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Article

Pollination patterns by Green-backed Firecrown hummingbirds

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SUMMARY

The Green-backed Firecrown is the only hummingbird species found throughout the temperate rainforests of southern South America and is among the region's most important pollinators. A diverse assemblage of the region's flora appears to rely on the Green-backed Firecrown for pollination, which makes the firecrown vital for ecosystem function. However, relatively little is known of firecrown ecology. We examined the foraging patterns of Green-backed Firecrowns of various ages and both sexes, using pollen samples taken from birds in southern Chile. We hypothesized that males and females would carry distinct pollen communities (sets of pollen morphospecies) and would differ in the number of pollen morphospecies carried. We found a clear difference between pollen communities carried by hummingbirds in summer and winter, but little differentiation by age and sex. We also found that females, on average, carried more pollen morphospecies than do males, and juveniles carried more morphospecies than do adults. All Green-backed Firecrowns carried significantly higher numbers of pollen grains in summer than in winter. Our results show intriguing differences in foraging behavior and pollination roles across ages and between sexes, which support anecdotal observations that adult males are territorialists while females and juveniles forage opportunistically. Since Green-backed Firecrowns are the only hummingbird species throughout most of their range, sexually divergent foraging patterns suggest that males and females may fill the ecological roles of different species. Our results add to the field's understanding of the foraging patterns of Green-backed Firecrowns and help us better appreciate the complexity of its ecological role.

INTRODUCTION

Pollinators play vital roles in ecosystem function. Seventy-eight percent of flowering plants in temperate regions worldwide depend on animal pollinators for reproduction, while a mean of 94% of angiosperms in tropical regions do so (1). In all, at least 299,200 known plant species, including most major food crops, rely on animal pollinators (1, 2). It is, therefore, very important to have a clear understanding of the ecology of pollinators and of the threats that face them. It is especially important to understand the ecology of keystone pollinators, species upon which a disproportionately large number of plant species depend for pollination.

The Temperate Rainforests of Southern South America (TRSSA) in southern Chile and Argentina contain a relatively simple pollinator community, in which the region's only hummingbird seems to play a particularly important role. The Green-backed Firecrown (*Sephanoides sephaniodes*) is endemic to the region and is the southernmost-ranging species of hummingbird in the world, occurring in areas where there are few, if any, sympatric animal pollinators (3, 4). However, the TRSSA's diverse flora is highly dependent on animal pollination (5). While long-proboscid insects (e.g., *Bombus dahlbomii* and Nemestrinidae spp.) may contribute to the pollination of some plant species, much of the floral community appears to be entirely dependent on the Green-backed Firecrown for pollination; in fact, about 20% of the region's woody plant genera feature ornithophilous (bird-pollinated) flowers (3, 5, 6). The reliance of such a large portion of the floral community on a single species is exceptional. In most ecosystems where hummingbirds are found, the ratio of hummingbird-pollinated plant species to hummingbird species is well below 5:1 (3). For instance, in temperate rainforests in the state of Washington, U.S.A., which are located about as far from the equator as are the TRSSA, only one species of plant depends on a hummingbird pollinator (7). The diverse floral community of the TRSSA relies, in large part, upon the Green-backed Firecrown alone, and consequently, the Green-backed Firecrown is often considered a keystone species, a species disproportionately important in maintaining the diversity and structure of its community (3, 5). Therefore, it is essential that the Green-backed Firecrown's ecological role be well studied and understood.

Adult Green-backed Firecrowns are sexually dimorphic. Males are larger than females, have relatively shorter bills, and exhibit bright iridescent crown feathers (8). While males are highly territorial, females are not known to defend discrete territories (9). Despite these morphological and behavioral differences, little information exists on sex-related differences in diet or contributions to plant pollination. We therefore examined pollen samples collected from wild Green-backed Firecrowns (**Figure 1**) in the Los Ríos Region, Chile, to investigate patterns of pollination with respect to differences in floral visitations between males and females, between adults and juveniles, and between birds captured in summer versus in winter. We hypothesized that morphological and behavioral differences between the sexes would cause males and females to differ in diet and to feed from distinct floral communities. Under this hypothesis, we predicted that females would carry a greater diversity of pollen, due in part to their longer bills, which likely enable them to visit a more diverse suite of plant species, and due also to the fact that females are not known to

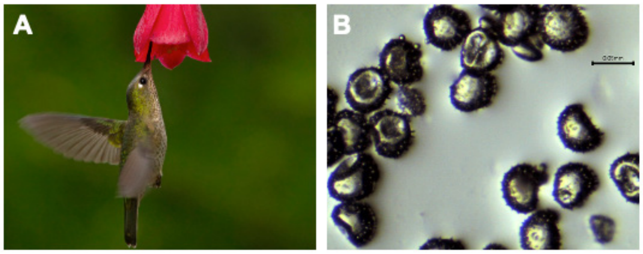

Figure 1: The Green-backed Firecrown and pollen examined. A) A female Green-backed Firecrown visiting a *Lapageria rosea* flower. Photo credit: Juan Andrés Vara Braun. B) Pollen from a *Lapageria rosea* flower viewed under the microscope. The black scale bar measures 0.05 mm.

defend discrete territories, and so are not confined to visiting the plant species present within a small area but rather are able to utilize a wider variety of flowers. Also, given that most hummingbird-pollinated plant species in the TRSSA bloom during the austral spring and summer (6), we hypothesized that hummingbirds would carry more pollen morphospecies in the summer months.

RESULTS

We collected pollen samples from 38 Green-backed Firecrowns (**Table 1**). Twenty-eight of the birds were successfully aged and sexed in the field in Chile and were therefore included in the analyses of differences in pollen richness (the number of unique morphospecies carried by an individual bird) and number of pollen grains.

During the process of pollen examination and identification, we identified 15 distinct morphospecies, based on pollen shape, size, and texture (**Table 2**). Five morphospecies corresponded directly to a plant species or group of species with pollen similar in appearance. The five known plants were *Tristerix corymbosus* (Loranthaceae), *Lapageria rosea* (Philesciaceae), *Greiga landbeckii* (Bromeliaceae), *Embothrium coccineum* (Proteaceae), and species from the Gesneriaceae family (including *Asteranthera ovata*, *Sarmienta repens*, *Mitraria coccinea*). *Lapageria rosea* and *Greiga landbeckii* were observed almost entirely in samples from the austral winter, while eight morphospecies, including *Embothrium coccineum*, were observed only during the austral summer. A non-metric multidimensional scaling (NMDS) plot showed clear differentiation in pollen community across the seasons, but little differentiation in the pollen community between juveniles and adults, or between males and females (**Figure 2**).

Birds in summer carried many more pollen grains than did birds in winter, with an average of nearly four times as many grains per bird in summer than in winter ($p = 0.0067$; **Figure 3**; **Table 3**). In summer, when juveniles and adults were reliably distinguishable, the two age stages carried similar numbers of pollen grains. There was no detectable difference in average grain counts between males and females. We used General Linear Models (GLMs) to further explore the drivers of grain counts and richness. The best model for explaining grain counts included season as the only predictor variable (**Table 4**). Sex, capture time, bill length, and body mass were not significant or included in the preferred model.

Differences in pollen richness between seasons and sexes were marginally significant (**Table 3**). Hummingbirds carried an average of 1.0 morphospecies more in the summer than in the winter ($p = 0.0516$; **Figure 4**) and females carried an average of 0.9 morphospecies more than did males ($p = 0.0662$). Summer juveniles carried an average of 1.4 more morphospecies than did summer adults, though this difference too was only marginally significant ($p = 0.0872$; **Table 3**). The best model for explaining morphospecies richness included both season and sex as significant ($p < 0.05$) predictor variables (**Table 4**). Capture time, bill length, and body mass were not significant or included in the preferred model.

DISCUSSION

We observed clear seasonal differences in pollen community composition, suggesting that hummingbirds feed from different flowers in summer than in winter. We also observed compelling patterns in pollen richness and grain counts related to sex, season, and age stage. However, as we analyzed variations in our data across these categories, we noted that these three factors were interrelated in our dataset – juvenile hummingbirds are only distinguishable in summer (though they are likely present year-round), and 86% of the juveniles we sampled were female. This correlation among the categories juvenile, female, and summer, makes it difficult to discern which of these variables are driving the patterns we

Hummingbird ID	Season	Age	Sex	Pollen richness	Number of pollen grains
A01501	Summer	Juvenile	U	2	738
A01508	Summer	Juvenile	F	5	1662
A01509	Summer	Unknown	M	2	14422
A01562	Summer	Adult	F	3	104
A01563	Summer	Unknown	F	2	195
A01564	Summer	Juvenile	U	7	4924
A01565	Summer	Juvenile	F	4	855
A01566	Summer	Adult	M	2	85
A01567	Summer	Juvenile	U	4	8972
A01568	Summer	Juvenile	M	3	4096
A01569	Summer	Unknown	M	1	3847
A01570	Summer	Unknown	M	0	0
A01572	Summer	Juvenile	F	7	4515
A01573	Summer	Juvenile	F	2	726
A01574	Summer	Juvenile	F	5	2611
A01575	Summer	Unknown	U	6	521
A01576	Summer	Adult	M	2	1000
A01577	Summer	Juvenile	U	2	4255
A01579	Summer	Juvenile	U	1	736
A01580	Summer	Adult	M	3	3084
A01620	Summer	Adult	M	2	145
A01631	Summer	Juvenile	U	5	784
A01634	Summer	Adult	M	3	3230
A01635	Summer	Adult	F	3	1821
A01636	Summer	Juvenile	F	2	1521
A01697	Winter	Adult	M	0	0
A01733	Winter	Adult	F	3	35
A01734	Winter	Adult	F	1	10
A01735	Winter	Adult	F	2	173
A01737	Winter	Adult	M	2	192
A01742	Winter	Adult	M	2	116
A01744	Winter	Adult	M	2	29
A01750	Winter	Adult	M	4	2959
A01766	Winter	Adult	F	2	1176
A01768	Winter	Adult	F	3	765
A01781	Winter	Adult	F	4	330
A01782	Winter	Adult	F	3	451
A01783	Winter	Adult	M	2	384

Table 1. Metadata for all 38 Green-backed Firecrown hummingbirds (Sephanoides sephaniodes) captured (M = Male, F = Female, U = Unknown).

Morphospecies	Summer incidence	Winter incidence	Plants included in morphospecies (if known)
A	0.73	0.29	Gesneriaceae (including *Asteranthera ovata*, *Sarmienta repens*, *Mitraria coccinea*)
N	0.50	0.00	
D	0.46	0.57	*Tristerix corymbosus*
G	0.38	0.14	
M	0.23	0.00	
H	0.19	0.00	
Q	0.19	0.00	
K	0.12	0.00	
O	0.12	0.00	
B	0.04	0.57	*Lapageria rosea*
F	0.04	0.07	
I	0.04	0.00	
J	0.04	0.00	*Embothrium coccineum*
C	0.00	0.64	*Greiga landbeckii*
L	0.00	0.00	

Table 2. Pollen morphospecies collected from Green-backed Firecrown hummingbirds (Sephanoides sephaniodes) in the Los Ríos Region, Chile in summer (Jan-Feb) and winter (July-Aug) 2018, ordered by summer incidence. Incidence is the proportion of hummingbirds carrying ≥5 grains of that morphospecies in summer or winter. Morphospecies were assigned a letter ID (A through O) in the order they were described. Corresponding plant species (if known) are reported to the highest taxonomic unit possible.

see in pollen richness and grain counts. For each comparison, we have attempted to identify the underlying drivers of our observed patterns by critically examining our data, drawing on other studies, and considering the life history of our study species. In addition, we use GLMs to attempt to further disentangle the effects of season and sex.

In the case of pollen grains, we noted that grain counts may have been affected both by the number of flowers a hummingbird visits and by the pollen characteristics of the flowers visited (e.g., number of pollen grains produced per flower and tendency of the pollen grains to adhere to the hummingbird). Given the clear differences in the composition of pollen carried in summer versus in winter (**Figure 2**), the most likely explanation for the greater number of pollen grains in summer is that these hummingbirds were visiting different plants in summer and that at least some of these plant species produced sticky or abundant pollen that increased summer pollen counts. Age and sex did not appear to be important drivers of pollen grain counts.

Morphospecies richness was greater in summer than in winter, among juveniles than among adults, and among females than among males (though each of these differences was marginally significant; see **Table 3**). The best supported GLM explaining pollen richness (year-round) included both season and sex as significant predictor variables, providing further evidence indicating that these both are important factors affecting morphospecies richness. All of these patterns seem plausible given our knowledge regarding the foraging behavior of Green-backed Firecrowns. Most hummingbird-pollinated flower species in our study area bloom in spring or summer (6), and so our data confirm our expectation that hummingbirds would carry more pollen morphospecies in the summer. Sex- and age-related differences in pollen richness likely reflect morphological and behavioral differences between juveniles, adult males, and adult females.

Our results suggest that juvenile Green-backed Firecrowns carry more diverse arrays of pollen than do adults. Juveniles are likely subordinate to adults, especially to territorial males, and might therefore be denied access to dense flower patches, which would likely force them to forage from a more dispersed and diverse suite of flowers, and therefore carry a more varied array of pollen. Alternatively, it is possible that juveniles have simply not yet developed preferences for certain flower groups, and so forage from a larger array of plants. Adults display a distinct preference for sucrose-rich solutions, but discrimination between sugar solutions has not been documented in juveniles (10); this suggests that juveniles may be less discriminating in their choice of floral food sources. Additionally, most juveniles sampled were female, and this also may contribute to the perceived disparity in the number of morphospecies characters between juveniles and adults.

Male Green-backed Firecrowns have, on average, bills that are significantly shorter than those of females (4, 8, 11). The average mass of male Green-backed Firecrowns in our study region was 6.2 g, in the center of the range for hummingbirds (8, 11, 12). These qualities—short bills and medium mass—align with those of territorialist hummingbirds (13, 14), and there is some behavioral evidence to suggest that males are also territorial also (11, 15). We found that males generally carried fewer pollen morphospecies than did females, and this too supports the idea that male Green-backed Firecrowns are territorial. It seems likely that territorialist hummingbirds would be more limited in their array of pollen than would generalists or hummingbirds with other foraging strategies, as territorialism allows hummingbirds to monopolize a narrow section of the available resources, limiting the flowers available—both to themselves and to other territorial hummingbirds—and eliminating the need to access a more diverse, less concentrated array of flora. Our finding that male firecrowns carry less diverse arrays of pollen provides additional evidence indicating that male firecrowns are territorial.

In contrast, we found that females carry, on average, more morphospecies of pollen, and other studies have found that females have lower body mass and longer bills (4, 8). A number of authors have suggested that the possession of longer bills by females may be favored as a result of intersexual food competition, as male hummingbirds of many

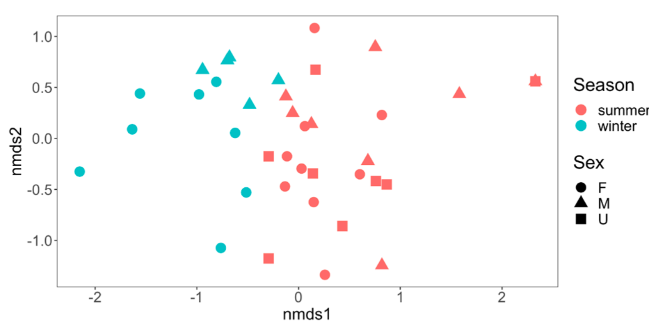

Figure 2. NMDS (non-metric multidimensional scaling) plot of community composition of pollen morphospecies collected from 38 Green-backed Firecrown hummingbirds. Each point represents the community composition of pollen collected from a single hummingbird. Points that are closer together indicate hummingbirds carrying more similar communities of pollen. Point shapes and colors indicate the sex of the hummingbird and the season in which it was captured. NMDS stress = 0.1383.

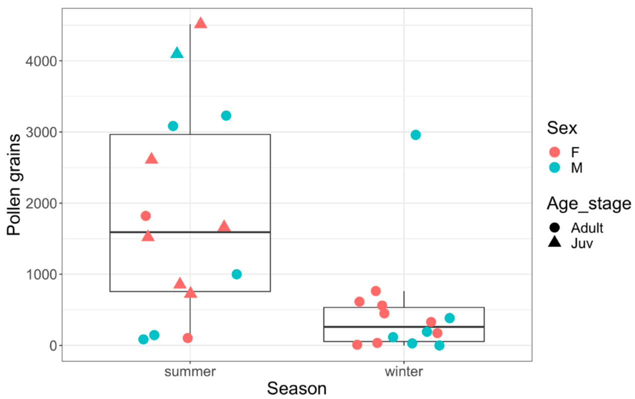

Figure 3. Number of pollen grains carried by 28 Green-backed Firecrown hummingbirds. Number of grains was greater in summer than winter (p = 0.0067), but similar among juveniles and adults (p = 0.2524) and among males and females (p = 0.6622). Points are jittered horizontally to facilitate interpretation.†).

	Response variable	Group	Mean ± SE (n)	p-value
Summer	Pollen richness	Adult Juvenile	2.6 ± 0.7 (7) 4.0 ± 0.2 (7)	0.0872†
	Number of grains	Adult Juvenile	2284 ± 573 (7) 1353 ± 523 (7)	0.2524
Year-round	Pollen richness	Summer Winter	3.3 ± 0.4 (14) 2.3 ± 0.3 (14)	0.0516
		Male Female	2.3 ± 0.3 (12) 3.2 ± 0.4 (16)	0.0662
	Number of grains	Summer Winter	1818 ± 395 (14) 473 ± 202 (14)	0.0067†
		Male Female	1277 ± 453 (12) 1047 ± 295 (16)	0.6622

Table 3. Summary statistics of between group comparisons of pollen richness and number of pollen grains collected from 28 Green-backed Firecrowns. Differences between groups were compared using two-sample t-tests or Welch's t-tests (indicated by †).

species defend flower patches and force females to forage more opportunistically among more scattered resources, occasionally filching from the territories of males, using a strategy referred to by some authors as facultative traplining (16, 17). A long bill is helpful when foraging in this manner, as it tends to allow visits to flowers to be briefer and more efficient. It appears that the Green-backed Firecrown exemplifies this phenomenon. While sexual dimorphism in bill length and body mass is fairly common among hummingbirds, especially in distinctly sexually dichromatic species such as the Green-backed Firecrown (12, 16), the way in which this dimorphism relates to foraging behavior and ecological niche has been documented thoroughly in relatively few species of hummingbird (18).

Our study contributes to a growing number of studies documenting sexual differences in foraging behavior and morphology in Green-backed Firecrowns (8, 9, 11, 19). Our results regarding sex- and age-related foraging patterns are similar to the range of values reported by Fraga *et al.* (11), the only other study of Green-backed Firecrowns that differentiated among males, females, and juveniles (although their study only reported approximate values). As the only hummingbirds throughout nearly all of their range, Green-backed Firecrowns seem to have adapted to occupy multiple pollination niches by developing different strategies for males and females—males seem to be territorialists, and females seem to be facultative trapliners. Interestingly, simple hummingbird communities on islands often consist of two species occupying two niches: facultative trapliners and territorialists (13). Here, male and female Green-backed Firecrowns evidently take on these two roles; in doing so, they seem to almost occupy the roles of two different species. Surprisingly however, despite differences in pollen richness, bill morphology, and apparent foraging behavior, we did not observe clear differences in pollen community composition between males and females as we had hypothesized.

The few other hummingbird species with well-documented sexual dimorphism in foraging strategy (e.g., Purple-throated Carib—see Temeles, *et al.* (18)) co-occur with other hummingbird species. However, throughout nearly all of its range, the Green-backed Firecrown is the only hummingbird present, at least in its habitat. The effects of interspecific competition on the foraging roles of males and of females would therefore be interesting to study more closely. For example, might pressure from interspecific competition result in a change in the foraging strategies of the sexes? Only on the Juan Fernandez Islands does the Green-backed Firecrown co-occur with an ecologically similar bird, its sister species, the critically endangered Juan Fernandez Firecrown *Sephanoides fernandensis* (12, 20). There, male Juan Fernandez Firecrowns appear to be the dominant territorialists, forcing female conspecifics and Green-backed Firecrowns of both sexes into more opportunistic roles (15, 20). It appears that interspecific competition does indeed affect the foraging strategy of males, forcing them into a role more similar to the role of female Green-backed Firecrowns elsewhere. Whether this pressure will result in any morphological changes remains to be seen.

The situation of the Green-backed Firecrown and the Juan Fernandez Firecrown provides an interesting case study that could shed light on niche partitioning, territoriality, and foraging ecology in other hummingbirds. However, the situation between the firecrowns is of special interest as the Juan Fernandez Firecrown is in imminent danger of becoming extinct (20, 21). Should this unfortunate event occur, resulting

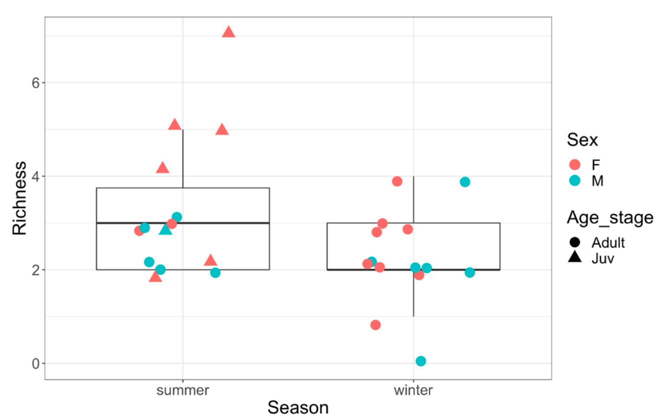

Figure 4. Richness (number) of pollen morphospecies carried by 28 Green-backed Firecrown hummingbirds. Richness was marginally greater in summer than winter (p = 0.0516), in juveniles than adults (p = 0.0872), and in females than males (p = 0.0662). Points are jittered vertically and horizontally to facilitate interpretation.

Response variable	Season	Sex	AIC_c	ΔAIC_c	AIC_c weight	Multiple R^2
Richness	1.2 ± 0.5 t = 2.404 *p* = 0.025	-1.1 ± 0.5 t = -2.277 *p* = 0.033	88.38	0	0.79	0.33
Pollen grains	1321 ± 441 t = 2.996 *p* = 0.006	–	425.91	0	1	0.28

Table 4. Explanatory models (parameter estimates and standard errors) of morphospecies richness and number of pollen grains derived from General Linear Models and selected by Akaike Information Criterion for small samples (AICc) with season, sex, capture time (minutes after sunrise), bill length (mm), body mass (g) evaluated as predictive variables. Only highly supported models (ΔAICc < 2) are shown. See text for details.

changes in foraging patterns of the Green-backed Firecrown would be very interesting to observe.

Our study has identified a number of interesting and ecologically relevant patterns in the foraging behavior of Green-backed Firecrowns. However, due to our relatively small sample size, we are unable to fully document, delineate, and understand many of these trends. In particular, future studies should examine 1) the surprising similarity of pollen communities carried by male and female Green-backed Firecrowns, despite their differences in bill morphology and foraging behavior; 2) the ways in which sexual dimorphism corresponds to sexual differences in ecological roles (especially as this may relate to competition with the endangered Juan Fernandez Firecrown); and 3) the potential similarity in foraging roles between juveniles (of both sexes) and adult female Green-backed Firecrowns. As our knowledge of important pollinators like the Green-backed Firecrown continues to develop, we will be better able to understand the roles they play in the maintenance of the plant community and the ways in which these roles affect ecosystem function.

MATERIALS AND METHODS

Study Area

We captured hummingbirds during the austral summer (January-February) and winter (July-August) of 2018 in native forests and exotic timber plantations in and adjacent to the Llancahue Forest Reserve in Los Ríos Region, Chile (39°50' S, 73°08' W, 1,300 ha). This reserve is located in the Intermediate Depression from 50 to 360 m a.s.l. and contains ~700 ha of old-growth Valdivian Temperate Rainforest and an additional ~400 ha of secondary native forest composed primarily of mixed evergreen broadleaf and *Nothofagus dombeyi*-dominated forest types (22). Annual rainfall averages 2,100 mm, occurring mostly from April–October (22). Temperatures are moderate, with maximum and minimum temperatures at the weather station in Valdivia (25 m a.s.l.) averaging 22.9 and 10.4 ˚C in January and 11.2 and 4.5 ˚C in July. Surrounding the reserve is a heterogeneous mosaic of exotic timber plantations (primarily *Pinus radiata* and *Eucalyptus* spp.), pastureland, and remnant patches of native forest.

Field Methods

Hummingbirds were captured with mist nets (9 x 2.5 m nets, 4–11 nets per day) in the understory of old-growth and secondary native forests, and both *Pinus radiata* and *Eucalyptus* spp. plantations. Nets were opened one hour after sunrise, operated for 5 hours, and checked every 15 minutes. Captures only took place on mornings without precipitation or high winds. Hummingbirds were removed from the nets and a numbered aluminum band was placed on the right tarsus. Once banded, we measured the following morphometric variables: mass (±0.1 g), wing chord (±0.5 mm), bill length (exposed culmen; ±0.01 mm), and tail length (±0.5 mm). Pollen samples were obtained by gently dabbing the bird's bill, head, and neck with a small piece of clear Scotch tape, which was subsequently adhered to a microscope slide for later examination. All birds were provided 20% sucrose nectar (v/v in water) from a glass dropper prior to release.

Pollen Identification

To count and identify the pollen grains sampled from each of the Green-backed Firecrowns, all pollen sample slides were carefully examined under a microscope (Micromaster, Fisher Scientific) at 80x magnification, and each grain of pollen assigned to a morphospecies based on pollen size, shape, and texture (**Figure 1**). Pollen grains for which the morphospecifies identity was unclear were examined more closely under 200x magnification. Tallies of individual grains belonging to each morphospecies were kept using manual clicker counters. Wherever possible, morphospecies were identified to plant species by comparison with standard pollen samples taken directly from flowers of known plants. To avoid potential bias due to sample contamination, morphospecies with < 5 pollen grains in a given sample were excluded from subsequent analyses. All pollen examination was performed at Stanford University.

Statistical Analysis

We evaluated seasonal, sex, and age-related differences in pollen community composition using non-metric multidimensional scaling (NMDS) performed in the R package 'vegan' (23). NMDS is a statistical ordination technique that takes information from many different dimensions (in this case, each dimension represented one pollen morphospecies) and collapses that information into a two-dimensional plot so that it can be visualized and interpreted. Each data point represents the community composition of pollen collected from a single hummingbird. Points that are close together indicate similar community composition, while points that are far apart indicate more distinct communities. Data points were then colored by category (e.g., summer vs. winter) to examine the drivers of community composition.

We used two-sample t-tests to statistically evaluate seasonal, sex, and age-related differences in pollen richness, calculated by counting the number of morphospecies in each sample and the number of pollen grains carried by each hummingbird. Specifically, we compared pollen richness and number of grains in summer vs. winter, male vs. female, and adult vs. juvenile hummingbirds. For these analyses, we excluded samples for which the hummingbird's age and sex were unknown, resulting in a sample size of 28 birds. Comparisons of adult and juvenile hummingbirds were made only for summer samples, since adults and juveniles in winter are indistinguishable. Normality was assessed using probability plots. We used Welch's t-tests for two comparisons in which groups had unequal variance (adult vs. juvenile richness, and summer vs. winter number of grains).

We used GLMs to further explore the factors that explain variation in pollen richness and grain counts. We included season, sex, capture time (minutes after sunrise), bill length, and body mass as predictor variables and used Akaike Information Criterion for small samples (AICc) to select the best models. We did not include age as a predictor variable because juveniles could only be distinguished during the summer season. We calculated AICc weights to infer the relative support of each model, as well as the multiple R2 value, which describes the proportion of variance explained by the predictor variables. T-statistics and p-values reported from the GLMs vary slightly from those reported from the two-sample t-tests because we only included hummingbirds (n = 25) in the GLMs for which we had information on all five predictor variables used. All statistical analyses were performed in RStudio (Version 1.1.383, ©2009-2016 RStudio, Inc.).

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REFERENCES

1. Ollerton, Jeff, *et al*. “How Many Flowering Plants Are Pollinated by Animals?” *Oikos*, vol. 120, no. 3, 2011, pp. 321–26.
2. Klein, Alexandra-Maria, *et al*. “Importance of Pollinators in Changing Landscapes for World Crops”. *Proc. R. Soc. B* vol. 274, 2007, pp. 303-313.
3. Armesto, Juan J., *et al*. “The Importance of Plant-Bird Mutualisms in the Temperate Rainforest of Southern South America.” *High-Latitude Rainforests and Associated Ecosystems of the West Coast of the Americas*, edited by R.G. Lawford, Springer, New York, NY, 1996, pp. 248–65.
4. Rozzi, Ricardo, and Jaime E. Jiménez. *Magellanic Sub-Antarctic Ornithology : First Decade of Long-Term Bird Studies at the Omora Ethnobotanical Park, Cape Horn Biosphere Reserve, Chile*. Edited by Ricardo Rozzi and Jaime E. Jiménez, University of North Texas Press, 2013.
5. Aizen, Marcelo A., and Cecilia Ezcurra. “High Incidence of Plant-Animal Mutualisms in the Woody Flora of the Temperate Forest of Southern South America: Biogeographical Origin and Present Ecological Significance.” *Ecología Austral*, vol. 8, 1998, pp. 217–36.
6. Smith-Ramirez, Cecilia. “Hummingbirds and their floral resources in temperate forests of Chiloé Island, Chile.” *Revista Chilena de Historia Natural*, vol. 66, 1993, pp. 65–13.
7. Franklin, Jerry F., *et al*. “The Forest Communities of Mount Rainier National Park.” *National Park Service Scientific Monograph Series*, vol. 19, 1988, pp. 1–222.
8. McFadden, Tyler N., et al. “Recommended Band Sizes and a Novel Technique for Sexing Immature Green-Backed Firecrown Hummingbirds (*Sephanoides sephaniodes*)”. *Ornitología Neotropical,* no. 30, 2019, pp. 179–84.
9. González-Gómez, Paulina L., and Cristian F. Estades. “Is Natural Selection Promoting Sexual Dimorphism in the Green-Backed Firecrown Hummingbird (*Sephanoides sephaniodes*)?” *Journal of Ornithology*, vol. 150, 2009, pp. 351–56.
10. Chalcoff, Vanina R., *et al*. “Sugar Preferences of the Green-Backed Firecrown Hummingbird (Sephanoides Sephaniodes): A Field Experiment.” *The Auk*, vol. 125, no. 1, pp. 60–66.
11. Fraga, Rosendo M., *et al*. “Interactions between the Firecrown Hummingbird *Sephanoides sephaniodes* and plants of the Nothofagus forests at Nahuel Huapi National Park, Argentina” *Hornero*, vol. 014, no. 04, 1997, pp. 224–34.
12. Fogden, Michael, *et al*. *Hummingbirds: A Life-Size Guide to Every Species*. Harper Design, 2014.
13. Feinsinger, Peter, and Robert K. Colwell. “Community Organization among Neotropical Nectar-Feeding Birds.” *American Zoologist*, vol. 18, no. 4, 1978, pp. 779-795.
14. Tinoco, Boris A., *et al*. “Effects of Hummingbird Morphology on Specialization in Pollination Networks Vary with Resource Availability.” *Oikos*, vol. 126, no. 1, 2017, pp. 52–60.
15. Wolf, Coral, and Erin Hagen. “Aggressive Interactions of Firecrowns (*Sephanoides* spp.; Trochilidae) during the Breeding Season of Robinson Crusoe Island, Chile.” *Ornitología Neotropical*, vol. 23, 2012, pp. 545-553.
16. Bleiweiss, Robert. “Joint Effects of Feeding and Breeding Behaviour on Trophic Dimorphism in Hummingbirds.” *Proceedings of the Royal Society B: Biological Sciences*, vol. 266, 1999, pp. 2491–97.
17. Temeles, Ethan J., and W. Mark Roberts. “Effect of Sexual Dimorphism in Bill Length on Foraging Behavior: An Experimental Analysis of Hummingbirds.” *Oecologia*, vol. 94, 1993, pp. 87–94.
18. Temeles, Ethan J., Irvin L. Pan, *et al*. “Evidence for Ecological Causation of Sexual Dimorphism In a Hummingbird.” *Science*, vol. 289, no. 5478, 2000, pp. 441–43.
19. González-Gómez, Paulina L., *et al*. “Aggression, Body Condition, and Seasonal Changes in Sex-Steroids in Four Hummingbird Species.” *Journal of Ornithology*, vol. 155, no. 4, 2014, pp. 1017–25.
20. Roy, Michael S., *et al*. “Evolution and History of Hummingbirds (Aves: Trochilidae) from the Juan Fernandez Islands, Chile.” *Ibis*, vol. 140, no. 2, 2008, pp. 265–73.
21. BirdLife International. “*Sephanoides fernandensis*.” *The IUCN Red List of Threatened Species*, 2018.
22. Donoso, Pablo J., *et al*. “Balancing Water Supply and Old-Growth Forest Conservation in the Lowlands of South-Central Chile through Adaptive Co-Management.” *Landscape Ecol*, vol. 29, 2014, pp. 245–60.
23. Oksanen, Jari, *et al*. *“vegan” Community Ecology Package.*

R Package Version 2.5-6. 2019.