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Me permito informar a usted que en la reunión ordinaria del Subcomité de Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el dia 2 de octubre de 2017, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **LOPEZ SEGOVIANO GABRIEL**, con número de cuenta **510021050** con la tesis titulada **"ESTRUCTURA DE LAS COMUNIDADES DE COLIBRÍES (TROCHILIDAE) EN UN GRADIANTE ALTITUDINAL Y SU RELACIÓN CON LA DISPONIBILIDAD DE ALIMENTO"**, realizada bajo la dirección de la **DRA. MARIA DEL CORO ARIZMENDI ARRIAGA:**

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Índice

Resumen

Las comunidades de colibríes han sido estudiadas en relación con sus recursos alimenticios desde hace cinco décadas. Se ha establecido que el principal factor que determina los patrones de abundancia y diversidad de las comunidades de colibríes es la abundancia de las flores que visitan. Así, se ha postulado que la separación ecológica de los nichos puede darse por diversos procesos que pueden ser morfológicos, fisiológicos o incluso conductuales. Otros factores de importancia son las fenologías florales y la migración; sobre todo en regiones altamente estacionales como el Noroeste de México donde un gran número de especies de colibríes son migratorias y existe una gran fluctuación de los recursos florales a lo largo del año. En el presente trabajo de tesis se abordaron cuatro estudios con la comunidad de colibríes en el Noroeste de México y como el uso de los recursos florales influye en su comportamiento, sus patrones migratorios así como la estructura de sus comunidades.

En primer capítulo, determinamos como la conducta y la dominancia influyen en la distribución de los recursos a nivel local. Donde encontramos que el comportamiento agresivo de los colibríes puede estructurar la comunidad y la jerarquía de dominancia está directamente relacionada con el tamaño corporal y no presenta relación con la carga del disco alar o el estatus migratorio. Además, el nivel de dominancia de cada especie está relacionada con la calidad del recurso floral.

En mi segundo capítulo, evaluamos si los patrones de fenología migratoria de dos especies de colibríes (*Selasphorus rufus* y *Amazilia beryllina*) están relacionados con abundancia floral. Los resultados muestran que la especie que presenta una ruta migratoria más larga no presenta cambios anuales en su migración (*S. rufus*), a diferencia de la especie con migración más corta que puede ajustar su migración anual en relación a la cantidad de recursos presentes en cada sitio visitado (*A. beryllina*). La migración de *S. rufus* por la región de estudio coincide con la floración de *Salvia iodantha*. Siendo *S. iodantha* la principales fuentes de alimento de *S. rufus* de la región templada del Noroeste de México.

En tercer capítulo, determinamos si existe una preferencia por un tipo de planta en particular utilizando como modelo a dos especies de colibríes de mayor abundancia en la región y de diferente estatus migratorio (*S. rufus* y *A. beryllina*). Encontramos que *S. rufus* se alimento de la especie con la cual coincide su migración en condiciones naturales y en exclusión experimental. A diferencia de *A. beryllina*, especie que cambio su preferencia en condiciones naturales y al ser ensayada en forma experimental en condiciones de exclusión. Así, la preferencia de un colibrí depende de múltiples factores donde destacan la calidad de los recursos florales, el estatus migratorio así como la jerarquía de dominancia de cada especie de colibrí.

Por último en el cuarto capítulo, se analizaron tres comunidades de colibríes en un gradiente altitudinal y las plantas de las que se alimentan, utilizando la teoría de redes de interacción mutualista. Encontramos que la topología de las redes de interacción cambia en el gradiente altitudinal y que la mayoría de las especies de colibríes las encontramos en dos pisos altitudinales pero desempeñaron papeles diferentes en cada sitio de muestreo. Otro resultado importante fue que las especies núcleo en cada red de interacciones fueron plantas ornitófilas y no ornitófilas. Por último determinamos que la abundancia de colibríes migratorios latitudinales está correlacionada con el número de interacciones así como con los enlaces entre colibríes y plantas.

Los resultados obtenidos en mi tesis, me permiten concluir que la comunidad de colibríes está directamente ligada a la oferta de recursos florales ya sean con síndrome ornitófilo o no-ornitófilo. Los patrones de abundancia de flores de estas plantas determinan los movimientos migratorios locales y regionales de los especies de colibríes, estando los migratorios latitudinales ligados a la floración de *S. iodantha* y su llegada anual presenta poca variación, mientras que la especie migratoria altitudinal parece depender de la cantidad de recursos disponibles. De la misma forma, las preferencias de estas especies por especies de plantas comunes en la región se mantiene constante para las especies migratorias latitudinales en condiciones naturales y de exclusión de otros visitantes, mientras que cambia para la migratoria altitudinal. Así, la estructura de la comunidad de colibríes está directamente relacionada con la cantidad de los recursos florales, su distribución y su temporalidad, así como la presencia y abundancia de otras especies de colibríes con las que se comparten los recursos.

Abstract

Hummingbird communities have been studied in relation to their food resources for five decades. It has been established that the main factor that determines the abundance and diversity patterns of hummingbird communities is the abundance of the flowers visited by them. Thus, it has been postulated that the ecological separation of the niches can occur through various processes that can be morphological, physiological or even behavioral. Other important factors are floral phenology and migration; especially in highly seasonal regions such as Northwestern Mexico where a large number of hummingbird species are migratory and there is a high fluctuation of floral resources throughout the year. In this work, four studies were undertaken with the hummingbird community in Northwestern Mexico and how the use of floral resources influences their behavior, their migration patterns as well as the structure of their communities.

In the first chapter, we determine how behavior and dominance influence the distribution of resources at the local level. Where we found that the aggressive behavior of hummingbirds can influence the structure of the community and determine the hierarchy of dominance which is directly related to the body size and not with the wing disc loading or migratory status. In addition, the level of dominance of each species was related to the quality of the floral resources.

In the second chapter, we evaluated the patterns of floral phenology and abundance and how they were linked to the seasonal patterns of abundance of two species of hummingbirds (*Selasphorus rufus* and *Amazilia beryllina*). The results showed that the species that presents a larger migratory route did not present annual changes in its migration (*S. rufus*), unlike the species with shorter migration that adjusted its annual migration in relation to the abundance of resources at each site visited (*A. beryllina*). The migration of *S. rufus* at the study region coincides with the flowering of *Salvia iodantha*, being the main food source for *S. rufus* from the temperate region of Northwestern Mexico.

In the third chapter, we determined if there was preference for a particular type of plant using as a model two species of hummingbirds abundant in the region and of different migratory status (*S. rufus* and *A. beryllina*). We found that *S. rufus* feeds on the species with which its migration coincides (*S. iodantha*) in natural conditions and experimental exclusion. Unlike *A. beryllina* that changed its preference when excluded from competition with other hummingbirds experimentally. Thus, the preference of a hummingbird depends on multiple factors that highlight the quality of the floral resources, the migratory status as well as dominance hierarchy.

Finally, in the fourth chapter, three communities of hummingbirds along an altitudinal gradient and the plants they feed on were analyzed, using the theory of mutualistic networks. We found that the topology of interaction networks changed in the altitudinal gradient and that most hummingbird species were found on two altitudinal levels but played different roles at each sampling site. Another important result was that the core species in each network of interactions were ornithophilic and non-ornithophilic plants. Finally, we determined that the abundance of latitudinal migratory hummingbirds was correlated with the number of interactions as well as with the links between hummingbirds and plants.

The results obtained in this work allowed me to conclude that the hummingbird community is directly linked to the supply of floral resources used, whether ornithophilic or non-ornithophilic syndrome. The patterns of abundance of flowers of these plants

determine the local and regional migratory movements of hummingbirds species being the latitudinal migrants tightly correlated with the flowering of *S. iodantha* being their annual arrival dates presents little variation, while the migratory species altitudinal seems to depend on the number of resources available. In the same way, the preferences of these species for common plant species in the region remain constant for latitudinal migratory species in natural conditions and for the exclusion of other visitors, while it changed for the altitudinal migrant. Thus, the structure of the hummingbird community was directly related to the quantity floral resources, their distribution, and temporality, as well as the presence and abundance of other species of hummingbirds with which resources are shared.

Introducción general

Las comunidades de colibríes han sido estudiadas en relación con sus recursos alimenticios desde hace cinco décadas. Se ha establecido que el principal factor que determina los patrones de abundancia y diversidad de las comunidades de colibríes es la abundancia de las flores que visitan (Wolf *et al.* 1976, Feinsinger 1976, Brown & Bowers1985, Abrahamczyk *et al.* 2015). Dentro de este arreglo de plantas y colibríes se ha propuesto que la competencia es uno de los factores que determinan el reparto de recursos y la distribución de las especies (Wolf *et al.* 1976, Feinsinger 1976). Así, se ha postulado que la selección natural en los colibríes ha favorecido la minimización de la competencia mediante la separación de los nichos ecológicos de las especies lo que permite la coexistencia (Feinsinger 1976, Wolf 1978). No obstante, la separación ecológica de los nichos puede darse por diversos procesos que pueden ser morfológicos, fisiológicos o incluso conductuales.

Los colibríes presentan una morfología que consiste en picos largos, lenguas largas y protráctiles, alas largas puntiagudas y musculaturas pectorales muy prominentes (Schuchmann 1999), lo que les facilita visitar flores largas, tubulares y suspenderse en el aire para conseguir alimento (Faegri & van der Pijl 1980, Brown & Bowers 1985). El pico es una estructura con la que acceden al néctar por lo que se ha establecido que su tamaño está correlacionado con el largo de la corola de las flores que visitan (Wolf & Stiles 1989, Arizmendi & Ornelas 1990, Lara & Ornelas 2001). Debido a esto, la presencia de un arreglo de especies de diferentes morfologías, fomenta que los colibríes con picos de diferentes largos visiten flores también de diferentes tamaños y curvaturas de corola, separando sus nichos alimenticios, lo cual es considerado uno de los mecanismos que explican la coexistencia las comunidades de colibríes (Feinsinger 1976, Brown & Bowers1985).

Los colibríes presentan dos patrones generales de conducta alimenticia: existen especies que defienden territorios monopolizando los recursos y peleando con otras especies a las que les impiden el acceso al néctar en su territorio (Territoriales) y otras que se alimentan siguiendo rutas externas de los territorios, o bien recursos que no son defendidos (Ruteros) (Feinsinger 1976, Wolf 1978). Estas conductas pueden cambiar en escalas espaciales y temporales (Rodríguez-Flores & Arizmendi 2016). Estos cambios dependen de la densidad de los recursos florales que ellos visitan pero también de la abundancia de las otras especies de colibríes presentes en el área de forrajeo, lo cual frecuentemente cambia a lo largo del año (Cotton 1998, Feinsinger 1978). Se ha descrito que los cambios de estrategia de alimentación pueden ser incluso a lo largo del día (Feinsinger 1976), como respuesta a la oferta de recursos y la competencia por ellos (Rodríguez-Flores y Arizmendi 2016).

Kodric-Brown *et al*. (1984) establecen que típicamente las comunidades de colibríes de las zonas templada de Estados Unidos de América son más homogéneas que las de sitios tropicales, siendo las especies de colibríes de una sola categoría de tamaño han evolucionado con especies de flores que han convergido en morfologías florales y recompensas similares. Estas especies de colibríes que se reproducen en Norte América realizan movimientos migratorios siguiendo los patrones temporales de floración de las plantas distribuidas a lo largo de sus rutas migratorias (Healy & Calder 2006). Los colibríes migratorios pueden llegar justo antes del pico de floración lo cual les provee de un suplemento abundante de néctar (Calder & Contreras-Martinez 1995). La disponibilidad de alimento acoplada con la llegada de las aves migratorias a los sitios de migración es un factor determinante para la supervivencia de estas aves migratorias (Calder 2004).

Los colibríes son aves nectarívoras, entre 85 y 90 % de su dieta constituye néctar floral (Gass & Montgomerie 1981). Un colibrí vista cientos de flores durante un día y transfiere el polen entre las flores (Hurly & Healy 1996, Healy & Hurly 2001). La interacción de colibrí y las flores que poliniza es catalogada como mutualista o de ganancia mutua (Jordano *et al* 2009), las cuales generan redes de interacciones mutualistas complejas (Jordano *et al*. 2009). Las redes de interacciones nos permiten integrar los sistemas y comprender mejor las comunidades a través de sus interacciones (Jordano *et al.* 2003, Bascompte & Jordano 2007, Jordano *et al.* 2009, García 2016). De hecho, las redes de interacciones colibríes y plantas se han usado para comprender como se estructuran las comunidades de colibríes y su recursos a una escala geográfica latitudinal (Dalsgaard *et al.* 2011) o altitudinal (Maglianesi *et al.* 2014), lo que nos permite establecer propiedades de la comunidad de colibríes y plantas en un gradiente geográfico.

En el presente trabajo de tesis se abordaron cuatro investigaciones realizadas con la comunidad de colibríes en el Noroeste de México y cómo el uso de los recursos florales influencia su comportamiento, migración y su estructura. Primero determinamos como la conducta y la dominancia influye en la distribución de los recursos a nivel local (Capítulo I). Después evaluamos los patrones de fenología y abundancia floral y como están ligados a los patrones estacionales de abundancia de los colibríes (Capítulo II). En tercer lugar, determinamos si existe una preferencia por un tipo de planta en particular utilizando como modelo a dos especies de colibríes abundantes en la región y de diferente estatus migratorio (Capítulo III). Por último, se analizaron tres comunidades de colibríes en un gradiente geográfico altitudinal y las plantas de las que se alimentan, utilizando la teoría de redes de interacción mutualista (Capítulo IV).

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

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

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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

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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 Rio & 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 iodantha*, *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. thyrsoideum* 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. thyrsoideum*, $n = 17$ 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 1EBX 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 ($Ds = w + w^{(2)} - l - l^{(2)}$). 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. thyrsoideum* (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. thyrsoideum* 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. thyrsoideum* had significantly more calories than patches of *S. iodantha* (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 Rio & Eguiarte 1986,

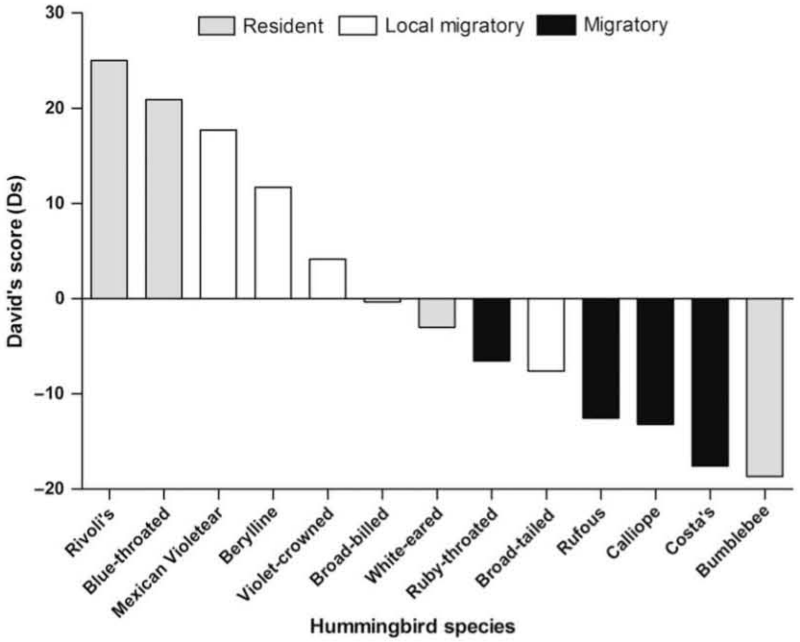

Figure 1. David's score for the 13 hummingbird species at El Palmito, Mexico. The resident Blue-throated Hummingbird and Rivoli's Hummingbird have the highest dominance index (Ds) score.

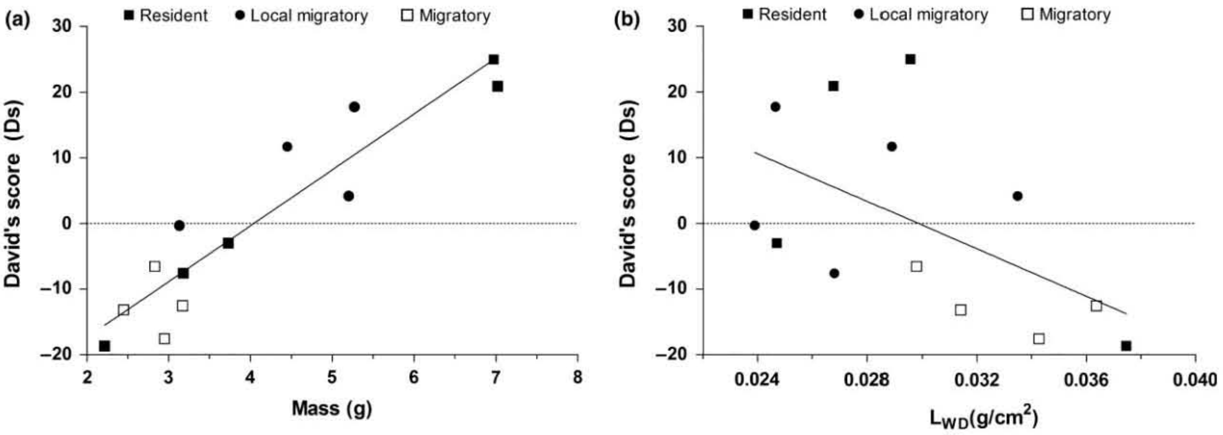

Figure 2. Relationship of the David's score index (Ds) with (a) body mass (g) and (b) wing disc loading L_{WD}; (g/cm^2) of 13 species of hummingbirds (Resident hummingbird solid square, Local migratory solid circle, and Migratory clear square). David's score (Ds) was positively related to body mass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

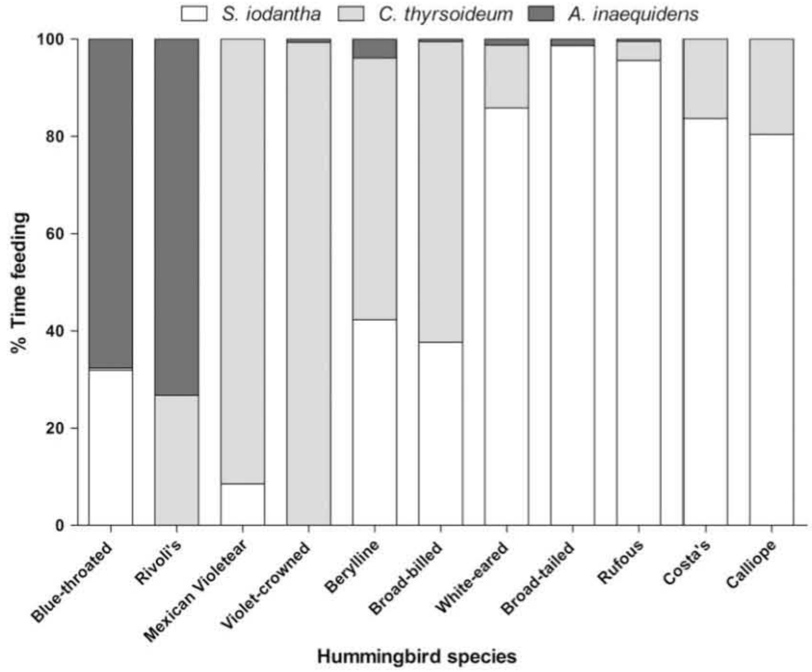

Figure 3. Percentage of time that each hummingbird species spent feeding in each type of flower patch (Bumblebee Hummingbird and Ruby-throated Hummingbird *Archilochus colubris* were excluded because of the small number of observations).

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

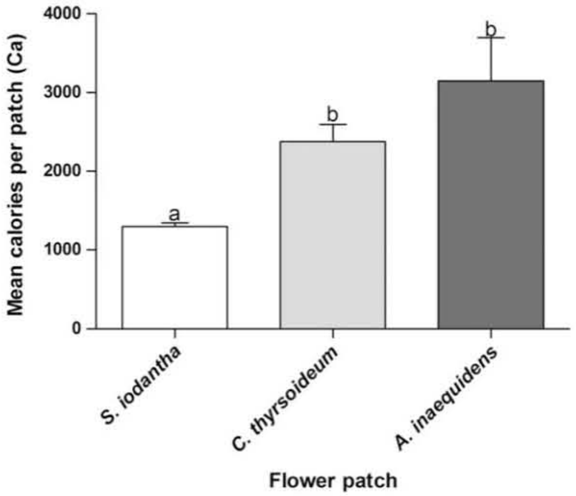

Figure 4. Mean (±se) calories produced by flowers in patches consisting of *Agave inaequidens*, *Cestrum thyrsoideum* and *Salvia iodantha* at El Palmito, Mexico. The Kruskal–Wallis test showed that flower patches of *S. iodantha* differed in the quantity of calories offered. Dunn's multiple *a posteriori* 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	*t*-Value	*P*
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 Rio & Eguiarte 1986, Ornelas *et al.* 2002). Although there was no significant difference in the average number of calories between flower patches of *C. thyrsoideum* and *A. inaequidens*, *C. thyrsoideum* 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. thyrsoideum* (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, Muchhala *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 Granges 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. thyrsoideum*. 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.

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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.

CAPÍTULO II. Hummingbird migration and flowering synchrony in the temperate forests of northwestern Mexico.

Sometido en PeerJ

Hummingbird migration and flowering synchrony in the temperate forests of northwestern Mexico

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ABSTRACT

Background. Climatic changes may affect pollination systems. For example, climate changes can cause mismatches in the phenology of migrant pollinators and the plants they pollinate, negatively affecting these mutualistic networks. As hummingbirds are highly dependent on floral nectar, their migration is synchronized with the phenologies of specific flowering plants. This phenomenon can be observed among latitudinal and altitudinal migratory hummingbirds. To explore this issue, we evaluated interannual variation in the phenology of two hummingbird species, one latitudinal migrant (*Selasphorus rufus*) and one altitudinal migrant (*Amazilia beryllina*), and their visited plants during three nonconsecutive years.

Methods. We assessed the relation between hummingbird migrations and flower phenologies in 20 fixed-radius plots (25-m radius) in El Palmito. The studied hummingbirds were counted, and all available flowers were also assessed along a transect 40 m in length and 5 m in width inside each plot. Sampling was performed every 10 days from November 12 through February of 2010–2011, 2013–2014, and 2015–2016, resulting in a total of 11 replicates of each plot per year. Monthly mean temperature (°C) and monthly mean precipitation (mm) were obtained from six national weather stations in the region. Migratory phenology was analyzed using a generalized additive model (GAM), and the relation between hummingbird and flower abundances was evaluated using a generalized estimation equation (GEE) model.

Results: *Selasphorus rufus* abundance was related with the time of the sampling over the years, although this relation was nonsignificant for the altitudinal migrant *A. beryllina*. The migratory phenology of *S. rufus* marginally differed during the second surveyed year in comparison to the other two years; this second sampling year was also more humid. A significant correlation was repeatedly found between the number of *S. rufus* hummingbirds and the number of *Salvia iodantha* flowers over the three surveyed years. Meanwhile, *A. beryllina* was related with the number of *S. iodantha* and *Cestrum thyrsoideum* flowers during the first year, with the number of both flowers as well as their interaction during the second year, and with the number of both flowers during the final year.

Conclusions. The migratory phenology of hummingbird species clearly depends on their type of migration. Long latitudinal migratory movements, such as those completed by *S. rufus*, remain constant over the years, as these are coupled with the blooming of their preferred feeding plants. Plant phenological shifts resulting from global climate change could likely place the existence of this species at risk. In comparison, the altitudinal migratory species *A. beryllina* responded to the availability of floral resources yet was not associated with a particular plant. The permanence of this species in the area will depend on multiple factors, including climate and demography (hummingbirds), but will especially depend on the supply of floral resources and the competition for these resources.

INTRODUCTION

Migration for most species is profitable in terms of fitness (*Hou & Welch Jr., 2016*). However, climatic changes can cause mismatches in the timing of key phenological events, thereby resulting in negative consequences for animal-plant mutualistic interactions (*Faaborg et al., 2010*). The El Niño phenomenon (ENSO), for example, can directly affect the timing of bird migrations and even influence the breeding success and their distributional range (*Crick, 2004*). Similarly, the flowering of plants can be advanced or delayed by climatic events, thus affecting the availability of resources along migratory corridors (*Kovács et al., 2012; Courter et al., 2013; Supp et al., 2015*). Such phenomena can lead to a mismatch between the migration of pollinators and the flowering of their preferred plants, thereby negatively affecting both pollinator and plant populations (*Faaborg et al., 2010*).

Only 4.26 % of hummingbirds can be considered long-distance migrants. Specifically, 14 out of the 328 known hummingbird species are long-distance migrants, and nine inhabit North America (*Schuchmann, 1999*). These species breed during the summer in Alaska, Canada, and the United States and then migrate southwards during autumn (*Howell, 2003*). Their migrations, unlike those of other larger birds, consist of short flights followed by short refueling stays at flowering grounds (*Hixon et al., 1983; Heinemann, 1992; Schuchmann, 1999; Calder, 2004*). The duration of their stay at a particular site may depend on the quantity and the quality of available feeding resources (*Russell et al., 1994*) and can be as short as one day (*Nemeth & Moore, 2012*). As hummingbirds are highly dependent on floral nectar (*Gass, 1979; Hixon et al., 1983; Schuchmann, 1999*), their migrations are synchronized with flowering phenologies (*Calder, 1987; Heinemann, 1992; Russell et al., 1994; Calder, 2004; Faaborg et al., 2010*). Similar behavior can be observed among tropical hummingbirds that move up or down foothills following the blooming of their preferred plant species (*Des Ganges, 1979; Arizmendi & Ornelas, 1990; Hobson et al., 2003; Tinoco et al., 2009; Fraser et al., 2010*).

In numerous cases, synchronous phenological cycles have been observed between flower and hummingbird species as well as correlations between their abundances (*Stiles, 1980; Schuchmann, 1999; Cotton, 2007; Abrahamczyk & Kessler, 2010; Abrahamczyk et al., 2011*). Changes in flowering phenology can influence the presence or the abundance of hummingbirds, promoting altitudinal or latitudinal movements or enabling their permanence at a given site (*Cotton, 2007*). These synchronized phenological corridors have been described as co-migration processes (*Feinsinger, 1978*). *McKinney et al. (2012)* stated that climate changes can affect such systems by producing asynchronous alterations that may even lead to local extinctions. Similarly, *Inouye (2008)* argued that changes in the phenological phases of pollinators and the plants they pollinate can also affect other organisms and interactions in trophic webs.

In this study, we evaluated interannual variation in the phenologies of two hummingbird species and their visited plants in three nonconsecutive years considering climatic conditions. We studied two hummingbird species: one latitudinal migrant, *Selasphorus rufus* (*Phillips, 1875; Calder, 2004; Schondube et al., 2004; Healy and Calder, 2006*), and one altitudinal migrant, *Amazilia beryllina* (*Des Ganges, 1979; Arizmendi, 2001*). These species have a comparable size and local abundance. In the latitudinal migrant, we expected to find a consistent pattern in its migratory phenology and flower choice, as its phenology must synchronize with that of its preferred plants along its flyway (*Calder, 1987; Heinemann, 1992; Russell et al., 1994; Calder, 2004*). Meanwhile, in the altitudinal migrant, we expected to find a more variable pattern in its migratory phenology, as this species is likely influenced by local flowering and the abundances of other hummingbird species in the local assemblage.

METHODS

Study Area

Study Area. The study site was conducted along a western slope of the Sierra Madre Occidental (SMO) mountain range at the El Palmito Concordia ejidal lands (23°34'16" N; 105°50'15" W) in Sinaloa, Mexico, between 1800 and 2200 masl. The SMO is the longest and most continuous mountain range in Mexico and represents an important temperate forest corridor (*González-Elizondo et al., 2012*). A vegetation gradient was present at the study site, including pine-oak forest, oak forest, and cloud forest mixed with riparian areas and secondary forest (*Díaz, 2005*).

Fourteen hummingbird species have been described for the region: four residents (*Hylocharis leucotis, Lampornis clemenciae, Eugenes fulgens, Selasphorus platycercus*, and *Atthis heloisa*), four altitudinal migrants (*Amazilia violiceps, A. beryllina, Cynanthus latirostris*, and *Colibri thalassinus*), and six latitudinal migrants (*Selasphorus rufus, S. sasin, S. calliope, S. platycercus, Calypte costae*, and *Archilochus colubris; Lopez-Segoviano, 2012*).

Hummingbird censuses

To determine the migratory phenology of the studied hummingbirds, we counted individuals in 20 fixed-radius plots (25-m radius) separated by at least 150 m. For 10 minutes, all detected hummingbirds were counted and sexed when possible (only *S. rufus*). The plots were located in a 300-ha area covered with different vegetation types (6 plots with oak-pine forest, 3 plots with cloud forest, 5 plots with forest edges, 5 plots with clear-cut vegetation, and 3 plots with riparian vegetation). The plots were fixed and distributed to represent the heterogeneity of the study site. All plots were sampled every 10 days from November 12 through February in 2010–2011, 2013–2014, and 2015–2016, resulting in a total of 11 replicates of each plot per year.

Flower censuses

To evaluate flower availability, all flowers inside the plots used for bird counts were also assessed along transects of 40 m in length and 5 m in width; these transects intersected the center of each plot. The abundance and the identity of all flowers present were recorded. Floral censuses were carried out at the same frequency as the bird counts: 11 times per year for each plot.

Climatic data

Temperature (°C) and precipitation (mm) were calculated as monthly means based on data obtained from the six meteorological stations of the National Meteorological System (Sistema Meteorológico Nacional) (*SMN, 2010*) closest to the study area. These were located along an altitudinal gradient and included data from November through February in 2010–2011, 2013–2014, and 2015–2016.

Statistical analysis

The synchronization between migratory phenologies and time was analyzed using a generalized additive model (GAM), as proposed by other researchers (*Zuur et al., 2009; Moussus et al., 2010*). We considered hummingbird counts to be dependent variables and date of sampling to be the explanatory variable and used a tensor (te) to compare these variables over the course of three years (*Wood, 2009; Zuur et al., 2009*).

To test the relation between hummingbird and flower abundances, we used a generalized estimation equation model (GEE). This model allows repeated measures with possible temporal correlations to be evaluated, especially when measures are taken in close time proximity to one another (*Zuur et al., 2009*). We used a Poisson distribution, specifying a temporal correlation (corstr= "ar1"), and considered the observations at each plot as a unit (id=plots); this operation was performed using the geepack package (*Højsgaard et al., 2014*) in R (2011). The numbers of *A. beryllina* and *S. rufus* hummingbirds were set as the dependent variables and the squared root of the numbers of *Salvia iodantha* and *Cestrum thyrsoideum* flowers and time, as well as the interaction among these flower abundances, as the explanatory variables. We choose the best model with the help of the anova function when comparing models with all variables and interactions with a model with fewer variables (*Crawley 2007*).

RESULTS

Migratory phenology

In the three studied years, *A. beryllina* and *S. rufus* were abundant in the region despite the presence of another resident species, *H. leucotis*. The migrant species *S. rufus* was the second most abundant species in the region, representing 10.6 % of the total hummingbirds recorded during the first period, 12.2 % during the second period, and 20.4 % during the third period (Table S1). *Amazilia beryllina* was the most abundant altitudinal migrant species in the region, representing 9.1 % of the total hummingbirds observed during the first period, 5.4 % during the second period, and 8.4 % during the third period (Table S1).

The GAM showed that only the abundance of *S. rufus* was related with the time of sampling over the years (X^2 =73.10, *p* <0.001; Table 1), as this relation was nonsignificant for the altitudinal migrant *A. beryllina* (X^2 = 10.31, *p* <0.13; Table 2). When testing the similarity of migrant phenologies among the sampled years, *S. rufus* phenology was marginally different during the second surveyed period (November 2013–February 2014; Table 1). Also, a comparatively higher level of precipitation was recorded during this year (Table 3). *Amazilia beryllina* phenology marginally differed between the first and third surveyed period (Table 2).

Flowering synchrony

Hummingbirds visited 15 plant species in the phenological transects. *Salvia iodantha* and *Cestrum thyrsoideum* were the most abundant species. Over the three surveyed periods, *S. iodantha* represented 69 %, 61 %, and 77 %, respectively, of total flowers registered in the region, followed by *C. thyrsoideum*, which represented 24 %, 35 %, and 14 %, respectively, of total flowers (Table S2). The flowering phenology of *S. iodantha* was similar during each sampling period and corresponded with the arrival of *S. rufus* hummingbirds to the study site (Fig. 1). Meanwhile, *C. thyrsoideum* presented a distinct blooming tendency in each sampling period (Figs. 1 and 2).

According to the GEE models, we found a significant correlation between the number of *S. rufus* hummingbirds and the number of *S. iodantha* flowers; this tendency was repeated in each of the three surveyed periods (Table 4 and Fig. 1). Also, we found a significant correlation between the number of *S. rufus* hummingbirds and the time of sampling over the first and third years (similar to GAM analysis; Table 1). We found a significant correlation between the number of *S. rufus* hummingbirds and *C. thyrsoideum* flowers on the first year and a significant interaction between *C. thyrsoideum* flowers and *S. iodantha* flowers and *S. iodantha* and time on the third year (Table 4 and Fig. 1). *Amazilia beryllina* was related with the number of *S. iodantha* flowers and with *C. thyrsoideum* flowers during the three surveyed periods, with the number of flowers of both plant species and their interaction during the second and third periods (Table 5 and Fig. 2). *Amazilia beryllina* was related to the time of sampling over the second year, with the time of sampling and number of flowers of *S. iodantha* during the three surveyed periods (Table 5 and Fig. 2).

DISCUSSION

Migratory phenology

Our study showed a relation between the abundance of *S. rufus* and the date of sampling although no similar relation was found for *A. beryllina*. *Supp et al. (2015)* found that hummingbird species like *S. rufus* that perform long-distance migrations have migratory periods with lower interannual variation in comparison to hummingbird species with shorter migratory routes. These authors attribute this finding to the capacity of hummingbirds with short migrations to adjust their route according to the environmental conditions of visited sites (*Supp et al., 2015*). In this sense, altitudinal migrant hummingbirds may perform movements of only a few kilometers but can search for resources along an altitudinal gradient. Also, altitudinal migration is generally optional in the short term and usually occurs when sedentary species migrate to avoid periods of adverse weather (*Faaborg et al., 2010*). Thus, the altitudinal migrant *A. beryllina* could move depending on local climate conditions and the quality of resources. In contrast, *S. rufus* performs one of the longest migrations known for hummingbirds (*Phillips, 1875; Healy and Calder, 2006; Supp et al., 2015)*, and this migration is temporally consistent over the years.

Even so, the analysis (GAM) showed that the migration phenology of *S. rufus* differed in the second sampling year. The high amount of rainfall in the region during the second sampling year could have affected the migration phenology of this hummingbird. *Gass and Lertzman (1980)* found that climatic phenomena such as hail storms can reduce the number of observed hummingbirds, decrease the available floral resources, and force hummingbirds to use suboptimal nearby habitats or to emigrate to other regions. *Graham et al. (2016)* proposed that periods with many climatic anomalies may be particularly problematic for animal populations and especially for those with strong physiological restrictions such as hummingbirds. In fact, hummingbirds may change their feeding behaviors in response to precipitation or other environmental factors that affect their energy balance (*Hou & Welch Jr, 2016*). During the second sampling period, we suppose that hummingbirds could have been forced to migrate to lower altitudes along the altitudinal gradient or to leave the region and continue their migration because of the greater frequency of storms.

In fact, annual variation in the climatic conditions of winter sites could decouple birds from their usual migratory phenology (*Cotton, 2007, Saino et al., 2007*). Migratory systems can be described as a series of sequential events wherein alternations to one of them can subsequently affect later events (*Gunnarsson et al., 2006*). For example, *Courter et al. (2013)* established that the migration of *Archilochus colubris* may be delayed depending on spring conditions at northern latitudes, which may result in a mismatch between the arrival of this hummingbird to lower latitudes, the initial food availability and the flowering plants dependent on pollination by this hummingbird. If migratory hummingbirds are unable to adjust their migration to the specific flowering dates or possibly brief flowering duration of their preferred plants along their migratory routes, will be less successful and their populations will likely be reduced (*Faaborg et al., 2010*). Thus, the decoupling of migrants and the availability of food resources along migratory routes can have direct consequences on the state of migratory populations.

Flowering synchrony

Our study found that the relationship between *S. rufus* and *S. iodantha* flowers was constant over the three sampled years, including during the second year that was an outlier in terms of precipitation. As the migration of *S. rufus* is the longest of all migrating hummingbirds that pass through Mexico (*Supp et al., 2015*), the coupling of its migratory route with a diverse assemblage of blooming plant species is expected (*Calder, 1987; Kodric-Brown & Brown, 1978; Russell et al., 1994*). In Mexico, the presence of *S. rufus* is synchronized with the flowering of *S. iodantha* along its migratory route; this was also found in another area of western Mexico (Manantlán, Jalisco) where *S. rufus* was the most abundant migratory hummingbird in winter and also visited *S. iodantha* flowers (vs. other flowers) most frequently (*Arizmendi, 2001*). This indicates the importance of the flowering phenology of *S. iodantha* for the migration of *S. rufus* along its migratory route in western Mexico. Our findings corroborate this widespread hypothesis based on multiyear sampling.

Migratory species' selection of refueling sites directly influences their survival. In an unknown environment, migratory species have limited time and energy to sample the habitat and experience greater susceptibility to predation and increased competition (*McGrath et al., 2009*). In response, *S. rufus* has been shown to establish territories at the best feeding places along its migratory route in the U.S., for example, in order to hoard food resources (*Gass, 1979, Carpenter et al., 1983, Hixon et al., 1983, Heinemann, 1992*). However, in Mexico, local hummingbird species have larger body sizes (including *A. beryllina*) and dominate smaller latitudinal migratory species, displacing them to floral patches with less energy resources (*Des Ganges, 1979, Calder and Contreras -Martinez, 1995, López-Segoviano, 2012, Rodríguez-Flores and Arizmendi, 2016*). For this reason, *S. rufus* individuals arrive at the beginning of the *S. iodantha* flowering period to feed on this widely distributed resource; these flowers do not provide maximum energy quality but are available to *S. rufus* because more dominant hummingbirds prefer other resources. This synchronization between the latitudinal migration of *S. rufus* and floral phenology may also be essential at other sites along the migration route of *S. rufus* in Mexico (*Calder and Contreras -Martinez, 1995*).

Meanwhile, we found that *A. beryllina* abundance was related to the flowers of both studied plant species, which had the greatest abundance in the study area. This confirms that altitudinal migratory hummingbirds primarily respond to the supply of local floral resources (*Stiles, 1985*). The morphological and physiological characteristics of hummingbirds need their rapid response to changes in the spatial distribution of food within their habitats (*Stiles & Wolf, 1970*). During periods with less abundance of floral resources, hummingbird species respond by altitudinal or partial migrations to areas with better supplies of floral resources (*Stiles, 1985*). Thus, hummingbird communities change depending on the availability of local floral resources (*Arizmendi & Ornelas, 1990; Feinsinger, 1976*). This is especially evident in species with short altitudinal migrations, such as *A. beryllina*, that can navigate through regions with different vegetation types and climate.

CONCLUSIONS

In conclusion, the migratory phenology of hummingbird species clearly depends on their type of migration. Long migratory movements such as those performed by *S. rufus* must be consistent over the years and also coupled with the blooming of their preferred feeding plants. In our study, the presence of *S. rufus* was related to a particular plant (*S. iodantha*), although this was not the case for the altitudinal migratory species *A. beryllina*. Furthermore, *S. rufus* prefers feeding on *S. iodantha* flowers in comparison to *C. thyrsoideum* flowers (unpublished data) and discriminates between these two resources. For these same reasons, *S. rufus* individuals may face risks in the face of global climatic changes (*Faaborg et al., 2010*). In contrast, *A. beryllina* responded to the availability of floral resources in general and was not associated with a particular plant. The permanence of this altitudinal migratory species in the area will depend on multiple factors, including climatic and demographic, and particularly on the supply of floral resources and the competition for such resources.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

Gabriel López-Segoviano conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, and reviewed drafts of the paper.

Maribel Arenas-Navarro performed the experiments, analyzed the data, prepared figures and reviewed drafts of the paper.

Ernesto Vega analyzed the data and reviewed drafts of the paper.

María del Coro Arizmendi conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, and reviewed drafts of the paper.

Table legends

Table 1. Results from GAM model of time and the abundance of Rufous hummingbirds for the three years sampled. The smoother estimated for the second sampling period showed a marginally significant difference.

	edf	Ref.df	Chi.sq	*P*
S(Time)	4.616	5.692	73.104	<0.001
S(Time)Year1	1.000	1.000	1.293	0.255
S(Time) Year2	1.072	2.528	6.922	0.052
S(Time) Year3	1.000	1.000	2.704	0.100

Table 2. Results from GAM model of time and the abundance of Berylline hummingbirds for the three years sampled. The smoother estimated for the first surveyed period marginally differed and third surveyed period differed in comparison to the other two years.

	edf	Ref.df	Chi.sq	*P*
S(Time)	5.218	6.352	10.315	0.109
S(Time)Year1	1.860	1.974	5.908	0.067
S(Time) Year2	1.001	1.102	1.227	0.268
S(Time) Year3	2.425	2.872	13.140	0.017

Table 3. Max Temperature, Min Temperature, Mean Temperature and coefficient of variation per sampling year corresponding yearly period (November–February). Max Precipitation, Min Precipitation, Mean Precipitation and coefficient of variation per sampling year corresponding yearly period (November–February). A considerable increase in rainfall can be observed during the second sampling period from November 2013–February 2014.

	AT (°C)				**AP (mm)**			
	Max	Min	Mean	cv	Max	Min	Mean	cv
2010-2011	22.9	6.4	15.5	0.3487	8	0	0.4	2.4596
2013-2014	26.1	5.4	15.3	0.4641	413.7	0	64.7	0.9961
2015-2016	26.6	3.7	16.4	0.4337	115.2	0	21.4	1.3882

Table 4. Results from the generalized estimating equation (GEE) model with an autoregressive correlation structure to assess relations between the abundances of migratory Rufous hummingbirds and flowering plants (*Salvia iodantha* and *Cestrum thyrsoideum*) and time per sampling year. Variables with Variables with *p* <0.05 are indicated in bold.

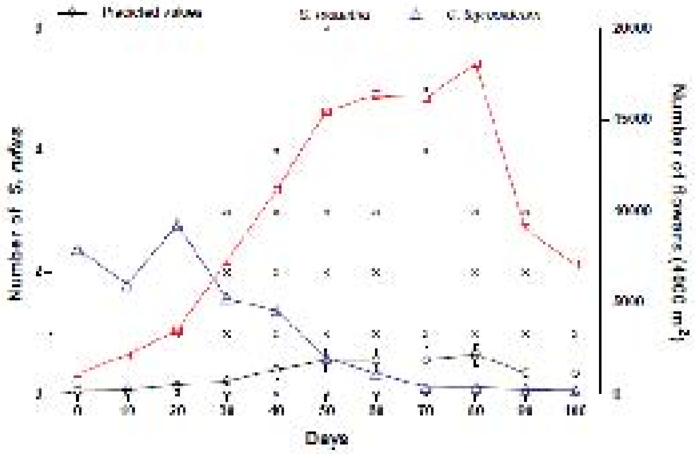
Parameter	Coefficient estimate	Standard error	Wald	*P*
Year 2010-11				
Intercept	-3.841	0.483	64.05	<0.001
S. Iodantha	**0.058**	**0.006**	**117.45**	**<0.001**
C. thyrsoideum	**0.033**	**0.007**	**17.19**	**<0.001**
Time	**0.147**	**0.050**	**8.58**	**0.003**
Year 2013-14				
Intercept	-2.757	0.402	47.06	<0.001
S. Iodantha	**0.056**	**0.004**	**129.80**	**<0.001**
C. thyrsoideum	0.006	0.006	0.86	0.35
Time	0.025	0.49	0.26	0.61
Year 2015-16				
Intercept	-3.947	0.528	55.80	<0.001
S. Iodantha	**0.140**	**0.022**	**39.03**	**<0.001**
C. thyrsoideum	0.053	0.028	3.52	0.060
Time	**0.221**	**0.053**	**17.43**	**<0.001**
S. Iodantha: C. thyrsoideum	**-0.002**	**0.001**	**7.80.**	**0.005**
***S. Iodantha*:Time**	**-0.005**	**0.002**	**7.55**	**0.006**

Table 5. Results from the generalized estimating equation (GEE) model with an autoregressive correlation structure to assess relations between the abundances of Berylline hummingbirds and flowering plants (*Salvia iodantha* and *Cestrum thyrsoideum*) and time per sampling year. Variables with p <0.05 are indicated in bold.

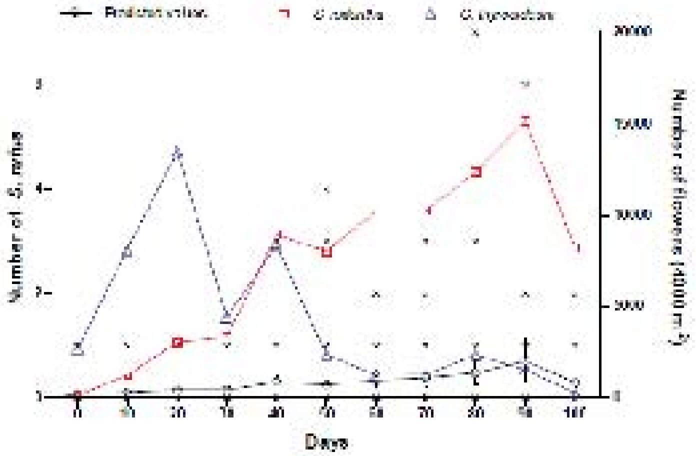
Parameter	Coefficient estimate	Standard error	Wald	*P*
Year 2010-11				
Intercept	-2.224	0.526	17.86	<0.001
S. Iodantha	**0.168**	**0.030**	**30.57**	**<0.001**
C. thyrsoideum	**0.032**	**0.005**	**32.68**	**<0.001**
Time	-0.102	0.089	1.29	0.26
***S. Iodantha*:Time**	**-2.022**	**0.005**	**18.94**	**<0.001**
Year 2013-14				
Intercept	-3.037	0.668	20.63	<0.001
S. Iodantha	**0.185**	**0.035**	**26.60**	**<0.001**
C. thyrsoideum	**0.070**	**0.009**	**60.89**	**<0.001**
Time	**-0.416**	**0.171**	**5.87**	**0.015**
S. Iodantha: C. thyrsoideum	**-0.001**	**0.0003**	**39.29**	**<0.001**
***S. Iodantha*:Time**	**-0.011**	**0.004**	**6.96**	**0.008**
Year 2015-16				
Intercept	-4.459	0.662	45.31	<0.001
S. Iodantha	**0.231**	**0.024**	**92.47**	**<0.001**
C. thyrsoideum	**0.079**	**0.016**	**24.29**	**<0.001**
Time	-0.049	0.073	0.46	0.497
S. Iodantha: C. thyrsoideum	**-0.0005**	**0.0001**	**9.06**	**0.002**
***S. Iodantha*:Time**	**-0.019**	**0.003**	**30.85.**	**<0.001**

Figures

Year 2010-11



Year 2013-14



Year 2015-16

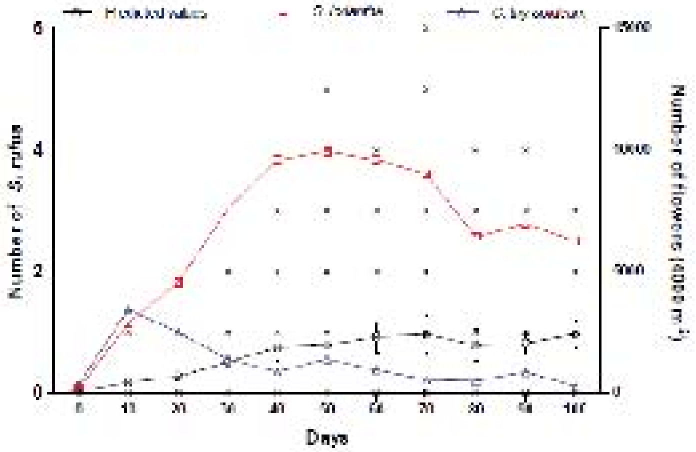
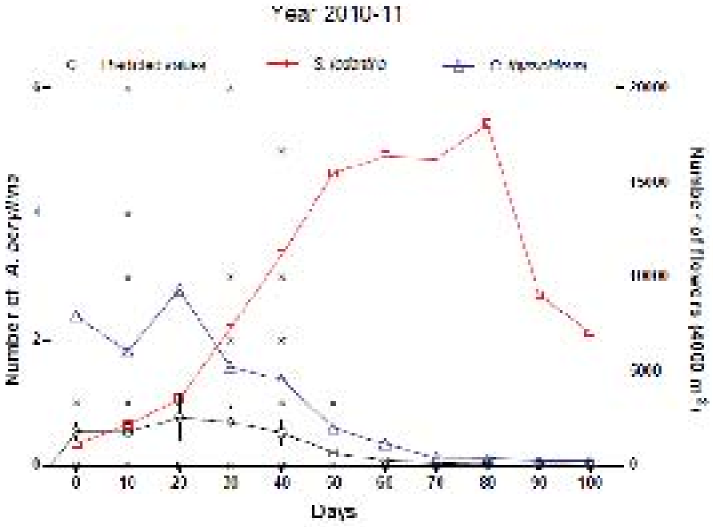
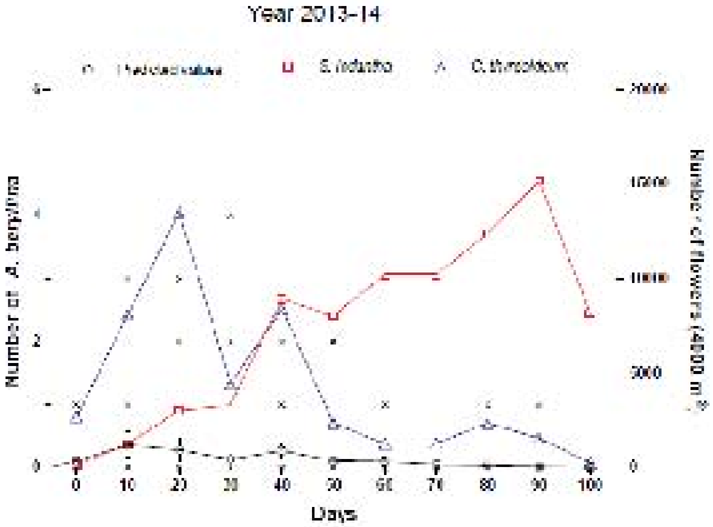


Figure 1. Abundance of Rufous Hummingbirds and flowers through sampling year. Mean (EE) predicted value of Rufous Hummingbirds (Table 4; black circle), number of Rufous Hummingbirds (x), the total of flowers of *S. iodantha* (red square), the total of flowers of *C. thyrsoideum* (blue triangle).


Year 2010-11
Predicted values
S. lobatho
C. thyrsoideum
Number of A. beryllina
Number of flowers (4000 m²)
Days
0
2
4
6
0
5000
10000
15000
20000
0
10
20
30
40
50
60
70
80
90
100


Year 2013-14
Predicted values
S. lobatho
C. thyrsoideum
Number of A. beryllina
Number of flowers (4000 m²)
Days
0
2
4
6
0
5000
10000
15000
20000
0
10
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70
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90
100

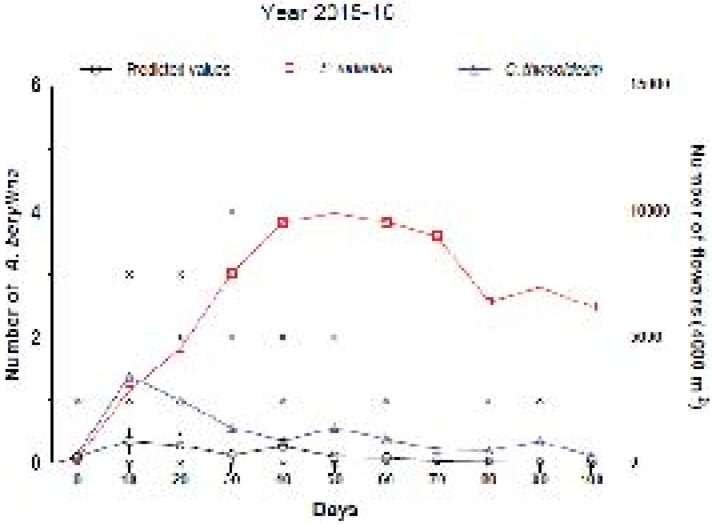
Year 2015-16
Predicted values
S. lobatho
C. thyrsoideum
Number of A. beryllina
Number of flowers (4000 m²)
Days
0
2
4
6
0
5000
10000
15000
0
10
20
30
40
50
60
70
80
90
100

Figure 2. **Abundance of Berylline hummingbirds and flowers through sampling year**. Mean (EE) predicted value of Berylline hummingbirds (Table 5; black circle), number of Berylline hummingbirds (x), the total of flowers of *S. iodantha* (red square), the total of flowers of *C. thyrsoideum* (blue triangle).

CAPÍTULO III. Hummingbird foraging preferences under natural and experimental conditions.

Hummingbird foraging preferences under natural and experimental conditions

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ABSTRACT

Background. Different studies have assessed hummingbirds' preferences for feeding resources, mainly according to floral characteristics such as shape, color, and morphology, in addition to nectar concentration, quantity, and sugar composition of visited flowers. Flower preferences can also depend on hummingbirds' life history with respect to flower use. Hence, latitudinal migrant hummingbirds likely differ from resident species as they are accustomed to use a wider range of resources. In this study, we assessed the flower preferences of a migrant and a resident species that are common during winter in northern Mexico using both observational and experimental methods.

Methods. We assessed hummingbird preferences for the most common plant species in the study region. In particular, we compared the preferences of two common hummingbird species, one resident (*Amazilia beryllina*) and one latitudinal migrant (*Selasphorus rufus*), for the most regionally common plant species, *Cestrum thyrsoideum* and *Salvia iodantha*, which have different flower color yet produce similar energetic rewards. We calculated the Jacob selectivity index from preference data obtained under natural field conditions and under and experimental flight cage in order to evaluate specific interactions.

Results: Both hummingbird species showed different visitation rates to the studied plants under natural conditions. *A. beryllina* visited the yellow flowers of *C. thyrsoideum* more frequently, while *S. rufus* visited the fuchsia flowers of *S. iodantha* with greater frequency. In the flight cages, both species preferred the fuchsia flowers of *S. iodantha* when presented in similar or lesser abundance than the yellow flowers.

Discussion. Under natural conditions, *A. beryllina* visited *C. thyrsoideum* to a greater extent in comparison with *S. iodantha* yet preferred *S. iodantha* in the flight cage when other hummingbirds were absent and even when *S. iodantha* was not the most abundant species. This could confirm that competition is an important process that drives the niche displacement of *A.*

beryllina. On the other hand, the latitudinal migratory species *S. rufus* maintained its preferences for flowers of a familiar color under both natural and experimental conditions.

Conclusions. Our results showed that the feeding preferences of the studied hummingbird species depend on the life history of each species. Therefore, the response of these migratory hummingbird to feeding resources and possible exclusion from their preferred resources, depends on their type of migration, territoriality, and possible associations with local plants.

INTRODUCTION

Hummingbirds are small birds with a high metabolic rate and, consequently, are highly dependent on feeding resources (*del Hoyo et al. 1999*). Feeding resources are selected based on a series of non-exclusive factors, mainly morphological (i.e., flower color, shape, position, and length; *Stiles 1976; Melendez-Ackerman et al. 1997; Lara & Ornelas 2001; Temeles et al. 2009; Handelman & Kohn 2014; Maglianesi et al. 2015*), environmental (i.e., abundance and distribution of hummingbirds and flowers; *Stiles 1976; Abrahamczyk & Kessler 2010*), physiological (i.e., energetic requirements of hummingbirds; *Martínez del Rio 1990; Schondube & del Rio 2003; Medina-Tapia et al. 2012*), demographic (i.e., abundance of other coexisting hummingbirds; *Maglianesi et al. 2015*), and behavioral (i.e., hummingbird foraging strategies and dominance; *Stiles 1976;Stiles & Wolf 1970; Rodríguez-Flores & Arizmendi 2016*) in addition to the quality and quantity of rewards offered by plants (*Temeles et al. 2009; Temeles et al. 2006; González-Gómez et al. 2011*).

In addition, flower color is another factor that has been proposed as an attractant that induces hummingbird visitation (*Stiles 1976; McDade 1983; Paige & Whitham 1985; Melendez-Ackerman et al. 1997; Lunau et al. 2011; Shrestha et al. 2013; Handelman & Kohn 2014*). Flower color provides a visual stimulus that can be detected at a distance to attract hummingbirds to energy-rich nectar sources (*Stiles 1976; Melendez-Ackerman et al. 1997*). In this respect, flower color has been regarded to have coevolved with the visual system of pollinators (*Shrestha et al. 2013*). Fenster (*2004*) stated that flower color is one the most important features in pollination systems, wherein red flowers were reported as being pollinated the most by hummingbirds (*Stiles 1976; Stiles 1981*). In particular, the color red has been shown to attract hummingbirds and repel bees (*Tadey & Aizen 2001;*

Lunau et al. 2011; Muchhala et al. 2014). One explanation rests in the fact that hummingbirds have tetrachromatic vision with photoreceptors sensitive to UV, blue, green, and red wavelengths, while bees have photoreceptors sensitive to UV, blue, and green wavelengths (*Lunau et al. 2011*).

Hummingbirds inhabiting the USA and Canada mainly feed on red flowers (*Healy & Hurly 2001*). Brown and Kodric-Brown (*1979*) showed that hummingbirds in Arizona pollinated plants with flowers that converged in shape, color, quantity, and quality of nectar produced, which reduced hummingbird selectivity and promoted high visitation rates. However, during winter migration, hummingbirds often face a wider array of flower colors, including non-typical ones (*Arizmendi & Ornelas 1990; Arizmendi 2001*). Lara et al. (*2009*) proposed that migrant hummingbird species might learn how to use novel resources, such as yellow flowers, following the lead of resident hummingbird species in their foraging bouts.

Hummingbird preferences for flower attributes have also been assessed experimentally, showing that hummingbirds prefer concentrated nectars (*Roberts 1996; López-Calleja et al. 1997*), conspicuous flowers (*Henderson et al. 2006b; Handelman & Kohn 2014*), and/or flowers that morphologically match their bill morphology (*Stiles 1976; Maglianesi et al. 2015*). The combination of experimental and natural studies can contribute towards a greater understanding of the ecological, physiological, and behavioral patterns that have been observed in studies on the community ecology of hummingbirds (*Stiles 1976; Maglianesi et al. 2015*).

We evaluated two hummingbird species' use of the most abundant plant species in our study region in northwestern Mexico. Specifically, we considered the preferences of two hummingbird species with different migratory status (a resident with seasonal altitudinal migrations, *Amazilia beryllina*, and a latitudinal migrant, *Selasphorus rufus*) for the plant species *Salvia iodantha* or *Cestrum thyrsoideum*, which had flowers of contrasting color (fuchsia and yellow, respectively). These plants represent the most abundant nectar resources during winter in the study region (*López-Segoviano 2012*), and this region also coincides with one of the main migratory pathways of Mexico (*Newton 2007*). The main purpose of this research was to assess the rewards offered by two flowering plants of contrasting color in order to determine both under natural and experimental conditions whether hummingbirds differentially use flowers and or exhibit preferences for certain flowers under isolation experiments. Differential flower use was expected for the two hummingbird species. The latitudinal migrant hummingbird was expected to prefer flowers similar to the ones found near their breeding grounds, i.e., reddish with tubular corollas, while the altitudinal migrant was expected to visit flowers according to their abundance in the region.

METHODS

Study Area

This experimental portion of this study was conducted in the ejido forestal El Palmito Concordia (23°34'16" N; 105°50'15"W), which forms part of the Sierra Madre Occidental in northwestern Mexico and has an altitudinal range of 1800 to 2200 masl. Vegetation types include mostly pine, pine-oak, and oak forest in addition to some cloud forest and riparian vegetation (*Díaz 2005*).

Fourteen hummingbird species have been registered for El Palmito, five of which are considered residents (*Hylocharis leucotis, Lampornis clemenciae, Eugenes fulgens,* *Selasphorus platycercus*, and *Atthis heloisa*), four residents with altitudinal migrations (*Amazilia violiceps, A. beryllina, Cynanthus latirostris*, and *Colibri thalassinus*), and five latitudinal migrants (*Selasphorus rufus, S. sasin, S. calliope, Calypte costae*, and *Archilochus colubris*; *Howell & Webb 1995; López-Segoviano 2012*). *Hylocharis leucotis* is the most abundant resident species, followed by the migrant *S. rufus* (latitudinal) and A. *beryllina* (altitudinal) (*López-Segoviano 2012*). Observations were carried out from November 2010 to January 2011 and experimental from November 2013 to February 2014, November 2014 to February 2015 and November 2015 to February 2016 during the fall and winter seasons.

Studied species

Selasphorus rufus J. F. Gmelin, 1788. Breeds in southern Alaska, western Canada, and northwestern USA and migrates to Mexico during winter (*Arizmendi & Berlanga 2014*). Small size (8.5 cm total length and 2.9–3.9 g; *del Hoyo et al. 1999*). Migrates up to 4000 km from breeding to wintering sites (*Phillips 1875; Calder 2004; Schondube et al. 2004; Healy & Calder 2006*). The migratory pathway of *S. rufus* follows the flowering season of its preferred plants (*Healy & Calder 2006*). However, in Mexico, little is known about the plants and migratory routes that this species uses (*Schondube et al. 2004*).

Amazilia beryllina W. Deppe, 1830. Distributed from southern Arizona throughout mountainous western Mexico (Sierra Madre Occidental, Eje Neovolcánico, Sierra Madre del Sur, and Sierra Madre de Chiapas; *Arizmendi & Berlanga 2014*) from 500 to 1500 masl and up to 3000 masl (*del Hoyo et al. 1999*). An altitudinal migrant that follows the flowering of plant resources (*Des Ganges 1979; Arizmendi 2001*).

Salvia iodantha Fernald 1900. Perennial shrub (height = 50 cm to 3 m) of the Lamiaceae family bearing pink, purple, or fuchsia flowers (*Cornejo-Tenorio & Ibarra-Manríquez 2011*). This plant species has been studied in Manantlán where it is visited by hummingbirds and bumblebees; the latter are nectar robbers (*Méndez Solís 2012*).

Cestrum thyrsoideum Kunth 1818. Perennial shrub (height = 50 cm to 3 m) of the Solanaceae family bearing white or yellow flowers (*Biblioteca Digital de la Medicina Tradicional Mexicana 2009*). In Sinaloa, it is reportedly visited by hummingbirds, mainly *H. leucotis* and *A. beryllina* (*Bribiesca 2012; López-Segoviano 2012*).

Nectar evaluation

To assess nectar quantity and quality, we used the standing crop procedure in which 20 flowers per plant were taken at random during each assessment period between 7:30 and 16 hrs (*Kearns & Inouye 1993*). The standing crop was used to assess nectar availability under natural conditions. Nectar was extracted using microcapillary tubes. After measuring the amount of nectar produced, a drop of nectar was placed in a handheld refractometer (ATAGO model N-1EBX rage 0-32 brix) to measure its sugar concentration. Using nectar quantity and sugar concentration, we calculated the calories produced per flower using the procedure described by Stiles (*1975*). Nectar was extracted from 2235 flowers of *C. thyrsoideum* and 7940 flowers of *S. iodantha* during the winter season (2010-2011).

Natural flower use

To determine flower use by hummingbirds under natural conditions, foraging observations were performed from 21 November 2010 to 11 January 2011 in flower patches of *S.*

iodantha and *C. thyrsoideum*, which have been recorded as the most abundant plant species in the study region overlap their flowering (*López-Segoviano 2012*). Other foraging plants were also observed and recorded, including 135 distinct floral patches of 8 different plant species in the region (*Salvia elegans*, *Cuphea hookeriana*, *C. calcarata*, *Loeselia mexicana*, *Castilleja tenuiflora*, and *Agave inaequidens barrancensis*). Observations were conducted for a period of 60 minutes from an approximate distance of 8 m from the floral patch (*Cotton 1998*). For each foraging bout, hummingbird species, sex, time of arrival, number of flowers visited, and duration of visit were recorded.

Hummingbird preferences

A flight cage (4.5–3.9 m) was placed over a flower patch of *S. iodantha* and *C. thyrsoideum*, each bearing the same number of flowers (e.g., 50 open flowers per flowering plant). Then, one individual of each hummingbird species was introduced into the flight cage and observed for 30 minutes. The number of flowers of each plant species visited by the hummingbird was recorded. This was repeated using different individuals of each hummingbird species (*A. beryllina*, N=21; *S. rufus*, N=18).

A second experiment was subsequently performed, noting that both hummingbird species concentrated their foraging activities on *S. iodantha* under isolation conditions. In this experiment, we covered flower patches bearing double the number of flowers of the non-preferred plant species to test if the abovementioned preference was maintained even in distinct abundance conditions (e.g., 50 *S. iodantha* flowers and 100 *C. thyrsoideum* flowers). Hummingbird visits were registered for different individuals of *A. beryllina* (N=19) and *S. rufus* (N=35), using the same protocol described above.

Preference experiments were performed in the study region during the winter seasons (November–February) of 2010–2011, 2013–2014 and 2015–2016.

Statistical Analysis

To evaluate differences in nectar quality and quantity, we used a Mann-Whitney test after considering the normality and the homogeneity of variance of the data (Kolmogorov-Smirnov tests).

We used Jacob's index of selectivity (D_i) to evaluate and to compare the feeding resources (plant species) used by hummingbirds under natural conditions, expressed as $D_i=(r_i-p_i)/(r_i+p_i -2 r_ip_i)$, where r_i is the proportion of flowers visited by each hummingbird species with respect to all flowers visited by this species and p_i is the proportion of resources represented by this species (*Jacobs 1974; Manly et al. 2002*). The index value (D_i) varies from 1 to -1, where positive values indicate a preference for a feeding item, negative values avoidance of the item, and a near zero value a lack of selectivity (Janeček et al. 2012). To determine resource availability in the region (p_i), we used the proportion of observed flower patches of each plant species with respect to all observed patches (Janeček et al. 2012). From the experimental data, we also calculated Jacob's index (D_i) (Jacobs 1974; Manly et al. 2002). In this case, we used total flowers available in each patch (p_i), and the selectivity index was calculated for each hummingbird evaluated in the flight cage. The resulting values were then analyzed using a Mann-Whitney test after evaluating the normality and the homogeneity of variance of the data.

RESULTS

Nectar

The volume of nectar produced by *S. iodantha* and *C. thrysoideum* did not differ statistically (*Mann-Whitney U*=8732000.00, *p*=0.250; Fig. 1), although the sugar concentration of the nectar of *S. iodantha* flowers was higher (*Mann-Whitney U*=172500.00, *p*<0.001; Fig. 1). The calories produced per flower did not differ statistically between the species (U=8649000.00, *p*=0.068; Fig. 1).

Natural flower use

In the 135 flower patches observed, *A. beryllina* visited flowers of four plant species (*S. iodantha*, *C. thyrsoideum*, *Loeselia mexicana*, and *Agave inaequidens barrancensis*) out of the eight plant species observed. *Amazilia beryllina* concentrated its foraging activities on *S. iodantha* (46.1%) and *C. thyrsoideum* (45.6%). Meanwhile, *S. rufus* only visited flowers of two plant species (*S. iodantha* and *C. thyrsoideum*), visiting *S. iodantha* (87.4%) more frequently in comparison with *C. thyrsoideum* (12.6%).

According to Jacob's index (D_i), *S. rufus* preferred to a greater extent flower patches with fuchsia *S. iodantha* flowers (0.66) and avoided those with *C. thyrsoideum* flowers (-0.47; Fig. 2). On the other hand, *A. beryllina* preferred flower patches with yellow *C. thyrsoideum* flowers (0.34) and avoided those with *S. iodantha* flowers (-0.24; Fig. 2).

Preference experiments

When both plant species were presented with the same number of flowers in the flight cages, *S. rufus* preferred the fuchsia flowers of *S. iodantha* and avoided the yellow flowers of *C. thyrsoideum* (Fig. 3), and *A. beryllina* followed the same pattern, preferring *S. iodantha* and avoiding *C. thyrsoideum* (Fig. 3). The Mann-Whitney test showed that these preferences were statistically significant for *S. rufus* (*Mann-Whitney U*=40.00, *p*<0.0001; Fig. 3) as well as for *A. beryllina* (*Mann-Whitney U*=85.00, *p*=0.0007; Fig. 3). Under isolation conditions, both hummingbird species preferred the fuchsia flowers of *S. iodantha*.

In the second experiment, when *C. thyrsoideum* was presented with twice the number of flowers of *S. iodantha*, the hummingbirds behaved similarly to the prior experiment (same number of flowers of both species), preferring the fuchsia flowers of *S. iodantha*. The statistical analysis showed that both *S. rufus* and *A. beryllina* individuals preferred to feed on fuchsia flowers and to avoid yellow flowers (*S. rufus Mann-Whitney U*=97.00, *p*<0.0001; *A. beryllina Mann-Whitney U*=44.00, *p*<0.0001; Fig. 4). Thus, both hummingbird species preferred *S. iodantha* flowers even when they were half as abundant as *C. thyrsoideum.*

DISCUSSION

Nectar quantity

Our results show that both plant species offered a similar quantity of nectar and calories per flower. However, *C. thyrsoideum* flowers had a lower sugar concentration than those of *S. iodantha* (24% and 29%; Fig. 2). Flowers pollinated by hummingbirds have a sugar concentration of around 20%, differing from those pollinated by bees, which usually have higher sugar concentration between 70% and 80% (*Baker 1975*). Heinemann (*1992*) proposed that the nectar of flowers visited by hummingbirds typically has a sugar concentration of around 26%, which is ideal for hummingbirds as it maximizes the energetic reward. In this case, nectar viscosity may be a factor and should be considered as a proxy of time dedicated to extraction. Similarly, Stiles (*1976*) stated that hummingbirds preferred plants with the highest nectar flow over concentration in native and exotic flowers of California. Also, he proposed that unlike experiments with feeders, where the concentration of sugars is the best measure of the quality of nectar, in the field, the volume of nectar produced could be the best measure of flower quality for ornithophilous species.

Natural and experimental preferences of *A. beryllina*

In this study, we found that the altitudinal migratory hummingbird *A. beryllina* visited the most abundant flowering plants species in the region, *S. iodantha* and *C. thyrsoideum*, as determined by López-Segoviano (*2012*) and Bribiesca (*2012*). Under natural conditions, *A. beryllina* preferred the yellow flowers of *C. thyrsoideum* and avoided the fuchsia flowers of *S. iodantha*. At the study site, *A. beryllina* has been observed to establish its territory in patches of *C. thyrsoideum*, excluding species such as *H. leucotis* and *S. rufus* (*Bribiesca 2012; López-Segoviano 2012*). These flower patches also represent the ones with the most flowers and calories produced (*López-Segoviano 2012*). *Amazilia beryllina* has been considered a territorial species (*Rodríguez-Flores & Arizmendi 2016*) that gains access to the best resources (*Stiles & Wolf 1970*). In this context, the feeding behavior of one hummingbird species can be strongly influenced by the feeding behavior of other hummingbirds, depending on the relative dominance and abundance of different species in the region (*Sandlin 2000a*).

However, when preferences were tested experimentally, *A. beryllina* individuals preferred to feed on the fuchsia flowers of *S. iodantha*. Maglianesi et al. (*2015*) stated that a hummingbird may change its natural feeding preference when subjected to experimental conditions and attributed this to the aggressive interactions that may occur with other hummingbirds under field conditions. In this sense, feeding preferences can be strongly influenced by the dominance strategies and the abundances of other hummingbirds (*Temeles et al. 2006*). Thus, hummingbirds are capable of adjusting their foraging niches depending on the abundance of flowers, the abundance of other hummingbirds, and their dominance strategies (*Rodríguez-Flores & Arizmendi 2016*).

Furthermore, the nectar of *C. thyrsoideum* could contain some secondary metabolites, like alkaloids, that repel hummingbirds. Within the Solanaceae family, many plants contain alkaloids in their fruits, leaves, stems, and even in their flowers (*Scott et al. 1957*). In fact, three plant species of the genus *Cestrum* have been reported as having an alkaloid in their leaves (*C. parqui, C. albotomentosum*, and *C. nocturnum*) and *C. parqui* in its flowers (*Scott et al. 1957*). In *Nicotiana attenuata*, the gene that produces the nicotine alkaloid was isolated, and the variation in the presence of nicotine among plants was shown to possibly have consequences on the pollinating behavior of hummingbirds (*Kessler et al. 2012*). In another study in South Africa, nicotine was added to artificial nectar, and the tolerance of nectarivorous *Pycnonotus tricolor*, *Cinnyris talatala*, and *Zosterops virens* to the alkaloid depended on the amount of nicotine and the sugar concentration of the nectar (*Lerch-Henning & Nicolson 2013*). Similarly, when a small amount of nicotine (10–25 µM) was added to nectar in artificial flowers, hummingbirds did not differentiate between flowers with and without nicotine, but when the amount of nicotine increased (50 µM), hummingbirds clearly rejected the flowers (*Kessler et al. 2012*). Therefore, future studies should be carried out to determine the non-energetic characteristics of nectar since these can influence the foraging behavior of hummingbirds and their feeding preferences.

Natural and experimental preferences of *S. rufus*

The latitudinal migratory hummingbird *S. rufus* preferred the fuchsia flowers of *S. iodantha* and discriminated the yellow flowers of *C. thyrsoideum*, confirming that it prefers to feed on a more familiar color resource. In this case, reddish flowers are more common in *S. rufus* breeding sites (*Brown & Kodric-Brown 1979*). However, this result could be a consequence of the feeding behavior dynamics of the regional hummingbird community. In fact, competitive pressures could be affecting the foraging decisions of these hummingbirds (*Sandlin 2000a; González-Gómez et al. 2011*) since the presence of a dominant hummingbird may influence the apparent preferences of subordinate hummingbirds (*Sandlin 2000b; Muchhala et al. 2014*). Accordingly, a hummingbird of low dominance can present an apparent preference for places with poorer resources (*Stiles 1976; Sandlin 2000b*). This dynamic could lead the subordinate *S. rufus* to forage in places with less energetic rewards in terms of amount of nectar per flower and number of flowers (*Des Ganges 1979; López-Segoviano 2012; Rodríguez-Flores & Arizmendi 2016*).

However, during the flight cage experiment with *S. rufus*, a preference for the fuchsia flowers of *S. iodantha* was confirmed, while this hummingbird discriminated against the yellow flowers of *C. thyrsoideum*. Thus, *S. rufus* likely fed on flowers of familiar color (*Brown & Kodric-Brown 1979; Ornelas & Lara 2015*), even when more yellow flowers were available. A study with *Mimulus aurantiacus*, a plant species with different flower colorations, showed that hummingbirds prefer to feed on flowers with stronger colors (orange-red) and discriminate flowers of opaque colors (yellow; *Heinemann 1992*). Similarly, *S. rufus* and *S. platycercus* prefer to visit red flowers (*Ipomopsis aggregata*) rather than flowers of paler colors (*I. tubatenuis* and hybrids) when the morphology and rewards of these flowers are similar; however, this may change if pale flowers have a greater amount of nectar (*Melendez-Ackerman et al. 1997*). Healy and Hurly (*2001*) established that color plays a minor role in the flower preference of *S. rufus* but can influence the speed with which this hummingbird learns the location of flowers with greater rewards.

For a hummingbird with low dominance that requires energy to carry out its latitudinal migration, the ability to rapidly learn which resources are the best is essential. In fact, *S. rufus* has been proven to incorporate information learned from the environment in its feeding behavior (*Healy & Hurly 1995; Healy & Hurly 2001; Henderson et al. 2006a*). For example, *S. rufus* has been shown to remember the characteristics of a visited floral patch: its location, amount of rewards, and color of its flowers (*Healy & Hurly 1995; Healy & Hurly 2001; Hurly & Healy 2002; Healy & Hurly 2004; Henderson et al. 2006a*;). Hurly et al. (*2010*) suggested that *S. rufus* uses the intrinsic visual cues of a flower to confirm that they have arrived at the correct place and are able to relocate exactly where they fed the previous year. Remembering the location of a place with shrubs or groups of flowers from one season to another is of great importance for a long-lived animal in a habitat with short seasonal blooms (*Stiles 1976*). Thus, migratory birds incorporate information learned on their migratory route and are able to afterwards locate and remember the best places in terms of resources (*Newton 2007*). In the context of the present study, adult *S. rufus* individuals may be remembering that in the study region, *S. iodantha* flowers are the best feeding resource.

CONCLUSION

Our results showed that a hummingbird species changed its feeding preference when another hummingbird species was excluded from resources. Under natural conditions, foraging niches are shaped by preferences but are also balanced with the costs of dominance. Cage experiments using captive hummingbirds may not always be representative of preferences under natural conditions. Therefore, the combination of both experimental and observational studies allows us to better understand hummingbirds' feeding behavior (*Stiles 1976; Maglianesi et al. 2015*).

In particular, our study showed that *S. rufus* had a strong preference for feeding on *S. iodantha* flowers in both natural and experimental environments. *Salvia iodantha* has flowers of a more familiar color for this latitudinal migratory hummingbird. In addition, *S. iodantha* flowers could be the best food source for *S. rufus* for several reasons: 1) *Salvia iodantha* flowers are the most abundant resource in the region. 2) The phenology of *S. iodantha* correlates with the dates of *S. rufus* migration in the region (*López-Segoviano 2012*). Finally, 3) the largest and most dominant hummingbirds in the region were observed to mainly use floral patches of *A. inaequidens* and *C. thyrsoideum* (*López-Segoviano* 2012).

Our results showed that the feeding preference of the studied hummingbird species depended on the life history of each species. The response of these migratory hummingbird species to exclusion from preferred feeding resources will depend on the type of migration they perform, their territoriality, and their possible associations with local plants. Further studies are needed to better understand the feeding strategies of *Amazilia beryllina* and *Selasphorus rufus*.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

Gabriel López-Segoviano conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, and reviewed drafts of the paper.

María del Coro Arizmendi conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, and reviewed drafts of the paper.

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Figures

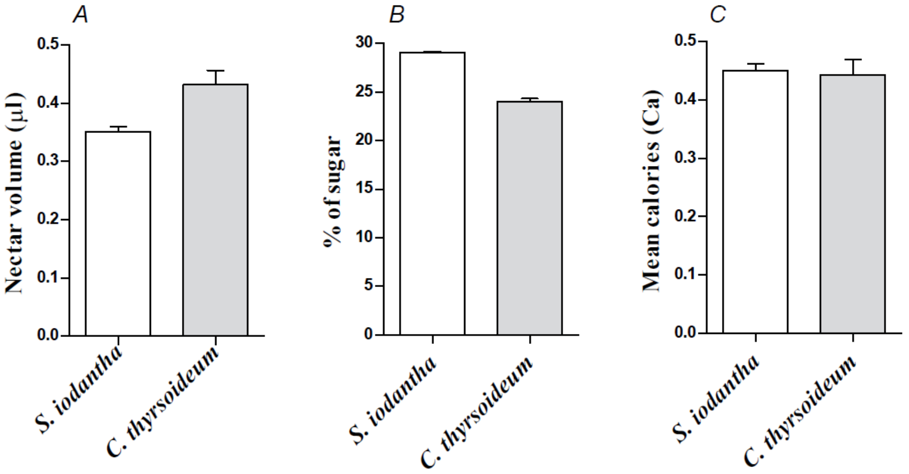

Figure 1. Mean values (SE) for nectar A) volume, B) sugar concentration, and C) calories for *S. iodantha* and *C. thyrsoideum* flowers. The calorie content of *S. iodantha* and *C. thyrsoideum* flowers is not significantly different.

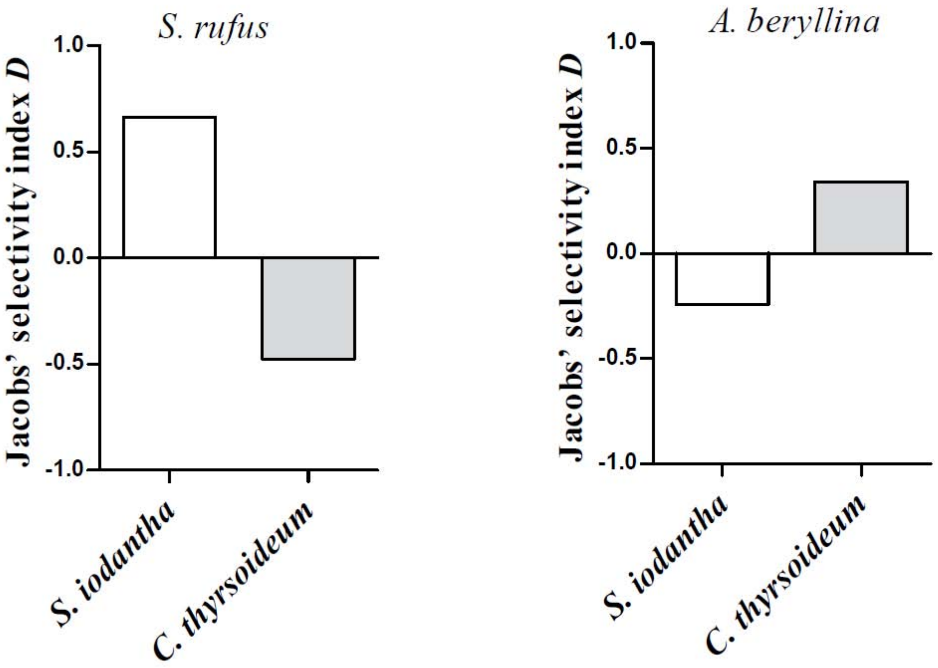

Figure 2. Jacobs' selectivity indices (D) for the hummingbirds *A. beryllina* and *S. rufus* considering *S. iodantha* and *C. thyrsoideum* flowers in the field. The two species have different feeding preferences.

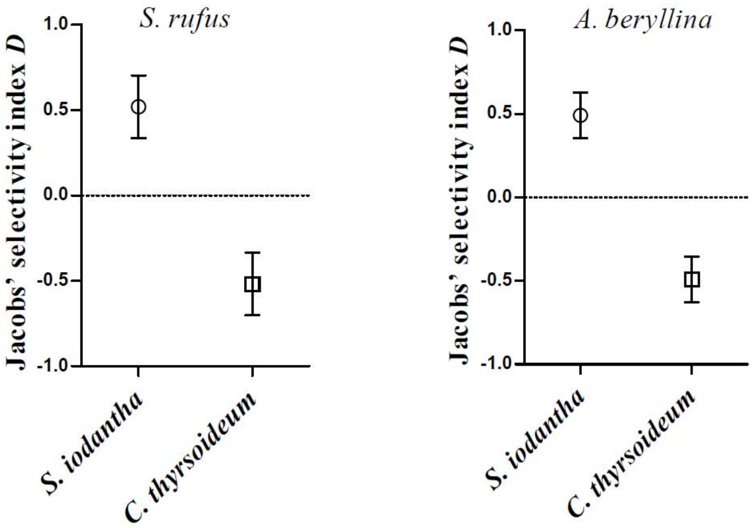

Figure 3. Mean values (SE) of the Jacobs' selectivity indices (D) for the hummingbirds *A. beryllina* and *S. rufus* considering a similar quantity of *S. iodantha* and *C. thyrsoideum* flowers under experimental conditions. There is a clear preference for the fuchsia flowers of *S. iodantha*.

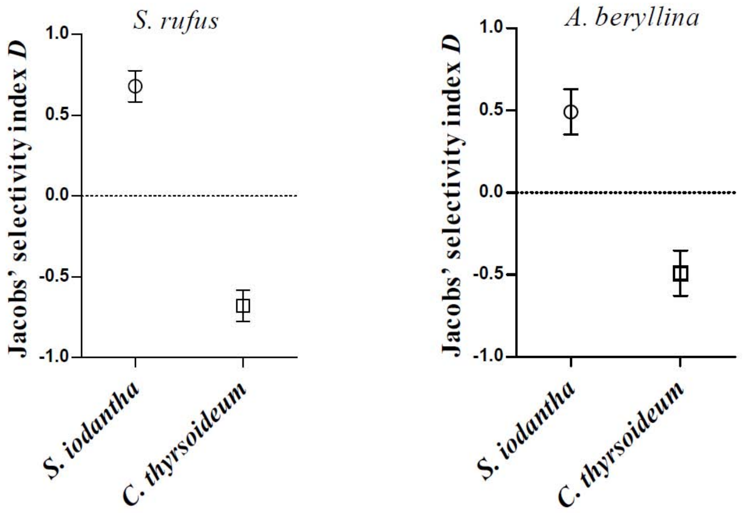

Figure 4. Mean values (EE) of the Jacobs' selectivity indices (D) of the hummingbirds *A. beryllina* and *S. rufus* considering *S. iodantha* and *C. thyrsoideum* flowers when the latter is twice as abundant under experimental conditions. A preference is observed for the fuchsia flowers of *S. iodantha* by both species of hummingbirds.

CAPÍTULO IV. Hummingbird-Plant Interactions in an altitudinal gradient in northwestern Mexico.

Será sometido a Biotropica

López-Segovian, Villa-Galaviz, and Arizmendi Hummingbird-Plant Interactions

Hummingbird-Plant Interactions in an altitudinal gradient in northwestern Mexico

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ABSTRACT

The interaction between hummingbirds and plants generate networks of complex mutualistic assemblages, which give us a better perspective of community interactions. In the present study, we analyzed the properties of three hummingbird-plants networks within an altitudinal gradient from 148 a 2218 masl. First, we evaluated network structure (specialization, connectance and nestedness) and how it changes depending on vegetation type. Then we determined the importance of the species that constitute each network (hummingbirds and plants). Finally, we analyzed if the abundance of migratory hummingbirds was correlated with the richness and abundance of floral resources. We established 30 observation and flower count plots on each of the altitudinal site (Temperate Forest, Ecotone, and Tropical Deciduous Forest) and registered once a month for 11 months. There were 1050 interactions between 20 hummingbird species and 64 plant species. We found that the parameters of specialization, connectance and nestedness are different in each altitudinal site. Hummingbird core species in networks were resident species and core plants were ornithophilous and non-ornithophilous. The abundance of migratory species was correlated with richness and abundance of flowers and other parameters of the structure of the network as the number of interactions and links. Most hummingbird species were found at two altitudinal sites, but these species played different roles at each site. We find several species of non-ornithophilous plants that are cores and of great importance in the structure of the network. Forest network was strongly correlated with the abundance of migratory hummingbird species and this correlation decreases as we go down to the Tropical Deciduous Forest.

Key words: biotic interactions; Ecotone; flower resources; hummingbird migration; mutualistic networks; ornithophilous; Sierra Madre Occidental; Temperate Forest; Tropical Deciduous Forest.

RESUMEN

Las interacciones entre colibríes y plantas generan redes mutualistas complejas, las que al ser analizadas nos pueden dar una mejor perspectiva de la estructura de la comunidad. En el presente estudio se analizaron las propiedades de tres redes de colibríes y sus plantas en un gradiente altitudinal de 148 a 2218 msnm. Primero, evaluamos la estructura de la red (especialización, conectividad y anidamiento) y cómo cambia dependiendo del tipo de vegetación. Luego determinamos la importancia de las especies que constituyen cada red (colibríes y plantas). Finalmente, se analizó si la abundancia de colibríes migratorios se correlaciona con la riqueza y la abundancia de recursos florales. Se establecieron 30 parcelas de observación y de conteo de flores a lo largo del gradiente altitudinal (bosque templado, ecotono y selva baja) y se registró una vez al mes durante 11 meses. Se registraron 1050 interacciones entre 20 especies de colibríes y 64 especies de plantas. Encontramos que los parámetros de especialización, conectancia y anidamiento son diferentes en cada sitio altitudinal. Las especies núcleo de colibríes fueron especies residentes y las plantas núcleo presentaron síndrome ornitófilo y no-ornitófilo. La abundancia de especies migratorias se correlacionó con la riqueza y abundancia de flores y otros parámetros de la estructura de la red como el número de interacciones y enlaces. La mayoría de las especies de colibríes se encontraron en dos sitios altitudinales, pero estas especies desempeñaron diferentes papeles en cada sitio. Encontramos diversas especies de plantas no-ornitófilas que son núcleo y de gran importancia en la estructura de la red. La red de Bosques estuvo fuertemente correlacionada con la abundancia de especies de colibríes migratorios y esta correlación disminuye a medida que bajamos a la selva seca.

THE POSITIVE INTERACTION BETWEEN TWO SPECIES IS CALLED MUTUALISM; there are many examples of mutualistic relationships in nature (Ricklefs & Miller 1999). In fact, these interactions play a fundamental role in the functioning of many ecosystems, as much of the reproduction and successful recruitment of many plant species depends on them (Jordano *et al*. 2009). For example, birds perform mutualistic interactions such as pollination and seed dispersal, generating complex networks of interaction (García 2016). The analysis of the complex networks of interactions allows us to integrate systems giving a better understanding of the complexity of communities (Jordano *et al.* 2003, Bascompte & Jordano 2007, Jordano *et al*. 2009, Garcia 2016). In addition, we can determine the susceptibility of communities to disturbance and which species are key for conservation (Bascompte & Jordano 2007, Verdu & Valiente-Banuet 2008, Jordano *et al*. 2009, García 2016). The relationship between hummingbirds and plants is a good example of a mutualism. This relationship is the result of many adaptations between the flowers and the vector of their pollen (Schuchmann 1999, Jordano *et al*. 2009). Interactions between hummingbirds and plants generate networks of complex mutualism interactions (Jordano *et al*., 2009). Networks that are constructed with interactions of hummingbirds and plants tend to be nested, a classic feature in pollinator interaction networks (Bascompte *et al*. 2003, Jordano *et al*. 2009, Gonzalez & Loiselle 2016). Nested networks have as their main characteristics to present hyperconnected species considered generalists and species with few connections that are considered specialists (Bascompte *et al*. 2003, Bascompte & Jordano 2007, Jordano *et al*. 2009, García 2016). Likewise, the level of functional specialization between hummingbirds and ornithophilous plants has been analyzed within the network of mutual interaction (Dalsgaard *et al*. 2008). It has been found that the hummingbird- plant interaction networks closely to the tropics tend to be more specialized than those at high latitudes (Dalsgaard *et al*. 2011). Similarly, high mountain regions are less specialized than low regions (Maglianesi *et al.* 2014).

It has been proposed that hummingbird communities depend on the abundance of flowers as the main factor determining their abundance and diversity patterns (Feinsinger 1976, Wolf *et al.* 1976, Abrahamczyk & Kessler 2015). The supply of floral resources can influence the behavior of hummingbirds (Rodríguez-Flores & Arizmendi 2016) and promote local and regional migratory movements (Arizmendi & Ornelas 1990). In fact, the arrival of the species at the replenishment sites coincides with the flowering of the plants in the region (Gass 1979, Hixon *et al*. 1983, Arizmendi & Ornelas 1990, Heinemann 1992). In addition, orographic elevations impose a challenge on hummingbird species as a filter that determines their establishment (Graham *et al.* 2009). Since ascending or descending in altitude implies a change in both climatic and vegetation composition that influence the hummingbird assemblage (Graham *et al.* 2009), and topology of pollinator interaction networks (Ramos-Jiliberto *et al*. 2010).Therefore, in the present study we analyzed the properties of three hummingbird communities and their relationships with plants within an altitudinal gradient in NW Mexico. Each of the sampling sites was located at different altitudes and consisted of different types of vegetation: temperate forest, ecotone with elements of pine-oak and tropical semideciduous forest, and tropical deciduous and semideciduous forest. We first evaluate the structure of the interaction networks (specialization, connectance and nestedness) and how this structure changes depending on the altitudinal sites. Then we determine the importance of the species that constitute each of the interaction networks both plants and hummingbirds. Finally we establish if the abundance of migratory hummingbirds correlates with the richness and abundance of floral resources and the number of interactions and links in the three altitudinal sites.

METHODS

STUDY AREA.—This study was carried out within the Sierra Madre Occidental at the municipality of Concordia, Sinaloa; in three altitudinal sites constituted by different types of vegetation. In the Sierra Madre Occidental (SMO) we can find a great variety of types of climates and vegetation distributed at different altitudinal intervals (González-Elizondo *et al*. 2012). The first site was located in the lower part of the SMO between 148 and 289 masl, consisting of tropical semideciduous forest, tropical deciduous forest, riparian vegetation, and secondary vegetation (Monte Mojino, Fig. 1). The second was located in the middle zone between 1131 and 1423 masl at the transition from oak-pine forest, oak forest and tropical semideciduous forest; in the same way we found riparian and secondary vegetation (Guacamaya, Fig. 1). The third site was located in the upper part of the SMO between 1800 and 2218 masl, and it was covered by pine forest, oak-pine, cloud forest, riparian and secondary vegetation (Palmito, Fig. 1). Although in all sampling sites, we can find secondary and riparian vegetation, this vegetation is characteristic of each study site and has little similarity in its composition with the other study sites. We choose each sample site considering vegetation type and greater altitudinal variability.

SAMPLING OF THE HUMMINGBIRD-PLANT INTERACTIONS.—To assess the interactions of hummingbirds and plants, we used circular plots that allowed us to represent the environmental and altitudinal heterogeneity of each of the altitudinal sites. Thirty plots were distributed in each altitudinal site separated at least by 200 meters. In each plot interactions between hummingbirds and flowering plants were recorded for 10 minutes by a team of two people. Subsequently a second team recorded the interactions by another 10 min. During each period of 10 minutes the hummingbird species that visited the plants were recorded; number of flowers visited was not counted. Records began at dawn and ended before noon, with a total of 330 hours of observation.

HUMMINGBIRD SAMPLING.—To determine the abundance of hummingbird species, in the 90 plots already established, hummingbird species and their abundance were recorded. In each counting plot, the number of hummingbirds, their species and sex (when possible) were recorded in a 25 meters radius for 10 minutes of focal observation using the method (Hutto *et al*. 1986).

FLOWER SAMPLING.— To determine the number of flowers per plant species visited along the gradient, 90 transects of 2 x 25 meters were established within each counting plot, where all open flowers of each species of plant that were visited by hummingbirds were counted. Flower sampling, abundance of hummingbirds and interactions of hummingbirds-plants were performed each month from November 2015 to September 2016. In total we registered 90 counting plots 11 times.

STATISTICAL ANALYSIS.—In order to analyze the properties of bipartite interacting networks, we used the Bipartite package (Dormann *et al*. 2008) and the R program (2017). The characteristics of the network topology analyzed were: specialization (H_2), nestedness (NODF) and connectance (C). We calculated network-level specialization by using the specialization index H_2. This index is defined as the diversity of species interactions within the network (H_2), considering the minimum (H_2min) and maximum (H_2max) number of possible interactions (Bluthgen *et al*. 2006, Dormann *et al*. 2009). Nestedness is a topological pattern that allows to see the separation of the systematic arrangement of the species by niche width (Guimarães & Guimarães 2006, Dormann *et al*. 2009). We calculated nestedness using the method of nestedness overlap and decreasing fill (NODF). If values of NODF are close to 0 there is no evidence of aggregation in the matrix and when it approaches 100 interactions are increasingly nested (Dormann *et al*. 2009). In addition, we evaluated whether the NODF of each of the networks is different than expected by chance, performing a null model for nestedness values with 1000 network replicates generated randomly, considering the observed species richness and heterogeneity of the interaction (Bascompte *et al*. 2003). Finally, we determined the connectance (C), where C is the fraction of interactions recorded with respect to the total possible. This is a characteristic of each community (Dormann *et al*. 2009) for which communities more interconnected tend to be more stable (Dunne *et al*. 2002). Connectance values go from 0 to 1 i.e. if each bird visited flowers of each plant species, then the connection would be equal to 1 (Gonzalez & Loiselle 2016).

In order to determine the importance of the species within the interaction networks, we used two indexes: Normalised degree, (ND) and core-periphery (Gc) analysis. The ND of each species is the proportion of species that interacts with the total possible in the network (Martín González *et al*. 2010). While Gc the core (Gc) and periphery species of each network are determined by: $Gc = (k_i/k_{mean})/ \sigma_k$ where k_i is mean number of links for a given hummingbird-plants species, k_{mean} mean number of links for all the hummingbird-plant species in the network and σ_k is the standard deviation of the number of links for hummingbirds and plants species (Dáttilo *et al*. 2013). Gc greater than one indicates species with greater number of interactions in relation to other species of the same trophic level, and can be considered as constitutants of the generalist nucleus (Dáttilo *et al*. 2013). In contrast Gc smaller than one, are species with less number of interactions in relation to other species of the same trophic level and are considered as species that constitute the periphery of the network (Dáttilo *et al*. 2013).

We used generalized linear models (GLM) to evaluate the relationship between the number of latitudinal migratory hummingbird species (*Selasphorus rufus, S. sasin, S. calliope, Archilochus colubris, A. alexandri, Calypte costae* and *Calothorax lucifer*; Howell 2003, Arizmendi & Berlanga 2014) and the richness and abundance of the visited flowering plants, the number of interactions and links. The model was done with a Poisson distribution using the R (2017) software. In addition, other models were constructed with the same variables, to which the non-ornithophylous plant species (sensu Faegri & van der Pijl 1979) were excluded. Each model was evaluated for over-dispersion, which was corrected (if applicable) using a Quasipoisson distribution (Crawley 2007).

RESULTS

NETWORK STRUCTURE—In the three study sites, 1050 interactions were recorded between 20 species of hummingbirds and 64 species of plants belonging to 28 families. The plant families were Lamiaceae (8 species), Convolvulaceae (6 species), Fabaceae (5 species), Bromeliaceae (5 species) and Plantaginaceae (4 species, Table S1). The network were constructed with 7 hummingbird species and 24 plants species in the lowland (Monte Mojino), 16 hummingbird species and 25 plants species in ecotono (Guacamaya) and 12 hummingbird species and 23 plants species in temperate forest (Palmito; Fig. 2, 3 and 4). The analysis of the characteristics of the networks in the three sites showed that Guacamaya presents a higher degree of specialization and a lower degree of connectance (Table 1). While in the lowland the network showed the highest nestedness and connectance but the lowest degree of specialization. It should be noted that nestedness in the Monte Mojino was not different from that expected by chance and in the Guacamaya and the Palmito nestedness is less than expected by chance (Table 1).

IMPORTANCE OF THE SPECIES—When analyzing the specific properties (ND, Gc) of each species of hummingbirds within the web, we found that most of the species are recorded on two altitudinal sites (*A. violiceps* and *S. rufus* on all three sties). But each species plays different role within each network; the species of hummingbirds that acted as core species having higher ND in each network were different. In the Monte Mojino core species were *C. latirostris* and *A. rutila* having the highest ND; in the Guacamaya the core species and with the highest ND was *A. beryllina* and in the Palmito *H. leucotis* and *L. clemencia*e were core species that presented the largest ND (Table 2).

When evaluating the properties of plant species within the networks at each sampling site, we found that the core and ND species of the three networks were of different growth habits. For the Monte Mojino network we found that two climbing plants (*Ipomoea bracteata* and *Combretum farinosum*) and three trees (*Pseudobombax ellipticum, Erythrina lanata* and *Ipomoea arborescens*; Table S2) were core species with higher ND. In the Guacamaya we found an herbaceous (*Lopezia semeiandra*) and two trees (*Inga vera* and *Ipomoea murucoides*) as the core species with greater ND (Table S2). In the Palmito, we found that a shrub (*Salvia iodantha*), a hemiparasitic (*Psittacanthus calyculatus*) and a species of sprouting growth (*Agave maximiliana*) were the core species with the highest ND (Table S2).

MIGRATORY HUMMINGBIRD— With the help of GLM analysis we found that the number of latitudinal migratory hummingbirds was related to richness (X^2 = 18.94, df = 3, R^2 = 0.366, P <0.001) and abundance of flowering plant species (X^2= 80572, df = 3, R^2 = 0.574, P <0.001). The relationship between the number of latitudinal migratory hummingbirds and the number of interactions (X^2 = 430.08, df = 3, R^2 = 0.491, P <0.001) and linkages (X^2 = 73.23, df = 3, R^2 = 0.475, P <0.001) was significant, however this relation changes depending on the altitudinal sites (Table 3).

When we excluded the non-ornithophilous plants from each network of interactions, GLM analysis showed a similar relationship of the number of latitudinal migratory hummingbirds with richness (X^2 = 24.16, df = 3, R^2 = 0.315, P < 0.001) and abundance of flowers (X^2 = 86411, df = 3, R^2 = 0.612, P < 0.001) and, number of interactions (X^2 = 509.13, df = 3, R^2 = 0.503, P < 0.001) and linkages (X^2 = 17.23, df = 3, R^2 = 0.380, P < 0.001). In addition, we found this relation is significant in the Palmito for all models, whereas in the Monte Mojino there was no relationship and in Guacamaya, we only found a relation with the number of links (Table 4).

DISCUSSION

NETWORK STRUCTURE—Our study revealed that the interaction network of hummingbird-mid-zone plants (Guacamaya; Table 1) presented the highest index of specialization. Similar to the results of Maglianesi *et al*. (2014), they found the highest specialization index of the network of hummingbird-plant interactions at the medium elevation (1000 m).

They establish that the specialization of the species within the web is a product of the morphological characteristics of hummingbirds, mainly the length and the curvature of the bill (Maglianesi *et al*. 2014). However, it has been established that in temperate regions of North America hummingbird species are morphologically convergent (Kodric-Brown *et al*. 1984, Brown & Bowers 1985) and interaction networks are less specialized than in tropical regions (Dalsgaard *et al*. 2011). In our study region, the morphology of the hummingbirds' bill is very similar in its curvature but differ in their feeding behavior and migratory status (López-Segoviano *et al*. 2017). In fact, the aggressive behavior of hummingbird species can influence the feeding preferences of different species of hummingbirds, depending on their level of aggressiveness (López-Segoviano *et al*. 2017).

On the other hand, we found that the networks of the Palmito (1800-2218 masl) and the Monte Mojino (148-289 masl) presented a similar indeces of specialization. Contrary to the study by Maglianesi *et al*. (2015) where they found that hummingbird-plant network are less specialized in highlands (2000 masl) in relation to lowlands (50 masl). Due to a low supply of plants with nectar available and a high rate of interspecific competition, that occurs in the mountain in Costa Richa, which could influence the low specialization (Maglianesi *et al*. 2015). However, in our study in the temperature forest (Palmito), we found a greater richness and abundance of migratory hummingbirds and a greater seasonality of floral resources, which may influence the parameters of the interaction network (Ramos-Robles *et al*. 2016). In this case, the matching of migratory hummingbirds and the floral phenology of some plants in the Palmito region can be considered as a co-evolutionary process (Feinsinger 1978), which could be related to the species specialization in the network (Benadi *et al*. 2014). Thus, the ecological species specialization in the plant-animal interaction networks influences multiple non-exclusive mechanisms (Maglianesi *et al*. 2014).

On the other hand, in Monte Mojino we find the highest nestedness index but this was similar to what was expected by chance, while in the Palmito and Guacamaya nestedness was lower than expected by chance. Unlike the network of Central Mexico that is highly nested (Lara-Rodriguez *et al*. 2012). The network nestedness is a measurmente of network cohesion, where low nestedness (such as those in the study region) are more susceptible to disturbance, unlike highly nested networks founded in temperate studies (Bascompte *et al*. 2003, Bascompte & Jordano 2007). Low nestedness in the region's networks may be an effect of variation on latitudinal migratory hummingbird species at sampling sites and of seasonality of floral resources. Because network parameters such as nestedness have been found to be negatively related to the proportion of migratory birds in frugivorous networks (Ramos-Robles *et al*. 2016). In fact, the structure of the hummingbird network of Peruvian high mountain (Andes) is strongly influenced by the phenology of the species that make up the network (Gonzalez & Loiselle 2016).

Our study revealed that the Monte Mojino connectance was higher than that of the Palmito and Guacamaya networks. A study in the Tehuacán-Cuicatlán Biosphere Reserve found that the connectance of the hummingbird interaction networks can be affected by the level of aridity or conservation of the place (Ortiz-Puido *et al*. 2012). Other study with several networks of central Mexico showed that the connectance of more conserved sites have low values, while those of disturbed areas have high connectance values (Lara-Rodriguez *et al*. 2012). In the case of our study, the level of disturbance is similar in the three altitudinal sites but we found smaller numbers of hummingbird species in Monte Mojino than in the other two sites. This can influence the connectance, since it decreases as species richness increases in the network of plant-pollinator interactions (Jordano 1987). In pollination networks in general, the connectance increases as the size of the network decreases (Olesen & Jordano 2002). Thus, at the local level species richness affects individual species and their biotic interactions (Olesen & Jordano 2002), directly influencing the structure of the interaction network.

IMPORTANCE OF THE SPECIES—Most species of hummingbirds are found in two altitudinal sites, however these species played different roles on each site (Table 2). Because species identity at the core of a network may change geographically by local species variation in relation to regional species groups (Bascompte & Jordano 2007). Thus, traits of hummingbird species can mediate the co-occurrence patterns of a hummingbird species through an environmental gradient (Graham *et al*. 2012). Similarly, the assemblage of hummingbird species depends on their morphology, functional roles and degree of specialization (Maglianesi *et al*. 2015). In addition, environmental variables and vegetation structure are important factors in the structuring of hummingbird communities (Graham *et al*. 2009). Core hummingbird species with higher index of normalized degree were the most abundant and resident species in the region (*A. beryllina*, *A. rutila*, *C. latirostris*, *H. leucotis* and *L. clemenciae*). Other studies in Mexico with interaction networks found that the species with greater abundance visited more species of plants (Ortiz-Puido *et al*. 2012, Martinez-Garcia & Ortiz-Pulido 2014). In the same way, in our study we found that resident species and most abundant species interact with a greater number of plant species supporting the idea that the generality of species is related to its abundance (Fort *et al*. 2016).

The core plants in the networks of the three altitudinal levels are of various growth habits. But, not all core plant species for the interaction network have ornithophile syndrome. For example, for core plant species such as *Agave maximiliana*, *Inga vera*, *I. arborescens* and *I. murucoides*, hummingbirds are not their main pollinators. In fact, direct observation methods have a strong limitation to represent the importance of pollinators to plants (García 2016). Thus, there is an unbalanced dependence between the community of hummingbirds and the plants from which they feed. However, the preference of hummingbirds for a type of plant could be influenced by the quality of the reward and the competition for this resource (Maglianesi *et al*. 2015, López-Segoviano *et al*. 2017). Maruyama *et al*. (2013) found in a Brazilian Cerrado that non-ornithophylous plants are as important for feeding hummingbirds as ornithophilous plants. They establish that flowers with bumblebee or bats/hawkmoth syndrome are commonly visited by hummingbirds and contribute greatly to the total availability of energy in their habitats (Maruyama *et al*. 2013).

In addition, other studies in Mexico have found a large number of non-ornithophylic plants within the hummingbird-plant interaction networks (Lara-Rodriguez *et al*. 2012, Martinez-Garcia & Ortiz-Pulido 2014), many of which are also core species of the network (Lara-Rodriguez *et al*. 2012). Maruyama *et al*. (2013) stated that studying the effect of the energy supply of non-ornithophylous flowers is important to better understand hummingbird communities. As is the case of the present study where the non-ornithophilous species are of great importance for the community of hummingbirds and the structure the interaction network.

MIGRATORY HUMMINGBIRD— Contrary to that established for frugivory networks where some species of migratory birds are the core species (Ramos-Robles *et al*. 2016), we did not find any of the seven species of migratory hummingbirds as core species. However, we found a correlation of the abundance of migratory species with the number of interactions and links. Similarly, the structure of the hummingbird-plant network in the Peruvian Andes is strongly influenced by the phenological periods of hummingbird and plant species (Gonzalez & Loiselle 2016). In fact, the overlap of phenology in conjunction with morphological coupling is of great importance for the structuring of hummingbird-plant networks (Maruyama *et al*. 2014, Vizentin-Bugoni *et al*. 2014). As well as the temporal dynamics of migratory species in the structuring of frugivorous networks (Ramos-Robles *et al*. 2016). Gonzalez & Loiselle (2016) found that phenological overlap in birds and plants led to a greater number of interactions between species pairs. Thus, the high seasonality of floral resources and the migration of the seven species of hummingbirds that breed in North America directly influence the structure of the interaction network and the assembly of the hummingbird community in the region.

On the other hand, flowering of the main ornithophilous plants in the temperature forest is synchronized with migratory periods of the hummingbirds that breed in the US and Canada (López-Segovia, Unpublished data). Feinsinger (1978) proposed that the phenological systems of ornithophilic plants and hummingbirds represent co-evolutionary processes. Thus, mutualisms can influence the evolution of flowering phenology through different paths, so that pollinator activity patterns can directly promote a certain time and duration of flowering (Aizen 2003). Since a pollinator may be a limiting resource to which plants may exhibit a temporal divergence of flowering, as a result of competition by pollinators (Stiles 1977, Waser 1978, Lobo *et al*. 2003). The relation of migratory hummingbirds to the richness and abundance of ornithophilous flowers was only present in the Palmito (temperature forest; Table 4). Since the arrival of migratory hummingbird species in the temperature forest increases the number of pollinators in the region (López-Segoviano 2012), which in turn increases the number of interactions with plants. In fact, increasing the plant visit rate also increases pollen flow (Mayer *et al*. 2012) and pollen deposition in flower estimates (Cayenne Engel & Irwin 2003).

In conclusion, our study showed that the topology of the interaction networks change through an altitudinal gradient, similar to other works with plant-pollinator interaction networks along different altitudinal gradients (Ramos-Jiliberto *et al*. 2010, Maglianesi *et al*. 2014, Maglianesi *et al*. 2015). Although, most species of hummingbirds were found at two altitudinal sites, these species played different roles at each site. In fact, key hummingbird species in each network were different but all were local and of great abundance. On the other hand, the key plant species on the three altitudinal sites were ornithophylous and non-ornithophylous. Finally, we established that the abundance of latitudinal migratory hummingbirds is correlated with network parameters such as the number of links and interactions. Similarly, the abundance of these hummingbirds correlates with that quantity and variety of floral resources in the temperate forest region.

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TABLES

Table 1. Properties of bipartite network structure, specialization (H2), connectance (C) and nestedness (NODF), in the three sampling sites: The network built with Guacamaya data presented the highest index of specialization and the Monte Mojino presented the highest index of connectance and nestedness.

Site	Hummingbirds	Plants	H_2	C	NODF	Z. score	*p*
Monte Mojino	7	24	0.246	0.345	46.88	-0.22	0.408
Guacamaya	16	25	0.310	0.165	30.90	-2.61	0.006
Palmito	12	23	0.248	0.264	40.11	-1.71	0.040

Table 2. Normalized Degree Index (ND) and core and peripheral analysis of hummingbird species in each of the altitudinal gradient networks. We can observe that networks of each site share species of hummingbirds but these species presented different functions in each network.

		Monte Mojino			Guacamaya			Palmito		
Species	Migratory Status	ND	Gc	Dat	ND	Gc	Dat	ND	Gc	Dat
A. beryllina	**Altitudinal**				**0.72**	**3.224**	**core**	0.22	-0.182	peri
A. rutila	**Resident**	**0.79**	**1.377**	**core**						
A. violiceps	Altitudinal	0.13	-0.679	peri	0.20	0.203	peri	0.04	-0.853	peri
A. alexandri	Latitudinal	0.08	-0.808	peri	0.04	-0.726	peri			
A. colubris	Latitudinal				0.08	-0.494	peri	0.04	-0.853	peri
A. heloisa	Resident							0.17	-0.349	peri
C. auriceps	Resident	0.21	-0.422	peri						
C. thalassinus	Local							0.09	-0.685	peri
C. costae	Latitudinal				0.08	-0.494	peri			
C. lucifer	Latitudinal				0.08	-0.494	peri			
C. latirostris	**Altitudinal**	**0.83**	**1.505**	**core**	0.16	-0.029	peri			
E. fulgens	Altitudinal				0.04	-0.726	peri	0.26	-0.014	peri
H. constantii	Altitudinal	0.25	-0.294	peri	0.04	-0.726	peri			
H. leucotis	**Altitudinal**				0.28	0.668	peri	**0.87**	**2.334**	**core**
L. clemenciae	**Altitudinal**				0.12	-0.261	peri	**0.57**	**1.160**	**core**
S. calliope	Latitudinal				0.20	0.203	peri	0.04	-0.853	peri
S. platycercus	Altitudinal				0.28	0.668	peri	0.43	0.657	peri

S. rufus	Latitudinal	0.13	-0.679	peri	0.24	0.436	peri	0.39	0.489	peri
S. sasin	Latitudinal				0.04	-0.726	peri	0.04	-0.853	peri
T. dupontii	Resident				0.04	-0.726	peri			

Table 3. Results of the generalized linear models of the number of latitudinal migratory hummingbirds in each altitudinal site and the richness of plants, number of flowers, number of interactions and number of links. It is possible to observe a relation of the number of latitudinal migratory hummingbirds with each one of the analyzed parameters in the Forest.

Parameter	Coefficient estimate	Standard error	Z/t	*P*
a) Plant Richness				
Intercept	1.489	0.099	14.988	<0.001
Forest:Migrants	**0.028**	**0.006**	**4.255**	**<0.001**
Ecotono:Migrants	**0.063**	**0.028**	**2.260**	**0.023**
Lowland:Migrants	-0.050	0.095	-0.526	0.598
b) Number of Flowers				
Intercept	7.183	0.325	22.097	<0.001
Forest:Migrants	**0.069**	**0.013**	**5.278**	**<0.001**
Ecotono:Migrants	0.042	0.100	0.425	0.674
Lowland:Migrants	-0.280	0.442	-0.634	0.531
c) Number of Interactions				
Intercept	3.081	0.199	15.448	<0.001
Forest:Migrants	**0.051**	**0.009**	**5.164**	**<0.001**
Ecotono:Migrants	0.084	0.053	1.597	0.121
Lowland:Migrants	0.056	0.166	0.336	0.739
d) Number of links				
Intercept	2.007	0.123	16.294	<0.001

Forest:Migrants	**0.039**	**0.007**	**5.640**	**<0.001**
Ecotono:Migrants	**0.088**	**0.032**	**2.749**	**0.010**
Lowland:Migrants	0.094	0.097	0.969	0.340

Table 4. Results of the generalized linear models of the number of latitudinal migratory hummingbirds in each altitudinal site and the richness of plants, number of flowers, number of interactions and number of links, only with plants with ornithophylous syndrome (Faegri and van der Pijl 1979). A relation of the number of migratory hummingbirds can be observed with each one of the parameters analyzed in the Forest.

Parameter	Coefficient estimate	Standard error	Z/t	*P*
a) Plant Richness				
Intercept	1.077	0.121	8.838	<0.001
Forest:Migrants	**0.037**	**0.007**	**5.343**	**<0.001**
Ecotono:Migrants	0.048	0.036	1.336	0.181
Lowland:Migrants	-0.048	0.117	-0.410	0.682
b) Number of Flowers				
Intercept	6.793	0.416	16.327	<0.001
Forest:Migrants	**0.078**	**0.015**	**5.013**	**<0.001**
Ecotono:Migrants	0.036	0.131	0.280	0.782
Lowland:Migrants	-0.379	0.655	-0.578	0.567
c) Number of Interactions				
Intercept	2.658	0.282	9.404	<0.001
Forest:Migrants	**0.061**	**0.0125**	**4.858**	**<0.001**
Ecotono:Migrants	0.079	0.076	1.038	0.308
Lowland:Migrants	-0.017	0.263	-0.066	0.948
d) Number of Links				

Intercept	1.119	0.119	9.380	<0.001
Forest:Migrants	**0.032**	**0.075**	**4.264**	**<0.001**
Ecotono:Migrants	**0.069**	**0.033**	**2.103**	**0.035**
Lowland:Migrants	0.003	0.106	0.029	0.976

FIGURES

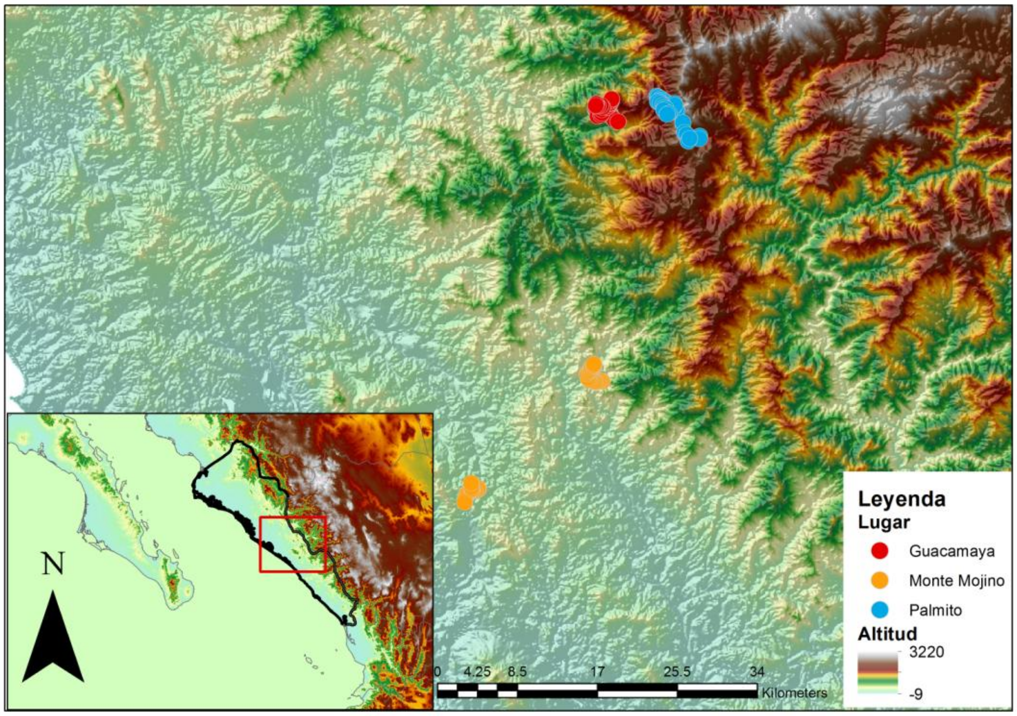

Figure 1. Map of altitudinal gradient of study area in the municipality of Concordia, Sinaloa.

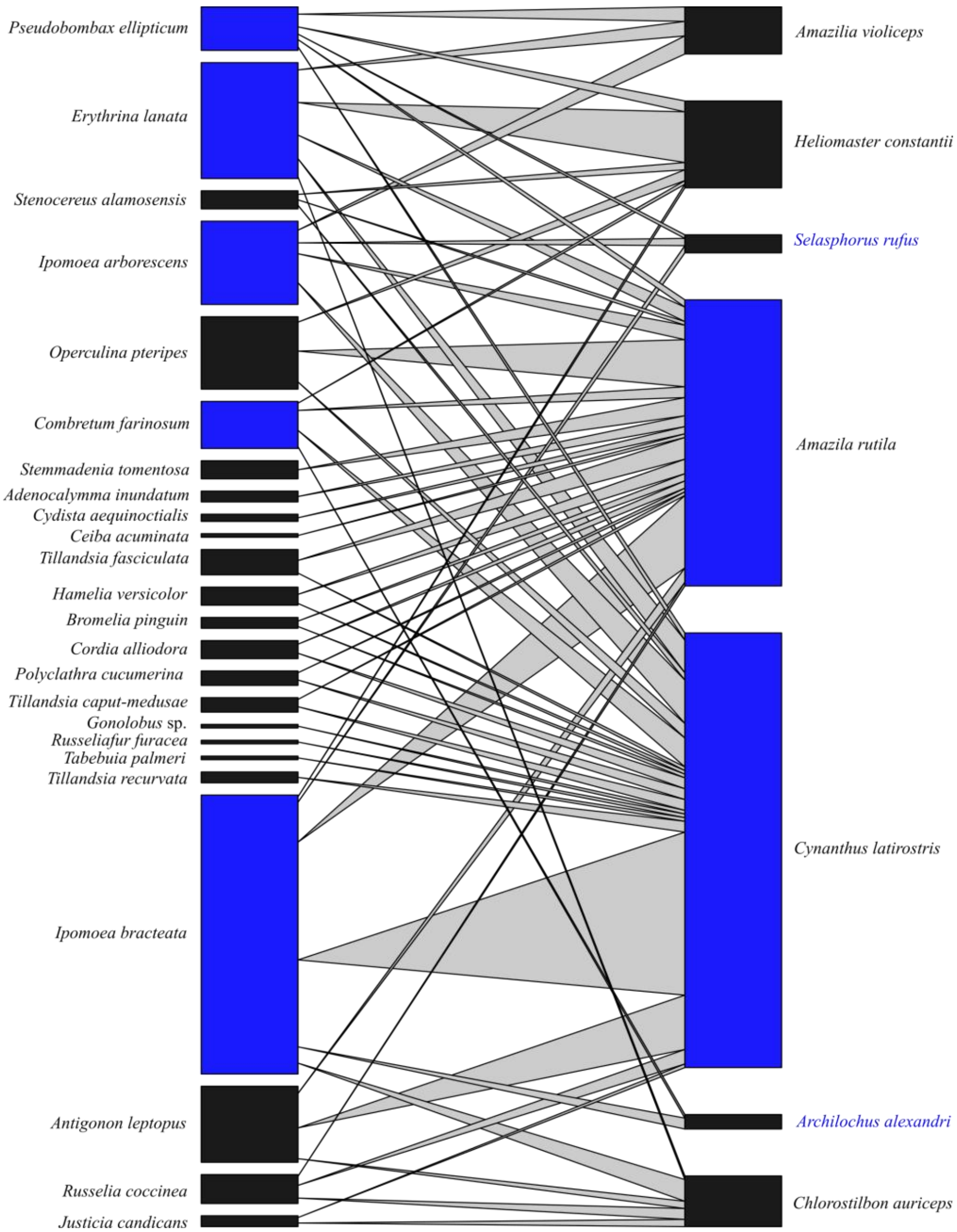

Figure 2. Interaction Network of hummingbirds-plants of the Monte Mojino. The species of migratory hummingbirds are written in blue and the core species of hummingbirds and plants in their box is represented with blue.

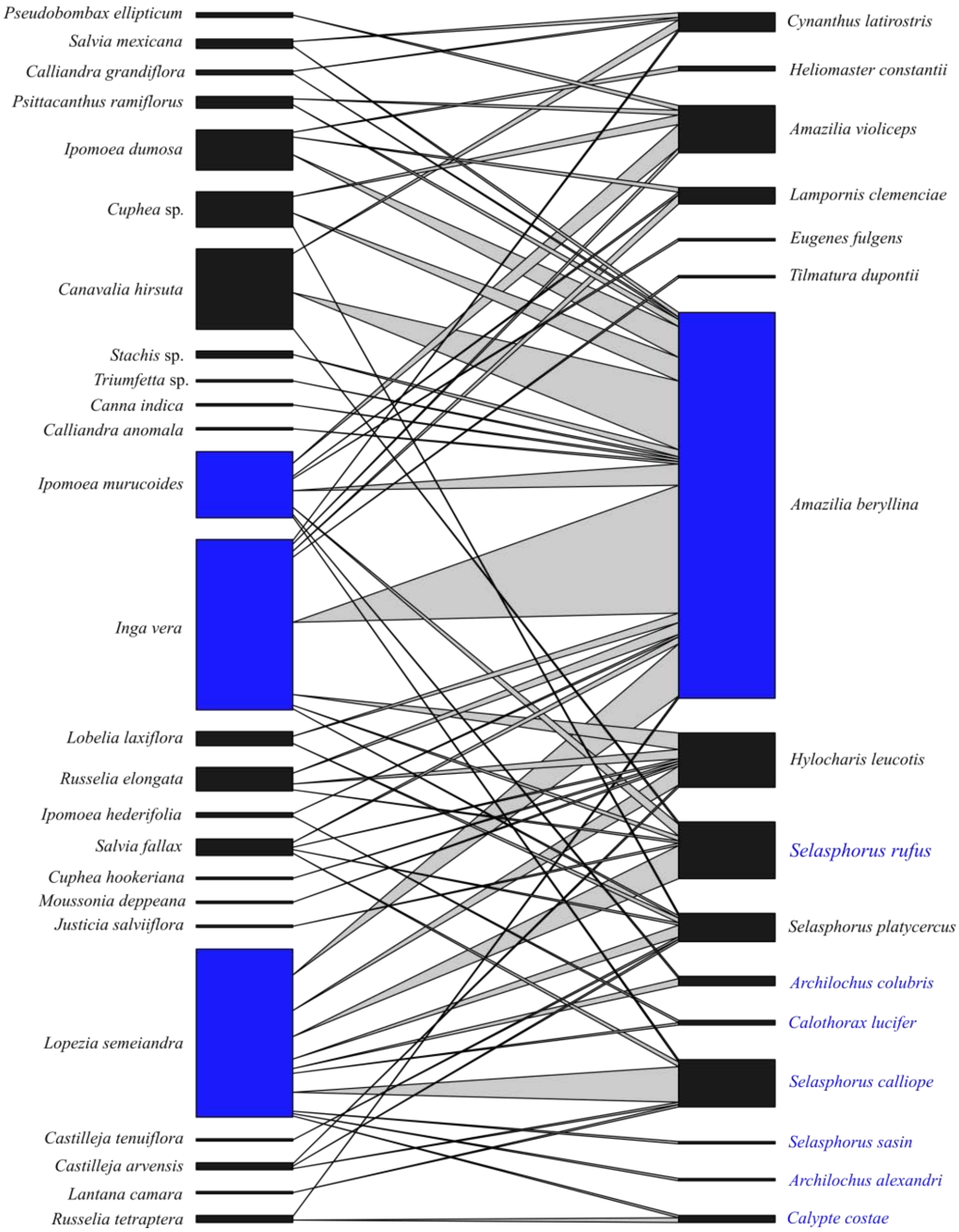

Figure 3. Interaction network of hummingbirds-plants of the Guacamaya. The species of migratory hummingbirds are written in blue and the core species of hummingbirds and plants in their box is represented with blue.

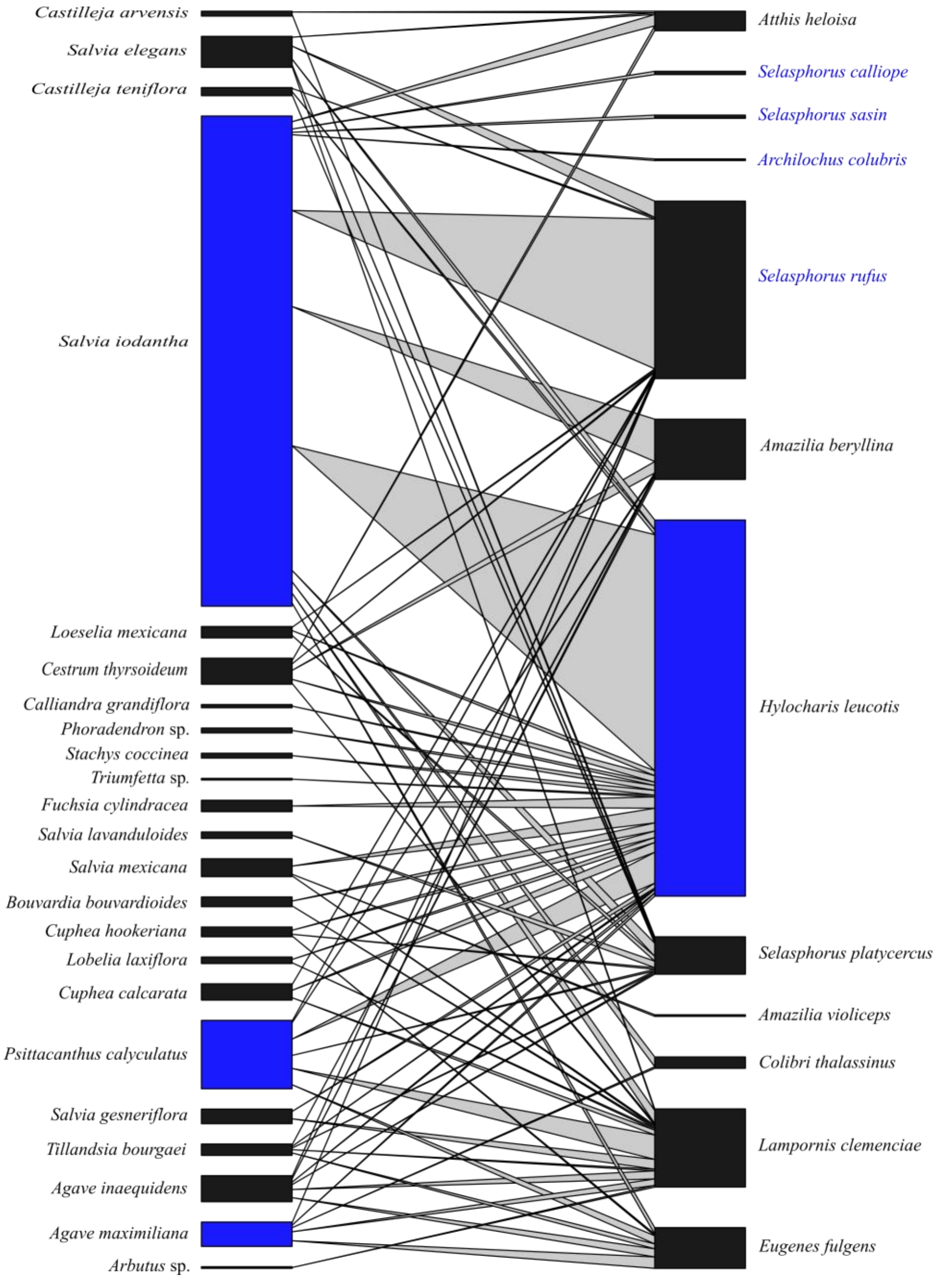

Figure 4. Interaction Network of hummingbirds-plants of the Palmito. The species of migratory hummingbirds are written in blue and the core species of hummingbirds and plants in their box is represented with blue.

Discusión general y conclusiones

Los resultados de mi trabajo de tesis permitieron entender como el comportamiento, la disponibilidad de recursos florales, la fenología floral y migratoria y la preferencia de los colibríes influyen en la estructuración de las comunidades de colibríes. Además, como la estructura de la comunidad de colibríes y las plantas de las que se alimentan cambia temporal y espacialmente analizando un gradiente altitudinal.

Al evaluar como el comportamiento agresivo de los colibríes puede estructurar la comunidad de colibríes, encontramos que la jerarquía de dominancia está directamente relacionada con el tamaño corporal y no presenta relación con la carga del disco alar y el estatus migratorio. Confirmando lo establecido por Martin & Ghalambor (2014) que las especies de aves grandes desplazan de manera agresiva a las pequeñas cuando comparten un recurso. Sin embargo, la dominancia de una especie de colibrí grande sobre una pequeña depende de la calidad del recurso defendido. Encontramos que el nivel de dominancia de cada especies está relacionada con la calidad del recurso floral defendido en cuanto a calidad energética medida como calorías totales producidas, pero no con el número de flores. Contrario a lo establecido por otros autores donde a mayor número de flores hay mayor defensa de los recursos (Feinsinger 1976, Cotton 1998, Justino *et al*. 2012). Lo cual puede ser un efecto de las plantas como *Agave inaequidens* que presentan una gran cantidad de calorías en un número reducido de flores. Así, el tamaño corporal de las especies de colibríes está relacionado con nivel de dominancia, que a su vez se relaciona con la calidad de los recursos florales de los cuales se alimenta y los cuales defiende.

En el segundo capítulo de esta tesis, analizamos los patrones fenológicos de las dos especies de colibríes migratorios de mayor abundancia en la región (*Amazilia beryllina* migratorio altitudinal y *Selasphorus rufus* migratorio latitudinal). Los resultados de tres años de muestreo no consecutivos, muestran que la fenología migratoria depende del tipo de migración que realiza cada especie. Ya que las especies con rutas migratorias más largas presentan menos cambios en su migración a lo largo de los años, en cambio especies con migraciones más cortas ajustan si migración anual en relación a las condiciones de cada sitio visitado (Supp *et al*. 2015). El patrón migratorio de *S. rufus* por la región de estudio (El Palmito) es similar el primer y tercer año de muestreo, pero el segundo es diferente, lo cual coincide con el año de mayor cantidad de precipitación en la región de estudio. Sin embargo, las asociación fenológica entre *S. rufus* y *Salvia iodantha* (planta con el mayor número de flores en la región) fue constante en los tres años de muestreo. Confirmando en conjunto con el estudio de Arizmendi (2001) que esta planta es la de mayor importancia para la migración de *S. rufus* por el occidente de México. Por su parte, *A. beryllina* presenta una asociación con todos los recursos disponibles en la región, durante los tres años de muestreo. Así, las especies de migración altitudinal parecen responder a los cambio en la disponibilidad de alimento (Stiles 1985) y las especies de migraciones latitudinales presentan una migración acoplada a la fenología de determinadas plantas en particular dentro de sus rutas migratorias.

Como continuación del segundo capítulo, en el tercer capítulo evaluamos si las preferencias de alimentación de las principales especies migratorias es acorde a los encontrado en el segundo capítulo. Es decir, si *S. rufus* prefiere alimentarse de las especies de plantas con la que se asocia durante su migración (*S. iodantha*) y *A. beryllina* se alimenta de todos los recursos disponibles por igual. Considerando lo establecido en el primer capítulo, que las preferencias de un colibrí son influenciadas por su jerarquía de dominancia. Usamos jaulas de vuelo para aislar la competencia y que así, un individuo de colibrí pudiera visitar su planta preferida de las dos plantas de mayor abundancia (*S. iodantha* y *Cestrum thyrsoideum*). Encontramos que *S. rufus* se alimentó de la especie con la cual coincide su migración natural y dentro de la jaula de vuelo. A diferencia de *A. beryllina*, especie que cambio su preferencia de manera natural y dentro de la jaula de vuelo. La preferencia de un colibrí depende de múltiples factores donde destacan la calidad de los recursos florales, el estatus migratorio y jerarquía de dominancia de cada especie de colibrí.

En el cuarto capítulo analizamos la estructura de la comunidad de colibríes y las plantas de las que se alimentan, en tres sitios dentro de un gradiente altitudinal (selva baja-bosque de pino). Encontramos que la topología de las redes de interacción cambian en el gradiente altitudinal y que la mayoría de las especies de colibríes las encontramos en dos pisos altitudinales pero desempeñaron papeles diferentes en cada sitio de muestreo. Así, los rasgos de las especies de colibríes pueden mediar los patrones de co-ocurrencia de una especies de colibrí a través de un gradiente ambiental (Graham *et al*. 2012) y el papel de cada especie en la comunidad depende del arreglo de las especies de cada sitio. Otro resultado importante fue que las especies núcleo en cada red de interacciones fueron plantas ornitófilas y no ornitófilas. Confirmando lo encontrado por Maruyama *et al*. (2013), donde se establece la importancia de las plantas no ornitófilas para la comunidad de colibríes. Por último determinamos que la abundancia de colibríes migratorios latitudinales está correlacionada con el número de interacciones así como con los enlaces entre colibríes y plantas. Además, encontramos que la riqueza y abundancia de recursos florales (ornitófilos) también se correlaciona con la abundancia de especies migratorias latitudinales. Sin embargo esto se presenta en el bosque de pino-encino, corroborando lo establecido en el segundo capítulo en donde encontramos la asociación de *Selasphorus rufus* (migrante latitudinal) y la planta con mayor número de flores en la región, *Salvia iodantha*. Estas asociaciones fenológicas de plantas y colibríes migratorios influye directamente en la estructura de la red de interacciones de colibríes y plantas. Al igual que se encontró en otro estudio donde la estructura de la red de colibríes-plantas en los Andes Peruanos está fuertemente influenciada por los periodos fenológicos de las especies de colibríes y plantas (Gonzalez & Loiselle 2016).

Los resultados obtenidos en mi tesis, me permiten concluir que la comunidad de colibríes está directamente ligada a la oferta de recursos florales ya sean con síndrome ornitófilo o no ornitófilo. En el primer capítulo encontramos que una especie de *Agave* polinizada por murciélagos y polillas es la principal fuente de alimento de las especies de colibríes más dominantes en la región dominada por bosques de Pino-Encino, marcando el tope de dominancia y el arreglo subsecuente de las especies menos dominantes. Al igual, la migración de la principal especie migratoria latitudinal está relacionada con la fenología floral de *Salvia iodantha* (ornitófila), especie fundamental para la permanencia de esta especie en la región. Incluso esta especie prefiere alimentarse de *Salvia iodantha* independientemente de su abundancia simulada bajo condiciones experimentales, lo que puede ser consecuencia de varios factores principalmente el acople fenológico y la jerarquía de dominancia. Así, la estructura de la comunidad de colibríes está directamente relacionada con la cantidad de los recursos florales, su distribución y su temporalidad.

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