rufus</i> ^b			187	43.85	42.78	57.75				Latitudinal migrant
	Juvenile	Female	12	25.00	25.00	83.33	SubO	Non-territorial	0	
	Juvenile	Male	45	51.11	46.67	82.22	SubD	Territorial	5	
	Adult	Female	94	45.75	45.75	52.13	SubD	Territorial	8	
	Adult	Male	1	0.00	0.00	0.00	SubO	Non-territorial	0	
<i>Tilmatura dupontii</i> ^b			33	9.09	0.00	78.79	SubO	Non-territorial		Altitudinal migrant
		Female	33	9.09	0.00	78.79	SubO	Non-territorial	0	

Bold values correspond to the dominance and foraging behavior at species level.

Records are classified at intraspecific level by age and/or sex.

Total, number of aggressive interactions recorded; WON, percentage of won encounters; BEG, percentage of encounters began by this hummingbird species; FLO, percentage of encounters that involved flower visitation; COD, categories of dominance; Dom, dominant; SubD, subdominant; SubO, subordinate; STR, foraging strategy; Terr, number of territories recorded.

^aMonomorphic hummingbird species.

^bHummingbird species with sexual dimorphism.

the end of winter (Fig S2). *E. fulgens* was non-territorial during the winter, but had an intermediate dominance with respect to other hummingbird categories (Table 1).

The test between size and the proportion of won interactions ($r_s = 0.345$; $n = 16$; $P = 0.095$) showed that dominant and subdominant hummingbirds were similar in size (Kruskal–Wallis test, $P = 1.000$). Although Fig. 1a shows that these two categories were larger than the subordinated hummingbirds, the size showed no significant effects (Kruskal–Wallis test, $P = 0.144$ and $P = 0.251$ respectively). Similarly, although no statistically significant, larger hummingbirds were

generally territorial compared with the smaller ones (Kruskal–Wallis test, $P = 0.288$, Fig. 1b), with exception of *E. fulgens*, a non-territorial large hummingbird (7.233 ± 0.764 g, Table 1).

Hummingbird community hierarchy and dynamic

As hummingbird community composition and abundance changed through winter (see below), the number of aggressive interactions changed too ($\chi^2 = 5.580$, d.f. = 1, $P = 0.018$) depending upon hummingbird dominance and foraging behavior

Table 2 Likelihood ratio test for the generalized linear mixed models fitted to test the differences in the proportion of interactions won by the different hummingbird species at the intraspecific level (sex and/or age)

Species	Level	χ^2	<i>P</i>
<i>Amazilia beryllina</i>	Age	2.698	0.100
<i>Amazilia violiceps</i>	Age	^a	
<i>Atthis heloisa</i>	Age	^a	
	Sex	2.132	0.144
		^a	
<i>Colibri thalassinus</i>	Age	^a	
<i>Eugenes fulgens</i>	Age	^a	
	Sex	0.257	0.612
<i>Hylocharis leucotis</i>	Age	0.062	0.804
	Sex	11.005	<0.001
	Age × Sex	0.911	0.340
<i>Lampornis amethystinus</i>	Age	0.050	0.823
	Sex	14.551	<0.001
	Age × Sex	1.330	0.249
<i>Selasphorus calliope</i>	Age	^a	
	Sex	^a	
<i>Selasphorus platycercus</i>	Age	^a	
	Sex	^a	
<i>Selasphorus rufus</i>	Age	0.493	0.483
	Sex	0.002	0.963
	Age × Sex	4.598	0.032
<i>Tilmatura dupontii</i>	Age	^a	
	Sex	^a	

Female and adult were the levels set as reference to the models. The statistically significant differences ($\alpha = 0.005$) are indicated with bold values.

^aModels not fitted because the response variable (win vs. lose) for these categories had constant or practically constant values (Table 1), causing problems with deviance estimations.

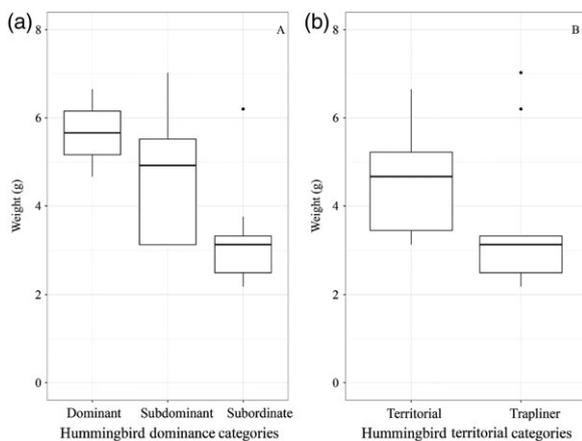


Figure 1 Relationship between hummingbird size (weight in grams), aggressiveness (a) and foraging behavior (b). Hummingbird records were analyzed at inter- and intraspecific level to classify hummingbirds into one dominance and territorial category (see text for details). Box encloses the 50% of the data and it is divided by the median (horizontal line); the upper and lower adjacent indicate 0.95 and 0.05 quantiles respectively. Points are considered to be outliers.

(Fig. 2). Also vegetation ($\chi^2 = 48.822$, d.f. = 1, $P < 0.001$), number of flowers ($\chi^2 = 9.819$, d.f. = 1, $P = 0.002$) and the time of observation ($\chi^2 = 15.938$, d.f. = 1, $P < 0.001$) had a significant effect in the model.

The proportion of interactions won by territorial and non-territorial hummingbirds did not change when comparing the beginning and the end of winter season ($\chi^2 = 2.902$, d.f. = 4, $P = 0.574$, and $\chi^2 = 5.294$, d.f. = 4, $P = 0.258$ respectively). However, during the last 2 weeks of March, non-territorial hummingbirds won more aggressive encounters (Fig. 2b).

In the same way, the proportion of aggressive interactions won by dominant hummingbirds did not change over time ($\chi^2 = 5.059$, d.f. = 4, $P = 0.281$), in contrast to subdominant and subordinate hummingbirds ($\chi^2 = 10.925$, d.f. = 4, $P = 0.027$, $\chi^2 = 16.796$, d.f. = 4, $P = 0.002$ respectively) (Fig. 2a). At the end of the winter season, the proportion of interactions won by the subordinate hummingbirds increased notably ($\chi^2 = 8.094$, d.f. = 1, $P = 0.004$), whereas the number won by the subdominant hummingbirds decreased ($\chi^2 = 4.996$, d.f. = 1, $P = 0.025$) (Fig. 2a). Specifically, the proportion of interactions won by *H. leucotis* males changed with time ($\chi^2 = 16.474$, d.f. = 4, $P = 0.002$), and these birds won significantly more aggressive encounters at the end of the winter season ($\chi^2 = 4.145$, d.f. = 1, $P = 0.041$) (Fig. S2c). The same pattern was observed in individuals of *A. heloisa* (Fig. S2c). In contrast, adult females of *S. rufus* were highly dominant at the beginning of the season, afterward the proportion of interactions won by them decreased significantly ($\chi^2 = 229.920$, d.f. = 1, $P < 0.001$) (Fig. S2b). For the subordinated latitudinal and altitudinal migrant categories, the number of won interactions did not change notably over time, moreover during the last 2 weeks of March, the adult males and juvenile females of *S. rufus* and the individuals of *S. platycercus* and *S. calliope* lost practically all the interactions where they were involved (Fig. S2c).

Hummingbird community composition

For a total of 90 net hours, we caught 117 individuals belonging to 10 hummingbird species (Appendix S1). Hummingbird community composition and abundance change over time ($\chi^2 = 19.967$; d.f. = 5; $P = 0.001$). We caught fewer hummingbirds toward the end of the winter ($\chi^2 = 11.772$, d.f. = 1, $P < 0.001$) and not all the species were caught in the same proportion ($\chi^2 = 131.992$; d.f. = 9; $P < 0.001$). Species such as *A. beryllina* and *S. rufus* were caught more frequently than the other species. Although the migratory status did not have an effect on the number of hummingbirds caught ($\chi^2 = 0.1552$; d.f. = 15; $P = 0.155$), as the sampling period advanced, the number of hummingbirds belonging to latitudinal migrant species diminished (Appendix S1).

Floral abundance and nectar resource availability

Fourteen plant species were used by hummingbirds as nectar resources (Appendix S3). The number of flowers available for the hummingbirds was different depending on vegetation

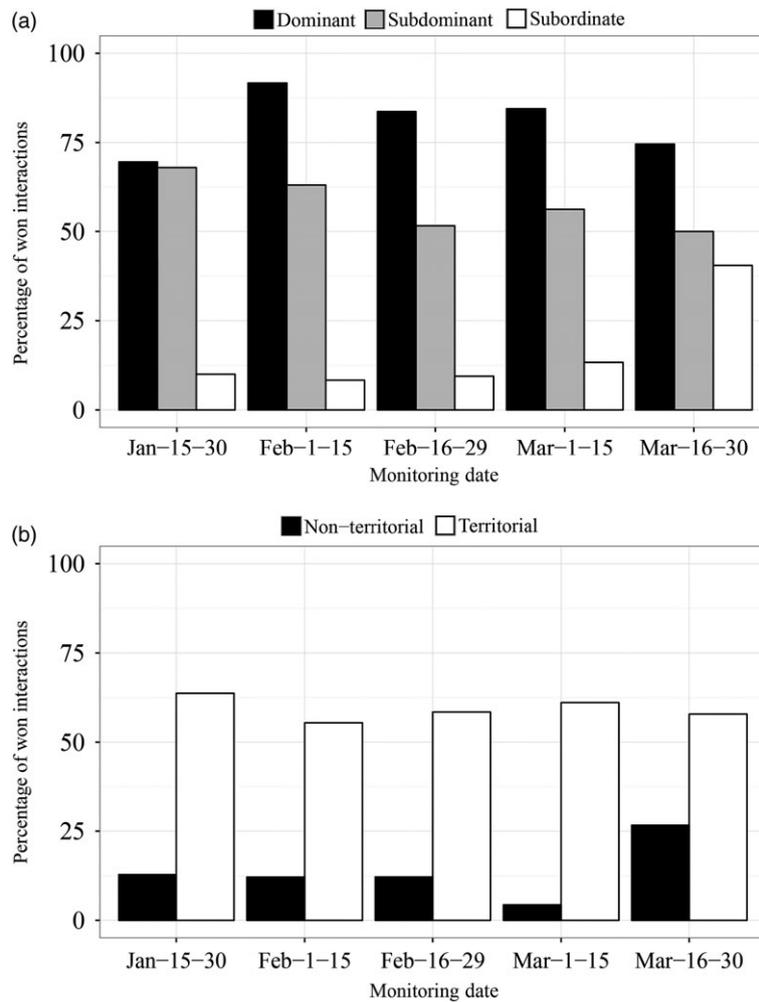


Figure 2 Proportion of aggressive interactions won by hummingbirds at Las Joyas Scientific Station during winter (2-week periods). Hummingbird species are discriminated by dominance categories (a) and foraging strategy (b).

and patch type ($L = 18.597$; d.f. = 15; $P < 0.001$), with more flowers in secondary vegetation (mixed patches) and cloud forest (large monospecific and mixed patches) (Fig. 3). Most species used by hummingbirds grew in disturbed areas, and only *M. depeana*, *Ipomoea hederifolia* and *Salvia albocaerulea* grew exclusively inside the forest (Appendix S3).

Resource availability and aggressive hummingbird interactions

The number of aggressive interactions changed significantly between the different types of floral patches ($\chi^2_{(0.05,26)} = 323.91$; $P < 0.001$), and almost all the interactions occurred at patches with abundant flowers (37.611% at large monospecific patches and 56.294% at mixed patches).

Hummingbirds responded differently to floral availability as a function of their dominance status and foraging strategy. Generally, a hummingbird that started an interaction would

win it ($r_s = 0.957$; $n = 16$; $P = 0.001$), and the majority of the interactions that involved subordinate hummingbirds happened when these birds were visiting flowers ($r_s = 0.587$; $n = 16$; $P = 0.008$) (Table 1).

Hummingbird aggressiveness and patch preferences were related with the number of flowers and the type of floral patch. In the small monospecific patches, we observed lower activity, with only a few hummingbirds showing aggressive behavior in these patches (males of *L. amethystinus* and individuals of *A. beryllina*) ($U_{\text{type of patch}} = 0.13$; $P < 0.001$, Table 3). Some species (*H. leucotis*, *E. fulgens* and *S. platycercus*) did not prefer a particular patch type between large monospecific and mixed, but we did find cases where the different dominance groups interacted more aggressively in one particular floral patch type than in others (Table 3). For example, in *L. amethystinus*, the males were more aggressive and visited the flowers of the large monospecific patches, while the females interacted in all type of patches indiscriminately. In the case of *S. rufus*, the subordinate individuals of

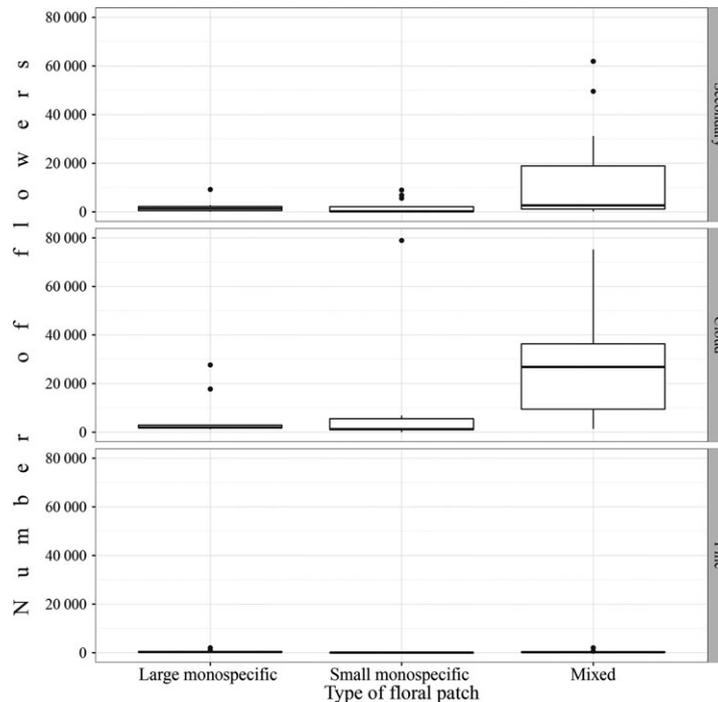


Figure 3 Number of flowers in the patches visited by hummingbirds during winter. Patches are classified by type of vegetation (secondary, cloud and pine forest), and according to the abundance and number of species found blooming together (large monospecific and mixed). Box encloses the 50% of the data and it is divided by the median (horizontal line); the upper and lower adjacent indicate 0.95 and 0.05 quantiles respectively. Points are considered to be outliers.

this species (juvenile males and adult females) interacted more frequently in mixed patches, compared to the subordinated individuals, which interacted principally in large monospecific patches (Table 3).

The number of flowers visited and the number of aggressive interactions were positively and significantly correlated with the number of calories produced by the flowers in the different patches studied ($r_s = 0.831$; $n = 91$; $P < 0.001$ for visits; $r_s = 0.724$; $n = 91$; $P < 0.001$ for aggressive interactions). However, the number of calories produced in floral territories defended by dominant and subdominant territorial hummingbirds were not statistically different ($n = 23$, $P = 0.4876$, $W = 64$, Mann–Whitney U test).

Discussion

Dominance and territoriality were not fixed attributes of the species in this hummingbird community, and changed as a function of hummingbird species, sex, age and size. Similarly, hummingbird foraging and dominance strategies change as a function of community composition, floral abundance and nectar resource availability. As expected, a close relationship between dominance and territoriality was found (Cotton, 1998): a dominant individual was generally a territorial one, while a subordinate hummingbird always acted as a non-territorial. In this community, size was not always the best predictor of dominance and territoriality,

and can be explored as a trait associated with phylogenetic clustering.

Effect of hummingbird size, age and sex on dominance and territoriality

Different authors have proposed that the pattern of dominance and foraging behavior between hummingbirds into a community may be defined by hummingbird body size and predisposition for territorial behavior (Feinsinger & Colwell, 1978; Des Granges, 1979; Justino *et al.*, 2012). In this community, large hummingbirds (because of their high energetic requirements) were dominant and moved between different habitats looking for resources with abundant nectar to establish feeding territories. Furthermore, latitudinal migrants (generally smaller) tended to be subordinate to the resident species and were forced to follow a non-territorial strategy (as observed by Wolf, Stiles & Hainsworth, 1976; Des Granges & Grant, 1980) (Fig. 1, Table 1).

The pattern where larger competitors exclude and influence the habitat use of the smaller and less dominant species support the ‘ideal despotic distribution’. Body size effect has been documented in other systems as nectarivorous birds in Australia, where bigger birds are limiting the access to nectar to the smaller birds (Bennett *et al.*, 2014). Specifically for the community studied here, the cases where this pattern was not supported exemplify as other factors are acting together with

Table 3 Number of aggressive encounters recorded at the different type of floral patches

Hummingbird dominance groups	Large		Mixed
	monospecific	monospecific	
<i>Amazilia beryllina</i>	329	8	333
<i>Amazilia violiceps</i>	0	1	1
<i>Atthis heloisa</i>	6	0	32
<i>Colibri thalassinus</i>	11	0	71
<i>Eugenes fulgens</i>	7	1	21
<i>Hylocharis leucotis</i> female	49	0	57
<i>H. leucotis</i> male	130	4	137
<i>Lampornis amethystinus</i> female	18	1	9
<i>Lampornis amethystinus</i> male	264	27	100
<i>Selasphorus calliope</i>	6	0	10
<i>Selasphorus platycercus</i>	16	1	27
<i>Selasphorus rufus</i> subordinate	42	1	110
<i>Selasphorus rufus</i> subordinate	9	0	6
<i>Tilmatura dupontii</i>	32	0	2

The interactions are discriminated by hummingbird dominance group. *Selasphorus rufus* subordinate included adult females and juvenile males; *S. rufus* subordinate include juvenile females and adult males.

body size to modify dominance and foraging behavior. Territoriality can be a very expensive strategy when resources are limited (Carpenter, 1987a), and in our community, a large territorial and dominant species as *E. fulgens* (Lyon, 1976; Des Granges, 1979) used a non-territorial behavior visiting the flowers defended by smaller territorial hummingbirds with impunity ('territory-parasite' *sensu stricto* Feinsinger & Colwell, 1978). This indicates that probably the amount of nectar offered by the flowers in our study site at this time was not enough to support a high population density and cover the energetic requirements related with a territorial strategy.

Other explanation to the lack of support for our predictions with respect to the dominance of larger competitor, is the hypothesis that suggests that smaller species can win aggressive contest against larger ones if these interact with distantly related species or with species poorly known (Martin & Ghalambor, 2014). This hypothesis could explain the fact that *Colibri thalassinus* (Mangoes clade *sensu stricto* McGuire *et al.*, 2009) and *A. beryllina* (Emeralds clade *sensu stricto* McGuire *et al.*, 2009), the two altitudinal migrants, won the majority of their interactions against *E. fulgens*, a resident and larger species that belongs to a different phylogenetic clade (Mountain gems clade *sensu stricto* McGuire *et al.*, 2009).

As expected, territoriality and dominance changed at intraspecific level depending on age and sex of the individuals (Carpenter *et al.*, 1993). The lack of sexual dimorphism in the plumage of some hummingbird species as *Panterpe insignis*, suggested that the females are dominant because both sexes converge in the color of the areas that are important for territoriality and aggressive displays (Wolf, 1969). In the community we studied, it was true for monomorphic species as *C. thalassinus* and *A. beryllina* (Tables 1 and 2). Also, in dominant hummingbird species with plumage sexual dimorphism (e.g.

L. amethystinus here), males and females usually have different foraging behaviors: adult and juvenile males are territorial and dominant over the adult and juvenile females that are subordinate and/or secondary territorial (Feinsinger & Colwell, 1978) (Tables 1 and 2). As observed with body size, our results showed that although the dominance and territoriality responded as expected in some cases, it was evident that other factors are modifying the dominance and territoriality at intraspecific level. In the particular case of *S. rufus*, our results suggested that hummingbird density modified the pattern expected for dominance. The adult males are dominant and highly territorial in the reproductive (Healy & Calder, 2006) and migratory (Kodric-Brown & Brown, 1978) areas of United States of America and Canada. However, in the LJSS (a wintering area), the adult males of *S. rufus* were subordinated to the adult females and juvenile males of the same species (Table 1, C. Rodríguez-Flores and M. C. Arizmendi pers. obs.). Stiles *et al.* (2005) stated that females of the majority of hummingbird species rarely defended territories during the winter, being generally subordinate to the males. But in the absence or low number of males, the females can show territorial behavior (Stiles *et al.*, 2005). We recorded adult males very occasionally during the observation periods, and only one was caught during the mist-net sessions. These results and the observations made during subsequent visits to different areas of the Reserve (C. Rodríguez-Flores, pers. obs.), supported the hypothesis of altitudinal segregation between sexes (Schondube *et al.*, 2004) with males establishing territories in the eastern side of the Sierra and at lower elevations, compared with females and juveniles. Additionally, Kodric-Brown & Brown (1978) suggested that at high elevation (>2500 m a.s.l.), the aggressive ability of male *S. rufus* decreased because of their high wing disk loading.

In the community studied by us, the majority of the aggressive interactions occurred between species of different migratory and dominance status. Des Granges (1979) found a similar pattern, and he interpreted it as a consequence of ecological segregation and co-adjustment of the niches of species that are coexisting. In our community, *L. amethystinus* (males) and *E. fulgens* interacted strongly with individuals of **other** dominance category but of the **same** migratory status. In the specific case of the males of *L. amethystinus*, their territorial and dominant behavior increased the number of aggressive interactions with individuals of *E. fulgens* and *A. heloisa*; two non-dominant species that as *L. amethystinus* were resident too.

Hummingbird community composition

We found that hummingbird foraging strategies and dominance were dynamic over time. This change occurred as a function of community composition (related with migration pattern) and the resulting change in hummingbird density of a particular species (or age/sex category) (Appendix S1, Fig. S2, Stiles, 1973; Lyon, 1976; Bennett *et al.*, 2014). The change in the composition and abundance of the hummingbird community occurred as expected, with few hummingbirds caught in the last 2 weeks of March because of the departure of the long-distance migrant species (Appendix S1, Arizmendi, 2001). This

pattern was supported by the number of altitudinal and latitudinal migrant hummingbirds caught with mist nets, and although these data are not conclusive with respect to the resident species (Appendix S1), our behavioral observations showed an increase in the number of aggressive interactions and visits to the flowers by resident species at the end of March, specially *H. leucotis*. Departure dates for the northwood latitudinal migration of *S. rufus* based on records at Nevado de Colima (69.5 km east of the study site) in previous years were between January 22nd to February 12th (Des Granges, 1979) and February 20th to March 21st (Schondube *et al.*, 2004). Our results showed that, even on March 21st, some individuals of *S. rufus*, *S. platycercus* and *S. calliope* were still at our study site.

Our data showed that *H. leucotis* and *A. heloisa* were subordinate species during winter, but at the end of March, the individuals of these species won a higher proportion of aggressive encounters against more dominant species such as *S. rufus*, *A. beryllina* and *L. amethystinus* (Fig. S2, Appendix S4), and additionally, its abundance increased over the following months with the highest density on summer (Arizmendi, 2001). In the particular case of *H. leucotis*, Lyon (1976) proposed that the flexible feeding behavior repertoire of this species was the factor that explained the success of this species in montane Mexico. These observations suggested that, over time, the foraging strategy and the dominance should change as a function of community composition (Sandlin, 2000b), with the resident species becoming more abundant with respect to the migrant species, and in consequence more territorial and dominant (Des Granges, 1979; Des Granges & Grant, 1980; Arizmendi & Ornelas, 1990).

Floral abundance and nectar resource availability

Different studies have suggested that hummingbird territoriality is determined by nectar availability (Feinsinger, 1976; Feinsinger & Colwell, 1978; Kodric-Brown & Brown, 1978; Cotton, 1998; Justino *et al.*, 2012). In our study site, the foraging strategy used by the different hummingbird dominance categories did not change as a function of habitat or the plant species they used as nectar resources during winter season. The only exception was the males of *L. amethystinus*. These birds visited the flowers of *M. depeana* and *I. hederifolia* at the cloud and pine forest (respectively) using a traplining strategy, but in secondary forest, these individuals were territorial and defended floral patches of *Salvia mexicana*, *S. albocaerulea* and *L. laxiflora* (Appendix S5). Change in foraging behavior is an alternative to get resources when the optimal feeding territories are occupied (Schondube *et al.*, 2004) or to exploit the difference in nectar availability between habitats (Lara, 2006). At regional scale, hummingbird nectar resources are not uniformly distributed, and these resources were located principally in the secondary vegetation and along stream banks in the cloud forest. Further, flower abundance was variable over time and decreased substantially in spring (Arizmendi, 2001). Restriction in nectar availability (at spatial and temporal scale) determines the competitive pressure between hummingbirds

(Carpenter, 1987b), which foraging strategies are profitable, and nectar exploitation patterns (Feinsinger, 1976). As expected, the nectar-rich areas at local scale (like large monospecific and mixed patches), attracted more competitors increasing territoriality and aggressive behavior between hummingbirds. The presence of small floral patches, generally undefended, acted as feeding areas where different hummingbird species, independently of the species, can feed with minimum conflict (Lyon, 1976).

Competition exerts a strong force on hummingbird behaviors (Sandlin, 2000a), and in this community, differences in the utilization of floral resources and habitat acted as mechanisms that favored hummingbird coexistence as suggested by Feinsinger (1976). In the case of floral use, these differences have been proposed as a mechanism that decrease the competition between species that use similar resources, favoring resource partitioning, and consequently decreasing the probability of injury during aggressive encounters with other individuals (Des Granges & Grant, 1980; Ritchie, 2002; Lara *et al.*, 2009). In our study site, *L. amethystinus* used principally the large monospecific patches, but the altitudinal migrant species, especially *C. thalassinus*, used the mixed patches more frequently (Table 3). Because these species are the more dominant species in our community, the more plausible explanation is the tendency to diverge functionally through segregation of nectar resources. Respect to habitat use, spatial segregation is one of the mechanisms that affect directly hummingbird community organization (Des Granges, 1979; Rodríguez-Flores, 2004), and in LJSS, species like *A. beryllina* and *S. rufus* used more the secondary vegetation areas in comparison with pine forest specialist species like *S. platycercus* (Contreras-Martínez, 2014). The preference of this species in pine forest corresponded to a behavioral strategy, where a low hierarchy species prefers habitats with low floral abundance and aggressiveness (Fig. 3) to avoid the more competitive habitats, while use poorer and dispersed resource patches (Carstensen *et al.*, 2011).

Conclusion

Hummingbird capability to evaluate and respond to changes in their environment is crucial to allow their coexistence and prevalence. Our study showed how hummingbird aggressiveness and territoriality are plastic traits that responded to spatio-temporal variations in community composition, hummingbird density and floral availability. Compared to other studies where nectar availability is the main factor controlling hummingbird distribution and territoriality (Lyon, 1976; Wolf, 1978; Des Granges, 1979; Gutiérrez-Zamora & Rojas, 2001), our results showed that local abundance and hummingbird migration pattern together with nectar availability are crucial components to explain the dynamic nature of dominance and territoriality in this community as found for other nectarivorous birds, the Noisy Miners (Bennett *et al.*, 2014). This complex and highly dynamic arrangement in which hummingbirds show high plasticity in resource use both in time and space and among species can be the key evolutive trait that has made hummingbirds one of the less threatened bird families in the Neotropics (Schuchmann, 1999).

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Supporting Information

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

Figure S1. Proportion of interactions won (number of interactions won/(number of interactions won + number of interactions lost)) by hummingbirds at Las Joyas Scientific Station during winter. Hummingbird species are discriminated by sex (a) and age (b).

Figure S2. Proportion of aggressive interactions won by hummingbirds at Las Joyas Scientific Station during winter (2-week periods).

Appendix S1. Number of hummingbird caught during the mist-net sessions at Las Joyas Scientific Station.

Appendix S2. Mean body weight for the different sex and age of the hummingbirds at Las Joyas Scientific Station, Mexico.

Appendix S3. Plants visited by hummingbirds in Las Joyas Scientific Station, Mexico.

Appendix S4. Aggressive interaction matrix between hummingbird dominance groups habiting Las Joyas Scientific Station (Mexico). In parenthesis is indicated the total number of aggressive interactions recorded between these two species.

Appendix S5. Interaction matrix between hummingbirds and plants at Las Joyas Scientific Station during winter.