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Arthropod Foraging in a Temperate Mountain Hummingbird Ensemble

Omar Maya-García [1,2], Elisa Maya-Elizarrarás [1], Carlos Lara [3] and Jorge E. Schondube [1,*]

[1] Laboratorio de Ecología Funcional, Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701, Col. Ex Hacienda de Sán José de la Huerta, Morelia 58190, Michoacán, Mexico; omar_maya@cieco.unam.mx (O.M.-G.); elimaya@cieco.unam.mx (E.M.-E.)

[2] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Unidad de Posgrado, Edificio D, Primer Piso, Circuito de Posgrados, Ciudad Universitaria, Coyoacán, Mexico City 04510, Mexico

[3] Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, Km 10.5 Autopista Tlaxcala-San Martín Texmelucan, San Felipe Ixtacuixtla, Tlaxcala 90120, Mexico; carlos.lara.rodriguez@gmail.com

* Correspondence: chon@cieco.unam.mx

Simple Summary: Hummingbirds use arthropods to obtain proteins, fatty acids, and micronutrients absent in their nectar diet. Despite arthropods' nutritional importance for hummingbirds, most studies on these birds have focused on nectar consumption (~97% of total studies), with arthropod ingestion requiring better study. Consequently, our understanding of the factors affecting hummingbirds' arthropod ingestion and their role as an energy source for these birds is limited. Our main objective was to describe the use of arthropods by a hummingbird ensemble during one annual cycle. We explored the effects of seasonal differences in nectar and arthropod availability on hummingbird arthropod foraging. We found that the arthropod capture attempt rate of the White-eared Hummingbird (*Basilinna leucotis*; the only species that forage for arthropods during the different seasons of the year) differed among seasons, being significantly higher during the warm-dry season of the year when arthropod abundance was at its peak. As a result, we found a significant and positive relationship between arthropod availability and arthropod foraging rate for this species. Our findings suggest that some hummingbirds can use arthropods as their only food source, covering all their nutritional and energy requirements. This capacity is vital when nectar is not available in the environment.

Abstract: Arthropods are hummingbirds' principal source of nitrogen, fatty acids, and micronutrients. Despite the nutritional importance of arthropods for hummingbirds, our understanding of the factors influencing their consumption and their relative role as an energy source remains limited. Here, we aimed to describe the use of arthropods by a hummingbird ensemble in a seasonal temperate mountain ecosystem in West Mexico during one annual cycle. We compared arthropod capture attempt rates among six different humming species. Also, we investigated the impact of seasonal variation in food availability on the arthropod capture attempt rates of the White-eared Hummingbird (*Basilinna leucotis*), the sole species observed foraging for arthropods in all seasons. We found that hummingbirds ingested arthropods from different orders (Araneae, Hemiptera, Psocoptera, Hymenoptera, and Diptera), with arthropod capture attempt rates varying wildly among species. The arthropod capture attempt rates of the White-eared Hummingbird showed a significant positive correlation with arthropod availability, peaking during the warm-dry season when floral nectar was scarce and arthropod availability was high. Our data show that arthropod ingestion is crucial for some hummingbird species, mainly when nectar availability is limited or absent in the environment.

Keywords: arthropods as an energy source; hummingbird nutritional requirements; food availability; seasonality

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1. Introduction

Although the nutritional importance of arthropods as a nitrogen source for hummingbirds is beyond doubt [1–3], our understanding of the factors influencing their ingestion in the field and their importance as an energy source for these birds needs to be improved. Some authors indicate that hummingbirds ingest arthropods solely to meet their nitrogen requirements and obtain essential fatty acids and micronutrients absent in floral nectar [2–4]. However, evidence indicates that some hummingbird species can ingest large amounts of arthropods and use them as an energy source when nectar is scarce in the environment [5–11].

Classical studies on arthropod ingestion by hummingbirds (e.g., [9,12]) have revealed a marked difference in arthropod use among different hummingbird species. This variation in arthropod ingestion among hummingbirds results from the interaction between intrinsic and extrinsic factors that affect their feeding decisions. Intrinsic factors include wing and bill morphology, which limit their capacity to capture arthropods, as well as their minimum nitrogen requirements and changes in their nutritional needs throughout their annual cycles (e.g., increases in protein and mineral requirements during egg production or molting [1,5,10,12,13]). Extrinsic factors include, among others, weather conditions and the availability of food resources (i.e., floral nectar and arthropods [6,9,10,14]).

While some intrinsic factors have been studied in the past (e.g., [2,3,12,15]), our knowledge of the role that extrinsic factors play in arthropod ingestion by hummingbirds remains preliminary at best (but see [9,11,12,16]). This lack of understanding stems from methodological constraints that limit our ability to measure arthropod foraging by hummingbirds in the field. These limitations include the small body size of the arthropods ingested by hummingbirds, the difficulty in determining the success of arthropod capture attempts, and the challenges associated with conducting prolonged focal observations of individual hummingbirds (i.e., minutes [11,12]).

Here, we tested the importance of arthropods for hummingbirds when birds face changes in arthropod and nectar availability in their environment. To do this, we studied the use of arthropods by members of a hummingbird ensemble in a seasonal temperate mountain ecosystem in West Mexico during one annual cycle. Our study aimed to (1) determine the diversity and quantity of arthropods ingested by hummingbirds, (2) compare arthropod capture attempt rates among hummingbird species, (3) describe the arthropod foraging tactics of the hummingbird ensemble, (4) quantify seasonal differences in arthropod use by hummingbirds, and (5) test the role of nectar and arthropod availability on arthropod ingestion.

Given that arthropod ingestion by some nectar-feeding birds like sunbirds and honeyeaters increases during periods of low nectar or high arthropod abundance in the environment [17–20], we hypothesized that hummingbird arthropod foraging would vary seasonally in response to nectar abundance. We predict that hummingbirds will increase their arthropod ingestion rates when nectar abundance is low or limited, using arthropods not only as a source of protein and fatty acids but also as a crucial energy source.

2. Materials and Methods

2.1. Study Site

We conducted fieldwork at the Nevado de Colima, an inactive high-altitude volcano (4260 m a.s.l.) located at the western end of the Trans-Mexican Volcanic Belt (19° N, 103° W; Figure 1), in the state of Jalisco, Mexico [21,22]. A portion of the mountain is designated as a National Park. Our study plot was located on the mountain's northeast slope at an elevation of 3194 m a.s.l., covering an area of 2 ha (Figure 1). The vegetation at the site comprises a blend of subalpine scrubland dominated by plants from the genera *Salvia*, *Ribes*, and *Festuca*, interspersed with patches of alders (*Alnus*) on exposed ridges, as well as pine and fir forests (*Pinus* and *Abies*) in ravines [23]. The most abundant flowering plants used by hummingbirds at the site include *Salvia elegans*, *S. gesneriflora* (Lamiaceae), *Ribes ciliatum* (Saxifragaceae), *Senecio angulifolius* (Asteraceae), and *Penstemon roseus* (Plantaginaceae) [24].

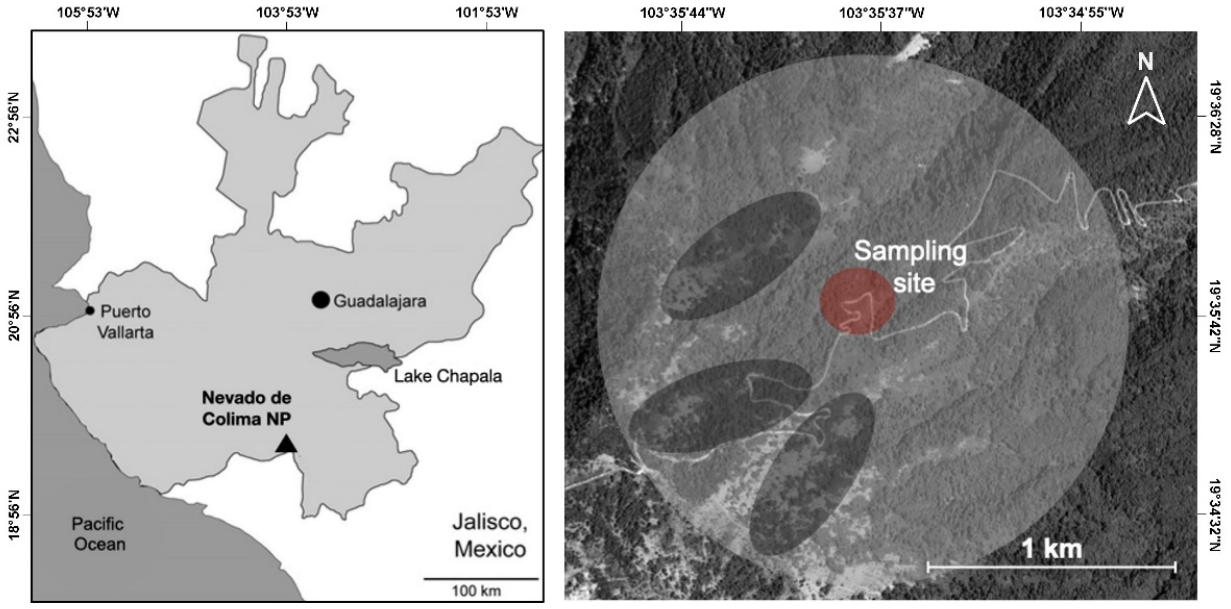


Figure 1. Map of our study area. We studied the hummingbird ensemble found around 3000 m a.s.l. in the Nevado de Colima volcano. This mountain is located in the state of Jalisco, Mexico (**left panel**). We sampled hummingbirds and their food resources in a 2 ha sampling plot (red polygon in the (**right panel**)). Additionally, we sampled flowers in a 1 km radius circular plot that surrounded our sampling plot by using two complementary approaches: (1) using roads (clear lines) as transects to sample flower abundance, and (2) conducting extensive area searches in three 6 ha areas that surrounded our sampling site (darker gray polygons). We could not search for flowers in several sections of the circular plot due to the complex topography of the landscape.

The region presents three climatic seasons as follows: (1) A rainy season (June to October) characterized by heavy daily rainstorms (monthly average precipitation: 360.5 mm) and temperatures ranging from 3.4 to 17.9 °C. (2) A cold-dry season (November to February) with occasional isolated rain and snowstorms (monthly average precipitation: 20.3 mm) and temperatures varying from −0.7 to 20.1 °C. And (3) a warm-dry season (March to May) marked by scarce rainfall (monthly average precipitation: 66.1 mm) and temperatures that fluctuate between 3.9 and 23.8 °C [23,25].

The hummingbird ensemble inhabiting the Nevado de Colima varied among the three climatic seasons, presenting a combined total of 15 species. Among these, the following eight species are year-round residents: Mexican Violetear (*Colibri thalassinus*), Rivoli's Hummingbird (*Eugenes fulgens*), Blue-throated Mountaingem (*Lampornis clemenciae*), Amethyst-throated Mountaingem (*L. amethystinus*), Bumblebee Hummingbird (*Selasphorus heloisa*), White-eared Hummingbird (*Basilinna leucotis*), Violet-crowned Hummingbird (*Ramosomya violiceps*), and Berylline Hummingbird (*Saucerottia beryllina* [24,26–28]). The remaining seven species are long-distance winter migrants found from November to March at our study site and are as follows: Black-chinned Hummingbird (*Archilochus alexandri*), Ruby-throated Hummingbird (*A. colubris*), Costa's Hummingbird (*Calypte costae*), Calliope Hummingbird (*Selasphorus calliope*), Rufous Hummingbird (*S. rufus*), Allen's Hummingbird (*S. sasin*), and Broad-tailed Hummingbird (*S. platycercus* [24,26–28]).

The hummingbird ensemble presented significant phenological differences among the three climatic seasons we used for sampling. During the rainy season, our study site hosts mainly resident species and some early arrivals of long-distance migrants (from mid-September). During this season, some resident species undergo flight feather molt (Amethyst-throated Mountaingem and Mexican Violetear; Maya-García and Schondube, unpublished data). During the cold-dry season, the following three significant phenomena occur: (1) the arrival of most individuals of long-distance migratory species [24,26–28]; (2) flight feather molting of long-distance migratory species (January and February); and

(3) breeding of resident species (from November to January; Schondube and Maya-García, unpublished data [29,30]). Finally, during the warm-dry season, the area presents only resident species, with the White-eared Hummingbird undergoing flight feather molt (Maya-Garcia and Schondube, unpublished data).

2.2. Field-Work

We conducted our study during one annual cycle, with sampling occurring once in each season as follows: warm-dry (May 2016), rainy (September 2016), and cold-dry (February 2017). Each sampling period lasted for 15 days. This sampling scheme was chosen due to the significant variations in weather conditions and food resource availability observed across the seasons. We organized our sampling to minimize the effect of our activities on bird behavior and the ecology of our study site. The first few days after arrival, we conducted behavioral observations of the hummingbird ensemble. This was followed by the colocation of mist nets and traps to capture arthropods at the site and to monitor the hummingbird ensemble. Finally, we measured the abundance of nectar and arthropods in our study plot and the surrounding area. Our seasonal sampling indicates that no plants were in bloom during the warm-dry season, while several plant species, mainly from the genera *Salvia*, *Ribes*, and *Penstemon*, bloomed during the rainy and cold-dry seasons. The composition and structure of the hummingbird ensembles exhibited seasonal variations, with long-distance migratory species appearing during the rainy and the cold-dry season [24,26–28].

We captured hummingbirds using ten mist nets (12 m long, mesh size of 24 mm) for three consecutive days during each sampling period. The mist nets were opened at sunrise and closed after six hours, with net rounds conducted every 5 to 15 min, depending on weather conditions. Mist nets were positioned within our 2 ha study area, and their location remained constant during the study [31]. We identified and banded all captured birds with aluminum bands and determined their age and sex using plumage characteristics and bill striations [32–34]. Hummingbirds have very small tarsi, and because their tarsi are covered by feathers while the birds are flying or perching, color bands cannot be used to identify individuals visually. Due to the small area size of our study plot we could not use point counts to determine hummingbird abundance. As a result, we decided to use capture rates as an indicator of relative abundance because we had good recapture rates during our mist netting sessions (40–60%). The abundance of each hummingbird species was standardized based on the number of individuals captured per 100 net hours.

2.3. Stomach Content Analysis

We obtained stomachs from individuals collected as part of an independent stable isotope study conducted at our study plot (n = 6 in May 2016, n = 8 in September 2016, and n = 18 in February 2017; see Table 1). This study collected blood, liver, pectoral muscle, and bones to extract collagen, facilitating the use of stomachs. The remaining feathers, skulls, and tongues were deposited at the collection of the Functional Ecology Laboratory of IIES, UNAM. Samples were collected with permission from the Secretaría de Medio Ambiente y Recursos Naturales, México (SGPA/DGGFS/712/2767/16). All collected captured birds were humanely euthanized by carefully placing their heads inside a small vial containing a cotton ball soaked in isoflurane, following the "Guidelines to the Use of Wild Birds in Research" [35]. Stomachs were deposited in plastic vials with saline solution (0.8% NaCl) and frozen in liquid nitrogen for subsequent analysis. In the laboratory, stomachs were thawed and dissected, and their contents were removed by washing them with 70% ethanol until their surfaces looked clean under the stereoscopic microscope. To determine the biomass of ingested arthropods (g dry mass), we dried our samples at room temperature for three hours and then weighted them using an analytical balance (Ohaus Adventurer, capacity/readability—110 g/0.0001 g, and a sampling error of ±0.0001 g). Samples were categorized as identifiable (partially fragmented; ≅90% of the materials) and unidentifiable (very fragmented; ≅10% of the materials; AmScope,

7–45× binocular stereo zoom microscope). Identification of arthropod taxa was carried out by Omar Maya-García, who had significant previous experience in the taxonomic identification of arthropods. Recognizable arthropods were identified to the taxonomic order level following Triplehorn and Johnson [36]. We initially intended to analyze the stomach contents using molecular techniques; however, we were unable to obtain quality DNA data from our samples.

Table 1. Biomass of ingested arthropods (g dry weight) by hummingbirds for each season. We show the mean and standard deviation values for species with two or more stomachs analyzed.

Season	Individual	Species	Age	Sex	Biomass of Arthropods Ingested (g Dry Weight)	Mean Biomass of Arthropods Ingested ± sd
Warm-dry	1	Amethyst-throated Mountaingem (*Lampornis amethystinus*)	Adult	Female	0.001	
	2	White-eared Hummingbird (*Basilinna leucotis*)	Adult	Male	0.0011	0.0019 ± 0.0007 ($n = 4$)
	3	White-eared Hummingbird (*Basilinna leucotis*)	Adult	Male	0.0027	
	4	White-eared Hummingbird (*Basilinna leucotis*)	Adult	Male	0.0024	
	5	White-eared Hummingbird (*Basilinna leucotis*)	Adult	Male	0.0014	
	6	Rivoli's Hummingbird (*Eugenes fulgens*)	Adult	Female	0.0038	
Rainy	7	Mexican Violetear (*Colibri thalassinus*)	Adult	Female	Traces	0.0009 ± 0.0005 ($n = 3$)
	8	Mexican Violetear (*Colibri thalassinus*)	Adult	Unknow	0.0012	
	9	Mexican Violetear (*Colibri thalassinus*)	Adult	Unknow	0.0012	
	10	Mexican Violetear (*Colibri thalassinus*)	Juvenile	Unknow	0.0003	
	11	Amethyst-throated Mountaingem (*Lampornis amethystinus*)	Adult	Female	0.0006	
	12	White-eared Hummingbird (*Basilinna leucotis*)	Juvenile	Female	Traces	
	13	Rivoli's Hummingbird (*Eugenes fulgens*)	Adult	Male	Traces	
	14	Rivoli's Hummingbird (*Eugenes fulgens*)	Adult	Female	Traces	
Cold-dry	15	Mexican Violetear (*Colibri thalassinus*)	Adult	Male	0.0007	0.0004 ± 0.0001 ($n = 4$)
	16	Mexican Violetear (*Colibri thalassinus*)	Adult	Unknow	0.0003	
	17	Mexican Violetear (*Colibri thalassinus*)	Juvenile	Male	0.0003	
	18	Mexican Violetear (*Colibri thalassinus*)	Juvenile	Unknow	0.0004	
	19	White-eared Hummingbird (*Basilinna leucotis*)	Adult	Male	Traces	0.0006 ± 0.0004 ($n = 2$)
	20	White-eared Hummingbird (*Basilinna leucotis*)	Adult	Male	Traces	
	21	White-eared Hummingbird (*Basilinna leucotis*)	Juvenile	Male	0.0009	
	22	White-eared Hummingbird (*Basilinna leucotis*)	Juvenile	Male	0.0003	
	23	Rivoli's Hummingbird (*Eugenes fulgens*)	Adult	Male	0.0025	0.001 ± 0.0013 ($n = 3$)
	24	Rivoli's Hummingbird (*Eugenes fulgens*)	Adult	Male	0	
	25	Rivoli's Hummingbird (*Eugenes fulgens*)	Juvenile	Male	0.0005	
	26	Broad-tailed Hummingbird (*Selasphorus platycercus*)	Adult	Female	0.0004	0.00075 ± 0.00037 ($n = 4$)
	27	Broad-tailed Hummingbird (*Selasphorus platycercus*)	Adult	Female	0.0009	
	28	Broad-tailed Hummingbird (*Selasphorus platycercus*)	Adult	Female	0.0012	
	29	Broad-tailed Hummingbird (*Selasphorus platycercus*)	Juvenile	Male	0.0005	
	30	Rufous Hummingbird (*Selasphorus rufus*)	Juvenile	Male	0.0003	$0.00036 \pm 5.77 \times 10^{-5}$ ($n = 3$)
	31	Rufous Hummingbird (*Selasphorus rufus*)	Juvenile	Female	0.0004	
	32	Rufous Hummingbird (*Selasphorus rufus*)	Juvenile	Female	0.0004	

2.4. Arthropod and Nectar Foraging Rates

During each sampling period, we observed the following two feeding behaviors of hummingbirds: (1) arthropod capture attempts and (2) flower visits for nectar. Our observations were conducted using the ad libitum sampling method [37,38], an approach previously used to quantify arthropod foraging behavior in hummingbirds [11,12]. We decided to use this method instead of trying to determine time budgets to quantify feeding behaviors for two reasons: (1) an insect capture attempt is an instantaneous behavior with no appreciable duration (much shorter than a second), making the time allocated to hunting for insects almost impossible to determine; and (2) at our study site, particularly during the cold-dry season, the high density of hummingbirds combined with frequent interspecific interactions, complex vegetation structure, and challenging topography limited our ability to follow individuals. As a result, observation periods typically ranged from less than 5 min to occasionally up to 10 min.

We want to point out that ad libitum sampling involves opportunistic observations without restrictions of one or several individuals, quantifying the frequency of targeted behaviors without specifying the timing or duration of these behaviors [37,38]. This sampling method allowed us to obtain multiple short observations of independent individuals, offering key advantages over traditional long focal observations of a few individuals as follows: (1) a broader individual representation reducing individual bias; (2) a larger sample size that enhances statistical power; (3) a minimized observer effect; (4) a better sampling suitability for complex environments; (5) an increased chance of capturing rare behaviors; (6) a population-level behavioral insight; (7) a reduced temporal autocorrelation; and (8) a more flexible and efficient data collection [39–43]. However, since banded birds could not be identified while foraging or perching, we may have counted some individuals multiple times while using this sampling method.

We conducted two pilot studies at our study site before beginning the main fieldwork for this project. During both pilots, J. E. Schondube (who has approximately 30 years of experience working with hummingbirds at the Nevado de Colima Volcano) trained the team to conduct accurate hummingbird foraging observations. As a result, Omar Maya-Garcia, Elisa Maya-Elizarrarás, Mauricio Ortega, and Concepción Pérez-Salaverria were well-trained to measure and distinguish different foraging behaviors during our fieldwork.

We identified birds to species level and recorded the number of feeding events per unit of time, including all attempts to capture arthropods or visit floral corollas. We used frequencies due to the nature of the behavior we were measuring. As previously mentioned, an insect capture attempt is an instantaneous behavior. Although the performance of any behavior takes time, measuring the duration of a hummingbird's insect capture attempt in the field is challenging. Therefore, without precise measurements of capture attempt durations, we cannot know or determine the percentage of time that hummingbirds spent foraging for arthropods, foraging for nectar, or performing other activities. Still, we can compare the frequencies of the two feeding behaviors.

Additionally, we recorded the foraging tactics of hummingbirds. We classified arthropod capture attempts made in mid-air as "hawking", while those conducted on a substrate were labeled as "gleaning" [12]. Similarly, when arthropod capture attempts were made while birds perched, they were categorized as "perch-foraging" [11].

When a hummingbird engaged in a gleaning event, we recorded the substrate on which it fed (tree foliage, tree bark, shrubs, herbs, or ground; following Recher et al. [44] and Recher and Davis [18,45]). The feeding intensity was measured using the frequency of capture attempts and floral visits, calculated by dividing the number of attempts by the observation time (events/min [37,38]). We defined "intense foraging activity" as birds presenting 60 or more feeding attempts per minute. Foraging observations were conducted simultaneously by three observers stationed in different areas of our study site. Observers were trained to follow the same protocol, systematically scanning an area until detecting a hummingbird and describing its foraging behavior until it flew away. Observations were

made using binoculars from 08:00 to 17:00 h during two consecutive days for each season (totaling 54 h/season).

2.5. Availability of Flowers and Floral Nectar

During each climatic season, we assessed the availability of flowers at our study site and the surrounding areas. Our sampling was conducted at the following two spatial scales: (1) a sampling plot and (2) a one km radius area around it. This allowed us to determine the abundance of floral resources in the landscape that surrounds our study plot (9.8 km^2; Figure 1). Inside the one km radius area, we sampled flowers by (1) using the main roads as sampling transects and (2) conducting area searches in three plots (≅6 ha each). The sampled plots were located on ridges or less steep slopes (20–30°), allowing for slow walking through the vegetation. We could not sample areas with steeper slopes (see Figure 1).

We only determined the availability of floral nectar inside our sampling plot using the standing crop method [46]. This technique allows for measuring nectar availability at a single temporal moment, facilitating comparisons [46,47]. We randomly selected ten individuals of each flowering plant species and ten flowers per plant (totaling 100 flowers for each species). Floral nectar was extracted using capillary tubes between 08:00 and 10:00 h (Drummond Microcaps, 20 µL, 64 mm). Nectar volume and concentration were measured to evaluate variations in energy standing crops during hummingbird activity. Nectar concentration was determined using a manual refractometer (Leica DC50, Wetzlar, Germany) and converted to energy units following the method described by Kearns and Inouye [46]. Additionally, to assess the representativeness of nectar data from our study site, we employed the same techniques to measure energy availability in two areas located within a 4 km buffer zone surrounding our study site.

Using the point-centered quarter method, we determined the density of flowering plants visited by hummingbirds [48–50]. To do so, we randomly selected 10 points within our study site using a grid overlaid on a map, and locations were chosen using a random number generator. Each sampling point was surrounded by four quadrants, delineated by the North–South and East–West axes. The distance between the central point and the nearest target plant species was measured in each quadrant at each sampling point. Plant density (plants/ha) was estimated using the equations proposed by Pollard [49]. Additionally, we determined the number of flowers (flowers/plant) by counting the flowers on one plant of each species at each of the ten randomly selected points where the point-centered quarter method was applied.

We quantified nectar resources using energy availability (kJ/ha) for each plant species used by hummingbirds, following Kearns and Inouye [46]. Briefly, this value was computed by multiplying the average nectar volume (µL/flower) by the average number of flowers per plant (flowers/plant) and then by the plant density (plants/ha). Subsequently, we converted this value to energy by considering the mean sugar concentration of the nectar for each plant species (1 mol of sucrose solution contains 56.41 J/mL [46]), thereby obtaining the total energy present at our site during each season (kJ/ha).

2.6. Arthropod Availability

We estimated arthropod availability using both the beating method and Malaise traps. Combining these methods allows for a more comprehensive and diverse sampling approach [51,52]. While these methods do not accurately measure total arthropod abundance, they allowed us to obtain a measure of arthropod availability at a given place and time, permitting comparisons across seasons [51–53].

We used the beating method to target arthropods that are either unable to fly or do not move fast when disturbed, particularly those associated with tree and shrub foliage (e.g., psocopterans, hemipterans, and spiders [51,52]). We randomly positioned seven linear transects (each 30 m long × 1 m wide) within our study site to implement this method. The branches of trees and bushes within each linear transect were hit three times

with a stick while a beating tray of 0.7 × 0.7 m was placed below the section of the plant. Arthropods deposited in the tray were collected using an insect pooter (Bioquip). Sampling was conducted by the same person on a single day per season, from 08:00 to 11:00 h, to minimize sampling bias.

We used Malaise traps to capture small, strong-flying insects such as wasps and flies [51,52,54]. We randomly selected two locations within our study site to place the Malaise traps (Bioquip, 110 × 110 × 110 cm). One trap was positioned at ground level, while the other was suspended from a tree, 2 m above the ground. Both traps remained in place for seven days (336 h/season). We preserved the arthropods captured with both trapping methods in 70% ethanol.

All collected arthropods were taxonomically identified to the order level and counted to determine their abundance. Subsequently, the arthropod samples were air-dried at room temperature for three hours and weighed using an analytical balance. To determine the relative availability of arthropods for hummingbirds, we only considered organisms within the size range and taxonomic groups found inside hummingbird stomachs (see results section below). We separately estimated the relative availability of arthropods (g of dry weight/season) collected by the beating method and the Malaise traps.

2.7. Data Analysis

Due to variations in our sample sizes, our ability to compare species across seasons was limited. This limitation forced us to include different species in the analyses designed to address each specific objective. To describe the diversity of arthropods ingested by the hummingbirds each season, we calculated the percentage of prey items from each arthropod order found in the hummingbirds' stomachs. Because some stomachs contained highly fragmented remains that could not be taxonomically identified, thereby reducing our sample size, we pooled data from all analyzed stomachs of each hummingbird species per season. Additionally, we quantified the quantity of arthropods ingested by hummingbirds during each season by measuring the biomass of ingested arthropods (both identifiable and unidentifiable remains) for each individual of each hummingbird species per season.

Due to the non-normal distribution of our data, we compared arthropod capture attempt rates among hummingbird species using a Kruskal–Wallis test [55]. We employed a post hoc Steel–Dwass non-parametric test to conduct multiple comparisons among hummingbird species. As we only observed one hummingbird species foraging for arthropods during the warm-dry season and had a small sample size for the rainy season, we restricted the comparison of arthropod capture attempt rates among hummingbird species to the cold-dry season.

We determined the arthropod foraging tactics used by hummingbirds by comparing the percentage of individuals engaging in gleaning, hawking, or perch foraging. Since we could not identify ~5% of the observed hummingbirds attempting to capture arthropods to the species level, we pooled the data from all hummingbird individuals per season.

Because the White-eared Hummingbird was the only species observed foraging for arthropods across all three sampled seasons, we exclusively focused on this species when examining seasonal variations in arthropod foraging. First, we used a generalized linear model (GLM) to examine seasonal variation in arthropod foraging, with the season (warm-dry, rainy, and cold-dry seasons) as the explanatory variable and arthropod capture attempts rate as the response variable, using an exponential distribution with a log link function. This analysis was performed using R Statistical Software (v4.3.2 [56]). Second, we used GLMs to assess the role that food resource availability has on hummingbirds' arthropod capture attempt rates. Specifically, we constructed three GLMs with the same response variable (arthropod capture attempts rate) but different explanatory variables as follows: (1) total energy availability (kJ/ha), (2) arthropod availability obtained via the beating method (dry weight/season), and (3) arthropod availability obtained from the Malaise traps (dry weight/season). In these three GLMs, we used exponential distributions

with reciprocal link functions. All statistical analyses (except the model to test the effect of season on arthropod foraging) were conducted using JMP version 9.0 [57].

3. Results

3.1. Hummingbird Ensembles

Hummingbird ensemble composition and abundance varied among seasons. Due to the low capture rates of some hummingbird species, we could not statistically compare their relative abundances. As a result, we present and compare the relative abundance data only to describe the main changes experienced by the hummingbird ensemble throughout the annual cycle. During the warm-dry season, the present ensemble consisted of the following three species: the Amethyst-throated Mountaingem, the White-eared Hummingbird, and Rivoli's Hummingbird. White-eared Hummingbirds presented a higher abundance, with 13.3 hummingbirds per 100 net hours, while the abundances of the Amethyst-throated Mountaingem and Rivoli's Hummingbird were lower, each at 0.5 hummingbirds/per 100 net hours.

During the rainy season, the hummingbird ensemble comprised the following four species: Mexican Violetear, Amethyst-throated Mountaingem, White-eared Hummingbird, and Rivoli's Hummingbird. The Mexican Violetear was the most abundant species, followed by Rivoli's Hummingbird (2.2 and 1.1 hummingbirds/100 net hours, respectively), with Amethyst-throated Mountaingems and White-eared Hummingbirds showing lower abundance values (0.5 hummingbirds/100 net hours each).

During the cold-dry season, the ensemble consisted of the following five species: Mexican Violetear, White-eared, Rivoli's, Broad-tailed, and Rufous hummingbirds. Once again, the White-eared Hummingbird dominated the ensemble by presenting the highest abundance value (7.7 hummingbirds/100 net hours), followed by Broad-tailed and White-eared hummingbirds (6.6 and 5.5 hummingbirds/100 net hours, respectively). Rivoli's and Rufous hummingbirds were the least abundant species, each presenting an abundance value of 1.6 hummingbirds/100 net hours.

3.2. Arthropod Ingestion by Hummingbirds

In all seasons, most of the collected stomachs contained arthropods, with only one stomach from the cold-dry season lacking arthropod remains. During the warm-dry season, arthropod biomass in hummingbird stomachs varied from 0.0038 g dry weight in an adult female of the Rivoli's Hummingbird species to only traces of insects (<0.002 g dry weight) in an adult female of the Amethyst-throated Mountaingem species (Table 1). During the rainy season, arthropod biomass in hummingbird stomachs varied from 0.0012 g dry weight in two adult individuals of the Mexican Violetear species to traces of insects in a Rivoli's Hummingbird adult female (Table 1). Lastly, during the cold-dry season, arthropod biomass ranged from 0.0025 g dry weight for an adult male Rivoli's Hummingbird to traces of insects present in an adult male Mexican Violetear (Table 1).

Our examination of identifiable arthropod remains indicated that hummingbirds ingested prey items from the orders Araneae (spiders), Hemiptera (bugs), Psocoptera (psocids), Hymenoptera (wasps), and Diptera (flies; Figure 2). In the warm-dry season, Diptera and Psocoptera were the most common arthropod orders ingested by White-eared Hummingbird individuals (37.6 $\pm$ 27.7% and 36.2 $\pm$ 33.0% of total arthropods in their stomachs, respectively). Diptera was the main order ingested by a Rivoli's Hummingbird individual (57.1%), while Psocoptera was the only order ingested by an Amethyst-throated Mountaingem individual (100%; Figure 2). Notably, spiders were only found in the stomachs of White-eared Hummingbird individuals during the warm-dry season. In the rainy season, Diptera was the primary arthropod order ingested by all sampled hummingbird species (Mexican Violetear: 40.3 $\pm$ 13.5%, Amethyst-throated Mountaingem: 66.6%, and White-eared Hummingbird: 100%; Figure 2). In the cold-dry season, Diptera remained the main arthropod order ingested by Rivoli's (46.4 $\pm$ 35.3%), Broad-tailed (36.7 $\pm$ 42.5%), and Rufous hummingbirds (31.5 $\pm$ 28.0%). In contrast, during this season, Hymenoptera was

the most ingested order by the Mexican Violetear (45.5 ± 5.0%), while Psocoptera was the most ingested order by the White-eared Hummingbird (62.0 ± 45.8%; Figure 2).

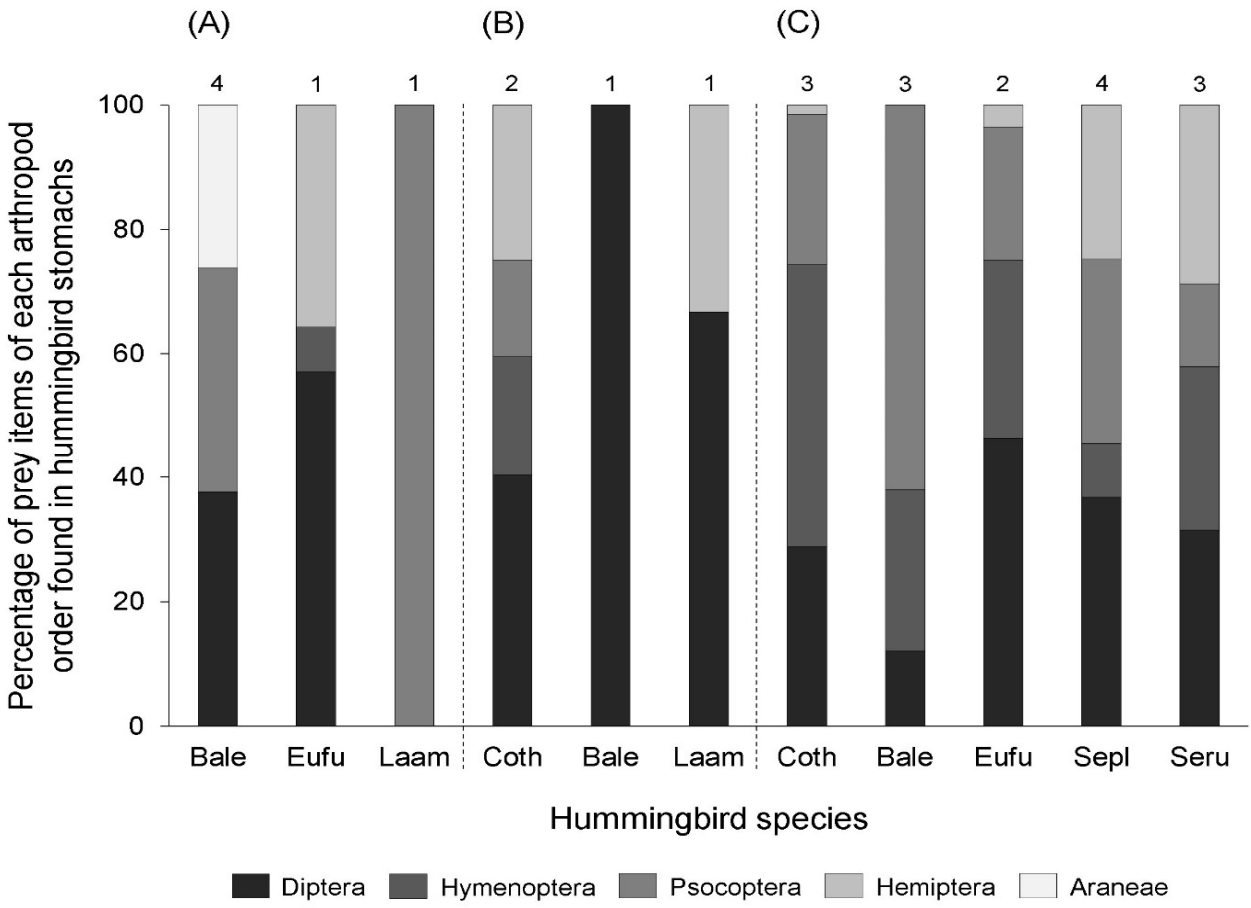


Figure 2. The relative importance of different arthropod orders in the diet of hummingbirds at our study site during (**A**) the warm-dry season (May 2016), (**B**) the rainy season (September 2016), and (**C**) the cold-dry season (February 2017). Values represent the mean percentage of prey items of each arthropod order ingested by hummingbird species. We excluded birds whose stomachs were empty or contained unidentifiable arthropods. The values at the top of the bars represent the number of analyzed stomachs. Coth = *Colibri thalassinus* (Mexican Violetear), Bale = *Basilinna leucotis* (White-eared Hummingbird), Eufu = *Eugenes fulgens* (Rivoli's Hummingbird), Laam = *Lampornis amethystinus* (Amethyst-throated Mountaingem), Sepl = *Selasphorus platycercus* (Broad-tailed Hummingbird), and Seru = *Selasphorus rufus* (Rufous Hummingbird).

3.3. Hummingbird Feeding Behavior

3.3.1. Foraging Rates

We observed only White-eared Hummingbirds foraging for arthropods during the warm-dry season, with no individuals visiting flowers. The proportion of White-eared Hummingbird individuals attempting to capture arthropods was relatively high (61.5% of the total observed), with a lower proportion engaging in other activities (38.5%; Figure 3). During this season, White-eared Hummingbird individuals foraged for arthropods at a rate of 28.84 ± 18.18 arthropod capture attempts per minute (mean ± sd, n = 80; Table 2, Figure 4A). Four White-eared Hummingbird individuals (one female and three males, representing 5% of the total observed) intensively foraged for arthropods, attempting to capture 60 or more arthropods per minute.

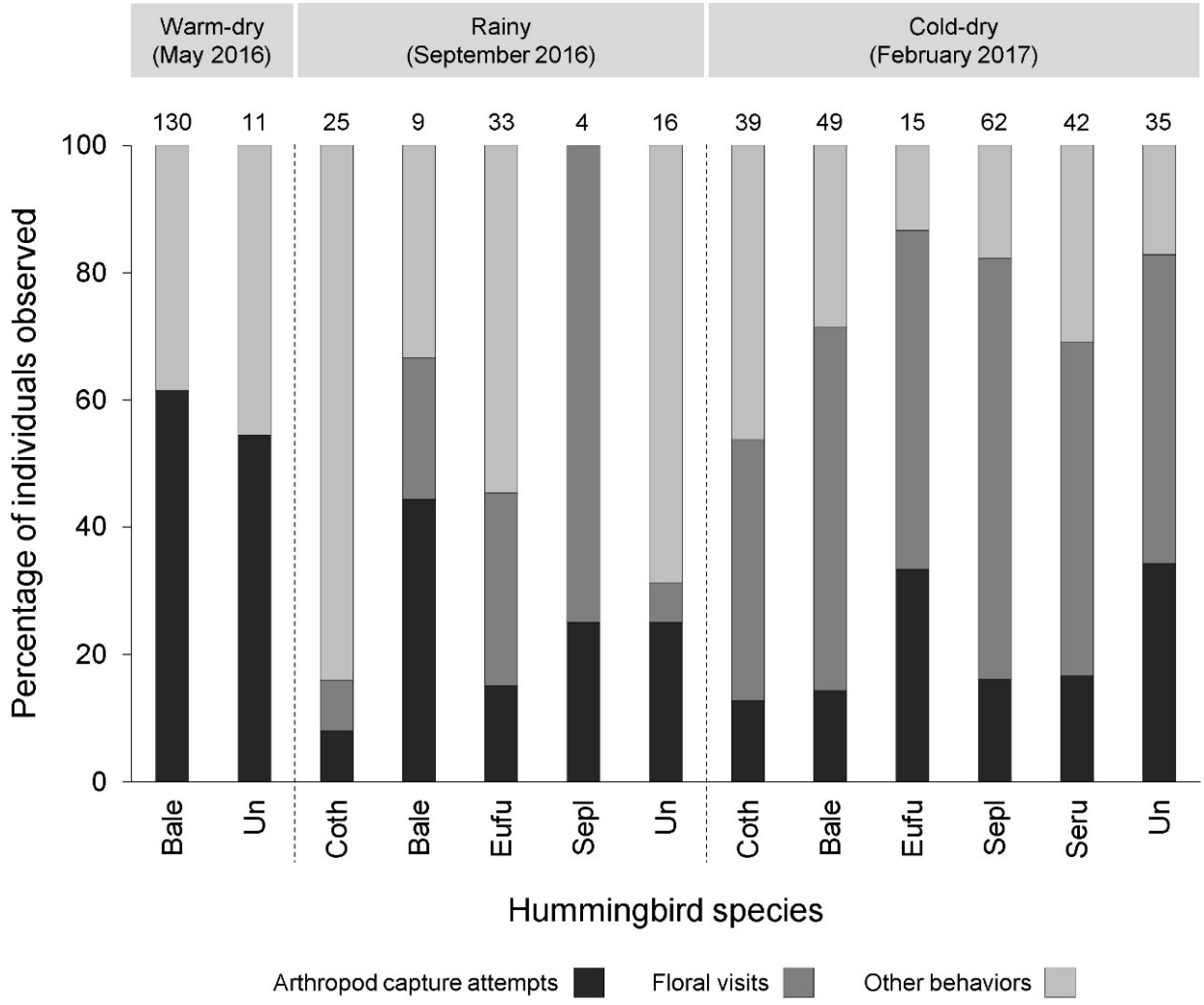


Figure 3. Percentage of individuals observed for each hummingbird species attempting to capture arthropods, visiting flowers, or performing other behaviors such as perching or hovering during the different seasons of the year. For each hummingbird species, we pooled data on female, male, and unidentified sex individuals. We excluded species with less than four observations. The values at the top of the bars represent the number of observed individuals. Coth = *Colibri thalassinus* (Mexican Violetear), Bale = *Basilinna leucotis* (White-eared Hummingbird), Eufu = *Eugenes fulgens* (Rivoli's Hummingbird), Sepl = *Selasphorus platycercus* (Broad-tailed Hummingbird), Seru = *Selasphorus rufus* (Rufous Hummingbird), and Un = Unknown.

Table 2. Hummingbirds' arthropod capture attempt and flower visit rates (events/min; mean ± sd) per species per season. For each hummingbird species, we pooled data on female, male, and unidentified sex individuals, and "*n*" represents the number of independent observations. The "Unknown" category includes individuals not identified at the species level.

Season	Species	Arthropod Capture Attempts/min	Flower Visits/min
Warm-dry	White-eared Hummingbird (*Basilinna leucotis*)	28.84 ± 18.18 (*n* = 80)	
	Unknown	23.41 ± 11.59 (*n* = 6)	

Table 2. *Cont.*

Season	Species	Arthropod Capture Attempts/min	Flower Visits/min
Rainy	Mexican Violetear (*Colibri thalassinus*)	16.43 ± 0.00 (*n* = 2)	19.54 ± 24.19 (*n* = 2)
	White-eared Hummingbird (*Basilinna leucotis*)	9.72 ± 3.82 (*n* = 4)	23.34 ± 8.00 (*n* = 2)
	Rivoli's Hummingbird (*Eugenes fulgens*)	15.94 ± 14.82 (*n* = 5)	26.38 ± 16.99 (*n* = 10)
	Amethyst-throated Mountaingem (*Lampornis amethystinus*)		20.93 (*n* = 1)
	Broad-tailed Hummingbird (*Selasphorus platycercus*)	2.90 (*n* = 1)	19.03 ± 6.50 (*n* = 3)
	Unknown	27.00 ± 24.24 (*n* = 4)	48.97 (*n* = 1)
Cold-dry	Mexican Violetear (*Colibri thalassinus*)	9.76 ± 14.72 (*n* = 5)	15.58 ± 11.01 (*n* = 16)
	White-eared Hummingbird (*Basilinna leucotis*)	15.38 ± 14.67 (*n* = 7)	27.28 ± 19.87 (*n* = 28)
	Rivoli's Hummingbird (*Eugenes fulgens*)	44.34 ± 24.31 (*n* = 5)	33.38 ± 21.61 (*n* = 8)
	Broad-tailed Hummingbird (*Selasphorus platycercus*)	5.31 ± 6.82 (*n* = 10)	24.19 ± 19.09 (*n* = 41)
	Rufous Hummingbird (*Selasphorus rufus*)	20.51 ± 32.69 (*n* = 7)	24.76 ± 15.59 (*n* = 22)
	Ruby-throated Hummingbird (*Archilochus colubris*)		20.00 (*n* = 1)
	Unknown	18.03 ± 19.05 (*n* = 12)	19.85 ± 19.70 (*n* = 19)

In the rainy season, Mexican Violetear, White-eared, Rivoli's, and a few Broad-tailed hummingbirds were observed attempting to capture arthropods and visiting flowers (Figures 3 and 4A,B). For White-eared Hummingbirds, the proportion of individuals trying to capture arthropods was higher than those visiting flowers (44.4% vs. 22.2%). However, among Rivoli's and Broad-tailed hummingbirds, more individuals were observed visiting flowers than foraging for arthropods (Rivoli's Hummingbird: 30.3% vs. 15.1%; Broad-tailed Hummingbird: 75% vs. 25%; Figure 3). For the Mexican Violetear, the proportion of individuals performing both behaviors was the same (8%; Figure 3). Despite the different proportions, all hummingbird species had higher floral visit rates than arthropod capture attempt rates during this season (Table 2, Figure 4A,B).

During the cold-dry season, all hummingbird species were observed trying to capture arthropods and visiting flowers for nectar (Figures 3 and 4A,B). The proportion of individuals visiting flowers was higher than those attempting to capture arthropods for all species (Figure 2). Similarly, except for the Rivoli's Hummingbird, all species had higher floral visit rates than arthropod capture attempt rates (Table 2, Figure 4A,B). We observed only one male individual of the Rivoli's Hummingbird species and one male Rufous Hummingbird foraging intensely for arthropods during this season (4.3% of the total observed).

We found a significant difference in arthropod capture attempt rates among hummingbird species during the cold-dry season ($\chi^2_{4,33}$ = 12.67, p = 0.01). The arthropod capture attempt rate was significantly higher in Rivoli's than in Broad-tailed hummingbirds (44.34 ± 24.31 vs. 5.31 ± 6.82 arthropod capture attempts per minute, adjusted p-value = 0.0268, from a multiple testing correction using the non-parametric Steel–Dwass test; Table 2, Figure 4A). Arthropod capture attempt rates did not differ among the other species (adjusted p-value > 0.05 for each pairwise comparison). Finally, we found that the arthropod capture attempt rates of White-eared Hummingbirds varied seasonally ($\chi^2_{2,91}$ = 12.41, adjusted p-value = 0.002), presenting significantly higher values during the warm-dry than during the rainy or the cold-dry seasons (Tables 2 and 3; Figure 4A).

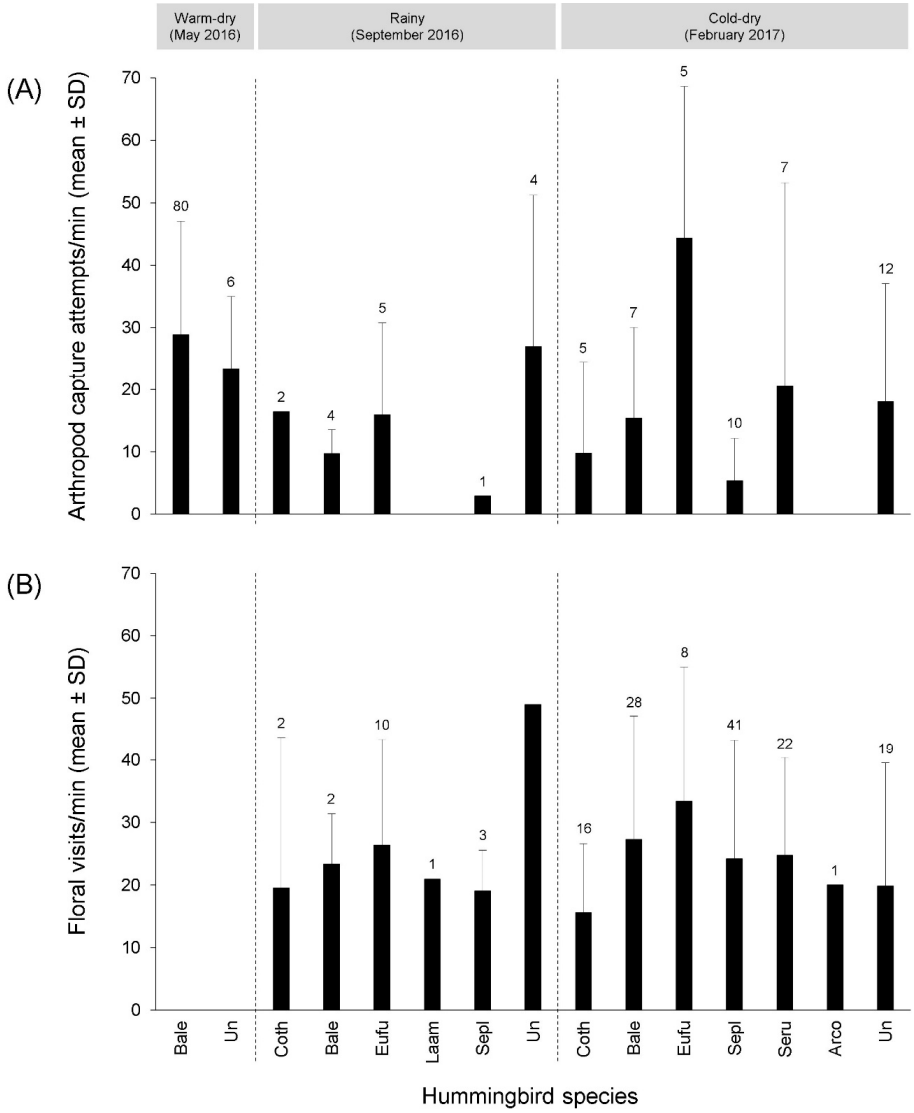


Figure 4. Number of arthropod capture attempts per minute (**A**) and floral visits per minute (**B**) for each hummingbird species during the three seasons of the year. We show the mean and standard deviation values, except for cases when $n = 1$. The values at the top of the bars represent the number of observed individuals. Coth = *Colibri thalassinus* (Mexican Violetear), Bale = *Basilinna leucotis* (White-eared Hummingbird), Eufu = *Eugenes fulgens* (Rivoli's Hummingbird), Laam = *Lampornis amethystinus* (Amethyst-throated Mountaingem), Sepl = *Selasphorus platycercus* (Broad-tailed Hummingbird), Seru = *Selasphorus rufus* (Rufous Hummingbird), Arco = *Archilochus colubris* (Ruby-throated Hummingbird), and Un = Unknown.

Table 3. Paired comparisons of arthropod capture attempt rates of White-eared Hummingbirds (*Basilinna leucotis*) between seasons of the year.

Variable	Levels	Ratio	SE	df	*t*-Value	*p*-Value
Season	cold-dry vs.rainy	1.583	0.6468	1	1.126	0.5010
	cold-dry vs.warm-dry	0.533	0.1378	1	−2.449	0.0427
	rainy vs.warm-dry	0.337	0.1128	1	−3.261	0.0045

3.3.2. Arthropod Foraging Tactics

During the warm-dry season, all the hummingbirds observed (both identified and unidentified individuals) attempted to glean arthropods directly from substrates (100% of individuals observed). In the rainy season, hummingbirds also captured arthropods

from substrates, with the majority using gleaning (92.9%) and a minority employing perch-foraging (7.1%). Finally, during the cold-dry season, the most common foraging tactic was gleaning (77.1%), followed by perch-foraging (14.6%), and hawking (8.3%).

Gleaning behavior differed among seasons and species. During the warm-dry season we only had foraging observations for the White-eared Hummingbird. Individuals from this species performed gleaning on tree foliage (44.6%) and shrubs (40.5%), while a smaller proportion conducted gleaning on herbs (9.4%), tree barks (2.7%), and the ground (2.7%; Figure 5). Similarly, during the rainy and the cold-dry season, White-eared Hummingbirds gleaned arthropods on a diverse array of substrates (Figure 5).

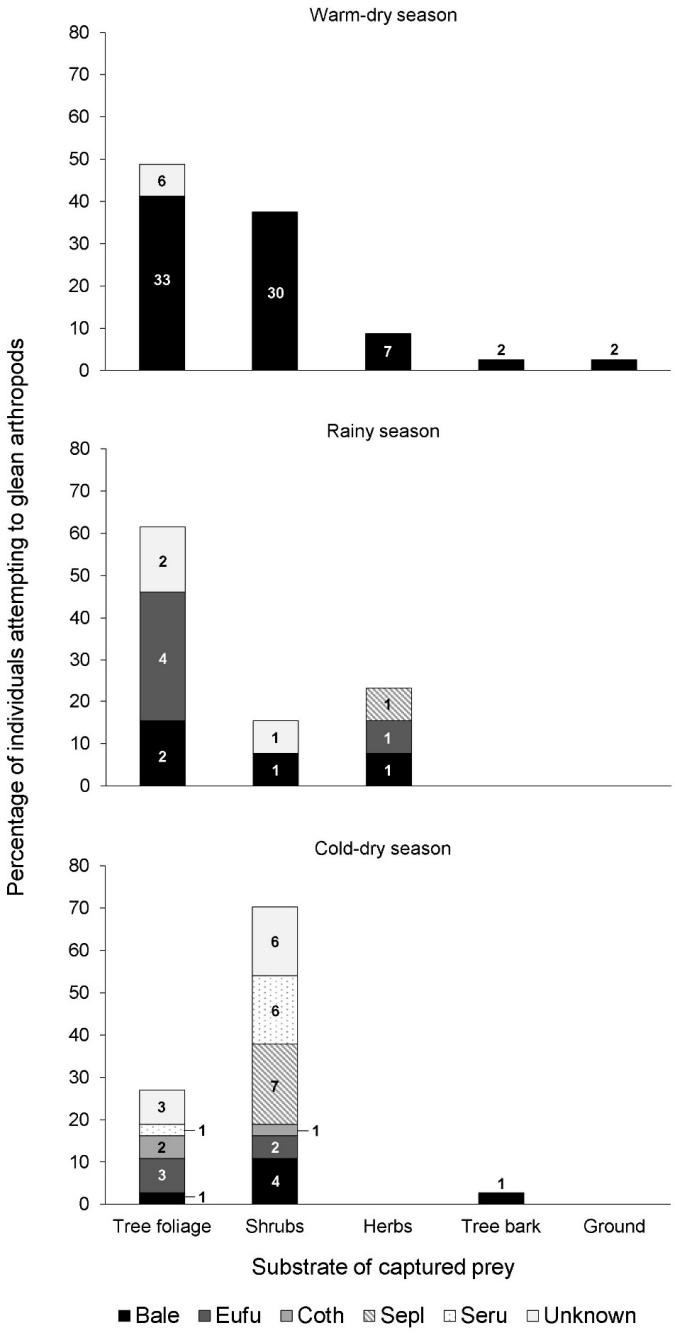


Figure 5. Percentage of hummingbird individuals observed attempting to glean arthropods on tree foliage, shrubs, herbs, tree bark, or the soil during the warm-dry, rainy, and cold-dry seasons. The different bands in the columns represent hummingbird species. Numbers inside the color bands represent the number of observed individuals.

White-eared Hummingbirds tended to glean on tree foliage and shrubs, presenting a similar behavior to the other two resident species (Rivoli's Hummingbirds and Mexican Violetears). This pattern differed from the gleaning behavior presented by the two long-distance winter migrant species (Broad-tailed and Rufous hummingbirds). During the winter months at our study site, the long-distance migrant species gleaned for insects mainly on shrubs and herbs (Figure 5).

3.4. Food Availability

No plants bloomed during the warm-dry season at our study site and the surrounding areas. In the rainy season, *Penstemon roseus* was the only plant in bloom, offering a total nectar availability of 4.71 mL/ha (0.09 kJ/ha; Table 4). In the cold-dry season, *Ribes ciliatum* and *Salvia elegans* bloomed, providing a nectar availability of 1609.92 mL/ha (53.38 kJ/ha; Table 4). We found that the availability of floral resources in our study plot did not differ from adjacent sites (Wilcoxon test: $\chi^2_{2,167} = 0.04$, $p = 0.83$).

Table 4. Nectar and arthropods are available at our study site per season. Arthropod availability only includes arthropod orders ingested by hummingbirds at our study site.

Season	Nectar Availability		Arthropod Availability	
	Abundance (mL/ha)	Energy (kJ/ha)	g dry weight/beating	g dry weight/Malaise
warm-dry	no nectar	no nectar	0.2464	0.0263
rainy	4.71	0.09	0.0517	0.0015
cold-dry	1609.92	53.38	0.0495	0.0124

The arthropods found at our study site using our two sampling methods included members of the orders Acari, Araneae, Collembola, Hemiptera, Psocoptera, Thysanoptera, Coleoptera, Hymenoptera, Diptera, and Lepidoptera. However, as our stomach analysis showed, hummingbirds only ingested prey items belonging to the orders Araneae, Hemiptera, Psocoptera, Hymenoptera, and Diptera (see Figure 2). During the warm-dry season, the availability of these arthropod orders collected using the beating method was 0.246 g dry weight/season, while in the rainy and cold-dry seasons, their availability was 0.051 and 0.049 g dry weight/season, respectively (Table 4).

3.5. Factors Affecting Arthropod Foraging by Hummingbirds

We found that the arthropod capture attempt rates of the White-eared Hummingbird were positively and significantly affected by arthropod availability, measured as both g dry weight/beating and g dry weight/Malaise (see Table 5, Figure 6). However, the arthropod capture attempt rates of this hummingbird species were not significantly affected by the energy available from nectar (Table 5, Figure 6).

Table 5. Results of the GLMs evaluating the effect of food availability on arthropod capture attempt rates of White-eared Hummingbird (*Basilinna leucotis*).

Model	Explanatory Variable	Estimate	Standard Error	χ^2_1	*p*-Value
GLM 1	intercept	2.1464	0.2342	83.9755	<0.0001
	nectar energy (kJ/ha)	0.0327	0.0279	1.9433	0.1633
GLM 2	intercept	5.1018	1.7001	30.7795	<0.0001
	g dry weight of arthropods/beating	−12.2675	6.9967	4.7114	0.0295
GLM 3	intercept	5.911	2.107	31.5378	<0.0001
	g dry weight of arthropods/Malaise	−145.7884	81.068	5.1908	0.0227

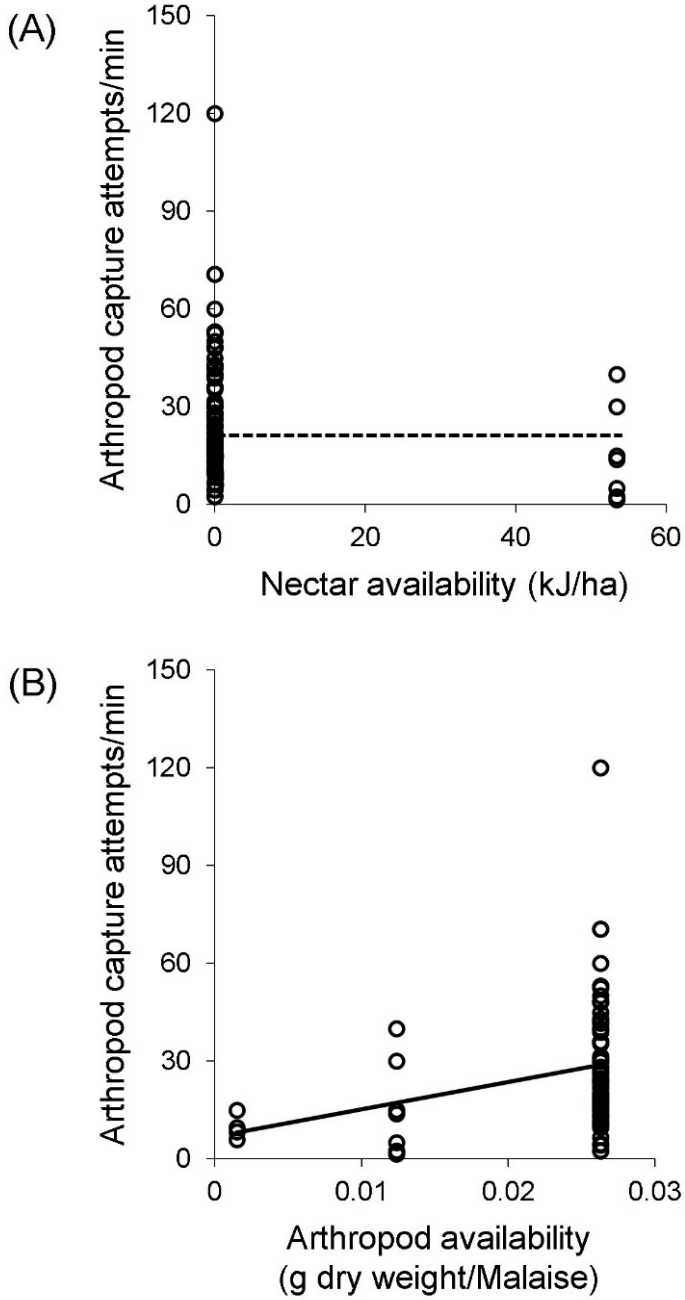


Figure 6. Relationship between the arthropod capture attempt rate of the White-eared Hummingbird (*Basilinna leucotis*) and the availability of two key resources: (**A**) nectar (kJ/ha), and (**B**) arthropods (standardized dry weight from Malaise traps). Arthropod capture attempt rates were independent of nectar availability (top panel) but showed a positive relationship with arthropod abundance (bottom panel, solid line). Arthropod biomass values represent pooled, standardized measurements from paired Malaise traps for each sampling period. This pattern of increased arthropod capture attempts with higher arthropod availability is consistent with observations in other nectar-feeding birds, such as honeyeaters and sunbirds.

4. Discussion

Our study reveals seasonal differences in arthropod capture rates among hummingbird species. Hummingbirds foraged more frequently for arthropods during the warm-dry season, when floral nectar was scarce, and arthropod availability peaked. Conversely, during the cold-dry season, when floral nectar was abundant and arthropod availability

was low, arthropod foraging activity decreased. Among the studied species, the White-eared Hummingbird exhibited the highest arthropod capture rate throughout the year. We found that arthropod availability in the environment positively influenced arthropod capture rates, while nectar abundance had no significant effect.

4.1. Seasonal Changes in Hummingbird Ensembles

Seasonal changes in hummingbird species composition and abundances occurred paired with significant fluctuations in floral nectar and arthropod availability at our study site. Changes in the hummingbird ensemble were caused by both altitudinal migrations of hummingbirds following floral phenology [26,28] and the arrival of latitudinal migrant hummingbirds during the fall and winter months [26–28]. Additionally, our data indicates that arthropod availability was crucial in determining the presence of some hummingbird species at our study site in those moments of the year when floral nectar was absent or presented low abundance.

Only three hummingbird species were present during the warm-dry season when flowers were absent, and arthropod availability was at its highest point, with the White-eared Hummingbird being the most abundant of them. The abundance of this species is related to its behavior and ecology. The White-eared Hummingbird is a small to medium-sized resident territorial species (3.2–3.6 g) that aggressively defends territories from smaller and larger hummingbird species [27,28]. This territorial behavior may contribute to its persistence during periods of nectar scarcity.

White-eared Hummingbirds have been previously reported as dietary generalists in our study area [28]. Their intense arthropod foraging during the warm-dry season was one of the highest we found throughout our sampling year, suggesting a physiological capacity to use food items with contrasting nutritional and physical characteristics. Our results also indicate that White-eared Hummingbirds can survive the absence of nectar during this season by increasing their arthropod ingestion, suggesting that this species can thrive by feeding solely on arthropods, as has been proposed for other hummingbird species in the past [6,7,11,28].

Hummingbirds can fly long distances and utilize food resources at the landscape level [58,59], with some species moving among suitable habitat patches or performing altitudinal movements in search of floral resources (see [24,26,28] as examples of previous studies that mention these movements in our study area). However, during the warm-dry season, when no plants were blooming at our study plot, only the White-eared Hummingbird was present. Our observations and mist-net captures showed that individuals of this species maintained territories and met their metabolic requirements by feeding on arthropods. We found no evidence of nectar use by this species during the warm-dry season; however, some individuals that were not defending territories may have moved to other areas to find flowers and consume nectar.

4.2. Effect of Availability of Food Resources on Arthropod Ingestion

The variations in nectar and arthropod availability across the warm-dry, rainy, and cold-dry seasons allowed us to identify two arthropod-use strategies employed by hummingbirds. The first strategy involves relying on arthropods as the primary source of nutrients (proteins, fatty acids, and micronutrients) and energy. In contrast, the second strategy entails utilizing arthropods to solely obtain specific nutrients while obtaining energy primarily from floral nectar. Our study reveals that the scarcity of nectar and the abundance of arthropods at our study site during the warm-dry season forced hummingbirds to rely on arthropods as their primary energy source. This finding is noteworthy as some hummingbird species may struggle to sustain themselves on high-protein diets due to the physiological costs of handling the byproducts of protein metabolism (Schondube and Maya-García, personal observations [2,60,61]). Our results suggest that hummingbird species equipped with the physiological capacity to survive only on arthropods should be capable of maintaining year-round populations at our study site, potentially becoming the

dominant species in the ensemble in the absence of nectar resources. Meanwhile, species unable to effectively metabolize protein-rich diets may be compelled to undertake local altitudinal movements in search of nectar, thereby influencing the composition of the hummingbird ensemble [26,28].

The White-eared Hummingbird was the only species that foraged for arthropods during all three seasons, ingesting a large quantity of arthropods during the warm-dry season when other hummingbird species did not. This finding correlates with the fact that the stomachs of this species from this season contained, on average, three times more arthropods than stomachs collected during the other two seasons, indicating the importance of arthropods for this species at a time when flowers were not available. Karasov [62] estimates that the metabolizable energy content of dry arthropods for birds is 19.3 kJ/g. If White-eared Hummingbird individuals were capturing arthropods of fruit-fly size and presented a 30% capture success rate, they could cover their daily energy expenditure in less than nine hours by feeding only on arthropods (Field metabolic rate of the White-eared Hummingbird = 26.71 kJ/day [24]). The high arthropod foraging rate of the White-eared Hummingbird indicates that this species could satisfy all its nutritional and energetic requirements by feeding exclusively on arthropods and being able to survive in the absence of floral nectar.

The arthropod foraging patterns of the White-eared Hummingbird were similar to those reported for other specialized nectar-feeding birds such as honeyeaters (Meliphagidae) and sunbirds (Nectariniidae). These groups of nectar-feeding birds, which are distributed throughout Oceania, Africa, and South Asia, increase their arthropod ingestion in response to the abundance of arthropods in the environment [17–20,63–66]. As far as we know, this is the first report of this foraging pattern in a hummingbird species. This result also indicates that when nectar, the basic food of these birds (food that is eaten daily, represents the primary portion of the diet by mass, and provides most of the nutrients or energy in the diet), is available and abundant, hummingbirds, like sunbirds and honeyeaters, use arthropods solely as complementary food (food that supplies a suite of nutrients that are present in low concentrations in the basic food of the diet) to obtain proteins, fatty acids, and micronutrients. However, when nectar availability is low or absent and arthropod abundance is high, arthropods play a role as alternative food (food that replaces the basic food when its' abundance is low, providing both nutrients and energy). Under this set of conditions, hummingbirds compensate by ingesting more arthropods to increase their energy intake and meet all their nutritional and energy requirements. In addition, during the warm-dry season, the proportion of individuals attempting to capture arthropods intensely ($\geq$60 arthropod capture attempts/min) was higher than during the rainy and cold-dry seasons. We consider that this arthropod "feeding frenzy" results from the high availability of small arthropods in the environment and the capacity of White-eared Hummingbird individuals to ingest and process large quantities of proteins.

4.3. Arthropod Foraging Tactics

Gleaning was the hummingbirds' primary arthropod foraging tactic throughout all three climatic seasons. This foraging method has been previously reported as commonly used among various hummingbird ensembles [10,12,67], suggesting that it represents a more energetically efficient strategy than capturing insects in flight [12]. Therefore, at our high-altitude study site, hummingbirds likely rely on gleaning more frequently than other foraging tactics to save energy, mainly during months when floral nectar is scarce, and night temperatures can drop below 0 °C.

The seasonal change we observed on the predominant gleaning strata, from tree foliage during the warm-dry and rainy seasons to the shrub layer during the cold-dry season, may be explained by the following two complementary hypotheses: (1) changes in gleaning strata are related to fluctuations in the abundance of different arthropod orders and their vertical distribution within the vegetation [36], and (2) the use of different arthropod foraging strata by resident and long-distance migrant hummingbirds.

Regarding the first hypothesis, bugs (Hemiptera) and psocids (Psocoptera) were the most prevalent arthropod groups found in tree and shrub foliage during the warm-dry and rainy seasons, whereas flies (Diptera) were the most abundant aerial insects in the subalpine scrub during the cold-dry season. Bugs and psocids inhabit bark and foliage, feeding on plant tissues [36]. At the same time, flies tend to concentrate around food sources like flowers, fruits, and decomposing plant and animal tissues, making them more abundant in lower plant strata [36]. Therefore, the seasonal variation in the proportion of the prey foraging substrate used by hummingbirds is shaped by differences in arthropod abundance and activity patterns.

Additionally, our results indicate that resident species tend to glean for arthropods predominantly on tree foliage, while the long-distance migratory hummingbirds use shrubs and herbs as their primary gleaning substrates. This behavioral difference is related to the behavioral dominance of the different species that comprise the ensemble. The three resident species (Mexican Violetear, White-eared, and Rivoli's hummingbirds) are behaviorally dominant and larger in body mass than the two long-distance migrants (Broad-tailed and Rufous hummingbirds [27,28]). As a result, to avoid aggressions while foraging, both migratory species tend to hide and forage for flowers at lower substrates than larger resident species (Schondube personal observations [26,28]). The lower arthropods gleaning substrates used by these two species could also be a strategy to reduce aggressions from more dominant resident species [10,11].

4.4. Differences in Arthropod Ingestion Among Hummingbird Species

The observed differences in arthropod capture attempt rates among hummingbird species were generated by the crucial differences in the observed species' foraging behaviors and ecological roles. For example, the arthropod capture attempt rates of the Rivoli's Hummingbird were higher than those of the Broad-tailed Hummingbird. At our study site, Rivoli's Hummingbird is a large, very aggressive species (7–8 g) known for trap-lining foraging, which involves visiting a series of widely spaced nectar sources [24,26–28]. This foraging strategy may increase their exposure to diverse microhabitats and thus lead to more arthropod encounters.

In contrast, the Broad-tailed Hummingbird is a smaller, long-distance winter migrant species (3–4 g) that defends territories from smaller hummingbirds to feed on floral nectar [24,26–28]. Their territorial behavior may limit their foraging range and, consequently, their arthropod encounter rates. Additionally, the larger size of Rivoli's Hummingbird might allow it to target a wider range of arthropod prey sizes, potentially contributing to its higher capture attempt rates. These behavioral and morphological differences illustrate how species-specific traits can influence nectar foraging and arthropod capture strategies in hummingbirds.

Therefore, during the cold-dry season when floral resources are abundant, Rivoli's Hummingbird individuals could increase their arthropod ingestion relative to nectar to reduce interspecific competition for floral resources and obtain additional energy from arthropods. Meanwhile, Broad-tailed Hummingbird individuals ingested arthropods at a meager rate, primarily to meet their nitrogen requirements while relying on nectar as their primary energy source to accumulate fat in preparation for migration at the end of the cold-dry season.

4.5. Effects of the Population Declines of Arthropods on Hummingbirds in a Changing World

In recent years, many studies have reported significant declines in the diversity and abundance of specific arthropod taxa worldwide (e.g., bees, ants, beetles, butterflies, and moths [68–70]). The primary factors contributing to these declines include (1) loss of natural habitats, (2) intensified agriculture and urban development, (3) pollution from agrochemicals, and (4) climate change [68–70]. Sánchez-Bayo and Wyckhuys [70] suggested that such declines could lead to the extinction of up to 40% of the insect species globally in the coming decades. While the reduction in arthropod diversity and abundance will

negatively impact all hummingbird species by limiting their protein intake [71,72], our findings suggest that this decline can also limit the energy intake of species that rely on arthropods when nectar is unavailable. The role of arthropods in the survival of hummingbirds could be further heightened when considering that climate change may dimmish nectar production and quality, which serves as the basic food for hummingbirds in many regions of the Americas [73,74]. Under this scenario, arthropods could become essential for the survival of hummingbirds in a human-altered environment.

4.6. Study Limitations

Studying insect foraging in hummingbirds poses numerous challenges due to their rapid movements, small body size, and inconspicuous behaviors during insect hunting, which contrast sharply with their more visible nectar-feeding activities [6,10–12]. When hunting arthropods, hummingbirds often employ subtle foraging techniques such as hover-gleaning, sally-gleaning, and hover-hawking. These behaviors are difficult to observe in dense foliage and can be mistaken for other activities, such as gathering nesting materials [11,12,75]. Additionally, the small size of the arthropods consumed by hummingbirds makes it difficult to confirm captures and identify specific prey species [11,12,75]. The high diversity of arthropod prey and their spatial and temporal variability further complicate these challenges, making systematic observations rare in the literature [6,10–12]. Researchers typically rely on resource-intensive methods, such as stomach content analysis or extended field observations, which often fail to capture the full complexity of hummingbird foraging habits [76,77].

Studying hummingbirds in small plots, such as our two-hectare site, offers valuable insights into resource abundance and behavior but also presents notable limitations. A small area may not represent the full range of habitats and resources these highly mobile birds exploit across the landscape, providing only a partial view of their foraging ecology [58,59]. Hummingbirds frequently traverse large areas, mainly when resources like nectar and arthropods are patchily distributed or present low abundances, making it difficult to generalize findings from small study plots. Furthermore, a limited plot size reduces the number of individuals observed while increasing the likelihood of repeated observations of the same birds, which weakens statistical reliability and diminishes the study's accuracy [37,38].

To overcome these challenges, we recommend expanding both the spatial and temporal scope of future studies to capture a more comprehensive picture of hummingbird foraging ecology. Emerging technologies, such as radio telemetry designed for hummingbirds, would enable the detailed tracking of their movements and habitat use [78,79]. Sampling should include diverse vegetation strata and extend across multiple seasons to reflect fluctuations in arthropod availability and foraging behaviors (e.g., [12,18,44,45]). Incorporating DNA metabarcoding could provide more precise information about prey diversity and diet composition. Finally, integrating these studies with long-term ecological monitoring programs would help contextualize seasonal and interannual variations, yielding more robust and generalizable findings.

5. Conclusions

Our results show that during the season when nectar is absent or scarce and the abundance of arthropods is the highest (warm-dry season), hummingbirds increase their arthropod capture attempt rates, suggesting they use them as an alternative food source for energy and nutrients. In contrast, when nectar is available and abundant in the environment (cold-dry season), most hummingbird species reduce their arthropod capture attempt rates, using this food source primarily to fulfill their nitrogen requirements (as complementary food). Additionally, our study suggests that seasonal changes in hummingbird ensemble structure correlated with variations in food resource availability. Hummingbird species with a high physiological capacity to ingest more arthropods, utilizing them as an energy source and surviving solely on this food resource, may establish year-round populations

and become abundant in a site where nectar production undergoes significant fluctuations. Meanwhile, species unable to subsist on rich-protein diets must migrate in search of floral resources.

Building on our findings, we recommend several directions for future research. Studies should investigate the physiological mechanisms enabling certain hummingbird species to rely heavily on arthropods when nectar is scarce, exploring digestive efficiency and nutrient assimilation under different diet compositions. The potential impacts of climate change on the synchronization between hummingbird presence and arthropod abundance peaks warrant examination, as this relationship could be crucial for hummingbird conservation. Future work should also explore how variations in arthropod availability influence hummingbird migration patterns, territoriality, and breeding success across different ecosystems. Additionally, investigating the cascading effects of hummingbird arthropod consumption on local insect populations and plant-pollinator networks would provide valuable insights into broader ecological dynamics. These research directions would contribute to a more comprehensive understanding of hummingbird ecology and inform effective conservation strategies in the face of ongoing environmental changes.

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