

## RESEARCH ARTICLE

# Phenotype predicts interspecific dominance hierarchies in a cloud-forest hummingbird guild

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## Abstract

Competition over resources often leads to intra- and interspecific interactions, which can be detrimental to the individuals involved. Thus, natural selection should favor communication systems that reliably convey information regarding the relative competitive abilities of an individual, reducing the need for physically damaging confrontation. Body size, sex, age, relatedness, and ornamentation are important factors determining dominance across diverse taxa in intraspecific interactions. These traits, when perceptible, may serve as signals across species in guilds that have frequent interspecific interactions. Hummingbirds provide a tractable system to study such community dynamics due to their high frequency of interactions, variable ornamentation, diverse body sizes, fast metabolism, and large overlap in resource utilization. Even in this system, potential interactions between morphology and coloration are rarely accounted for together when analyzing dominance between species. We take a novel approach to understanding interspecific dominance by assessing behavior, morphology, and coloration across different types of behavioral interactions. Across 11 tropical montane hummingbird species, we find that dominance is predicted by wing size and some metrics of plumage coloration. However, the biological significance of these factors varies between the different dominance behaviors performed. These results inform our understanding of interspecific signaling and its role in the evolution of intraguild communication and resource competition.

## KEYWORDS

community ecology, dominance, ecology, interspecific interactions

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## 1 | INTRODUCTION

Competition for resources is a major cause of intra- and interspecific interactions in ecological systems. Direct, physical confrontation for the same resource can be detrimental to all individuals involved. However, natural selection may dampen potentially harmful physical disputes by favoring communication systems that reliably convey information regarding the (relative) competitive abilities of an individual (Bergman et al., 2003; Zahavi, 1975). Signals in such communication systems can then be used to quickly and effectively establish dominance hierarchies without the need for individuals to engage physically. Given the vast array of different communication signals used throughout the animal kingdom, identifying which key traits are associated with dominance within and across species remains difficult. Many studies looking at these factors have focused on intraspecific dominance hierarchies, serving to highlight a handful of signaling traits that emerge repeatedly across taxa (Allee & Dickinson, 1954; Cheney, 1977; Francis et al., 2018; Satoh & Ohkawara, 2008).

Unsurprisingly, body size has repeatedly been identified as an important phenotypic factor determining dominance within most taxa where examined (Escudero et al., 2020; Galbany et al., 2015; Halley & Gjershaug, 2008; Wright et al., 2019). Sex, age, relatedness, and ornamentation likewise frequently play a role in an individual's intraspecific dominance and social standing (Chiarati et al., 2010; Foerster et al., 2016; Holekamp et al., 2012; Moreno-Opo et al., 2020; Rohwer, 1982; Silk et al., 2003; Stapley & Whiting, 2006; Tibbetts et al., 2022). Other evolutionary pressures, such as sexual selection, can play an important part in the evolution of any trait tied to reproduction (e.g., intrasexual dominance rank and social status). Critically, these same traits may also evolve or be coopted as cues for interspecific signaling. For example, plumage ornamentation is a common example of a trait frequently serving as a cue both to attract opposite-sex mates and to display competitive ability to the same sex (Berglund & Pilastro, 1996; Emlen, 2008; Zahavi, 1975). Nevertheless, ornamentation, such as coloration, can also serve as a display trait in antagonistic interspecific interactions (Dijkstra et al., 2007; Falk et al., 2021; Kohda, 1998; Seehausen & Schluter, 2004). While body size also seems to play an important role in interspecific interactions (Francis et al., 2018; Leighton et al., 2023; Rabinowicz et al., 2020), relatively little is known about how individuals communicate their competitive ability to members of a different species.

Better understanding of interspecific behaviors can elucidate the importance of community ecology as a driver of niche segregation, phenotypic polymorphisms, and behavioral plasticity. Hummingbirds, a focal and frequently observed lineage for interspecific interaction studies, are well suited to tackling this topic because of their wide distribution, high frequency of interspecific interactions, variable ornamentation, diverse body sizes, fast metabolism, and large overlap in resource utilization (Skutch, 1974). These characteristics have led to a relatively large number of studies looking at the interspecific interactions of hummingbird communities

(Bribiesca et al., 2019; López-Segoviano et al., 2017; Márquez-Luna et al., 2018; Rodríguez-Flores & Arriaga, 2016). Although few of these studies have looked at the importance of plumage ornamentation in interspecific signaling, dominance has been repeatedly linked to body size (Bribiesca et al., 2019; Márquez-Luna et al., 2018), abundance (Bribiesca et al., 2019), foraging behavior (Tiebout III, 1996), resource quality (Justino et al., 2012), and food preference (López-Segoviano et al., 2017; Rodríguez-Flores & Arriaga, 2016). Whereas body size is now a well-established predictor of dominance in this avian guild, its relevance seems to decay with phylogenetic distance. Accordingly, Martin and Ghalambor (2014) looked at interspecific species interactions across a suit of different avian taxa, including hummingbirds, and found that body size becomes a weaker predictor of winning an interaction as the phylogenetic distance between two species increases. One possible explanation for this pattern is that as the genetic distance between species increases, their physiology becomes more dissimilar, allowing for them to adopt contrasting and perhaps increasingly size-independent competitive abilities. In the case of hummingbirds, the maneuverability and flight performance of larger species are dependent on their increased muscle capacity and lower wing loading (Dakin et al., 2018; Skandalis et al., 2017). These differences in flight performance suggest that species play to their strength when it comes to tasks demanding maneuvering behaviors. For this reason, it is critical to assess the linearity (sometimes termed "transitivity"; McDonald & Shizuka, 2013) of interspecific dominance hierarchies in this clade.

In this study, we observed a long-term set of artificial feeders to (1) assess the factors related to dominance and (2) compare the species ranks according to different kinds of dominance behaviors. Based on the results of previous studies with hummingbirds, we predicted that the dominance rank would strongly and positively correlate with a species' average mass, wing length, tail length, and the intensity of plumage coloration used in displays. Given that differences in hummingbird maneuverability may favor certain behaviors, we also predicted that the dominance rank would change markedly based on the type of interaction (e.g., displacement, chasing, or standing ground).

## 2 | METHODS

### 2.1 | Field site and study population

We conducted our study at Reserva Las Tangaras, situated on the outskirts of Mindo, Ecuador (−0.7770042, −78.7903148). The research site is located 1320 m.a.s.l. in a secondary-growth cloud forest. The reserve has placed nectar feeders with a 25% sucrose solution daily for more than 10 years, establishing a consistent and reliable food source for nectivorous birds. More than 10 hummingbird species reliably visit the nectar feeders during the rainy season (February–May). The four feeders are placed in different positions around the research site's cabin, but never separated by more than 10 m. We collected data from April–June

2019 ( $n = 57$  days) between 0650 and 1700 h. Of the 15 hummingbird species that visited the feeder during the study, we limited our analysis to the 11 species that had more than 100 interactions and visited the feeder more than once a day (on average) during the focal watch.

## 2.2 | Morphometrics

All morphometric data were sourced from a long-term banding station run at our study site by D. Becker (Table 1). Starting in 2013, banding data for hummingbirds coming to the feeders was collected annually every year. Hall traps were used to capture hummingbirds consistently coming to the nectar feeders over the span of 2 weeks in December. All birds received an aluminum USGS-style hummingbird band, and the following measurements were recorded: weight, wing length, tail length, and culmen length. All banding was done under permit No. 006-2019-IC-FAU-DPAP-MA issued annually by the Ministerio del Ambiente, Agua y Transición Ecológica, Ecuador. As highlighted through the STRANGE framework (Webster & Rutz, 2020), we acknowledge that our morphometrics may be biased toward individuals that have a higher propensity to be caught (reviewed in Webster & Rutz, 2020). We are cognizant that there are certainly potential biases in this study (as with any study) and we address them more extensively in the Discussion section. We trust that this transparency motivates future studies to account for as many biases as possible and improves the overall quality of research.

## 2.3 | Observations

During 1-h focal watch periods ( $n = 57$  watches on separate days), we recorded any interaction between pairs of hummingbirds, within half a meter of a nectar feeder, when each of the two individual species

could be identified. For sexually dimorphic species, the apparent sex of the interacting individuals was noted as well. For each interaction, we noted the “aggressor” and the “receiver.” The “aggressor” and the “receiver” were categorized as the individual that instigated the interaction and the one that received the instigating behavior, respectively. From preliminary observations, we subdivided the interactions into the three most common interactions we had seen: displacement, chasing, and standing ground. Thus, the subsequent hierarchies were each constructed according to the behavioral interaction type, and the overall hierarchy was constructed by combining all of these behaviors together.

Displacement was defined as an interaction where the receiver was actively feeding (bill inserted into the feeding port), and the aggressor drove out the feeding individual and began feeding themselves. Chasing was defined as an interaction where the receiver was actively feeding, or positioned at a feeding port, and the aggressor ousted the feeding individual by chasing them away from the feeder without then proceeding to feed themselves. Standing ground was defined as an interaction where the receiver was actively feeding, and the aggressor unsuccessfully attempted to drive out the feeding individual (independent of either individual perching or hovering). For simplicity of annotation, for each of these interactions, one individual was recorded as the “dominant” individual while the other was noted as the “subordinate” individual based on whether they “won” their contest. Thus, for the first two interaction subtypes described (displacement and chasing), the aggressor was marked as the “dominant” individual, and the receiver was marked as “dominant” for the third subtype (standing ground) since all three were the winners of their respective contests. All feeders had a perch at each of their ports; however, given the difficulty of recording the amount of time spent perched for each interaction, whether an individual was hovering or perching for the interaction was not recorded. Additionally, vocalizations seem important as communication signals in this clade but, regrettably, our equipment did not capture enough acoustics data to be incorporated in this study.

TABLE 1 The species assessed in this study and their respective average morphometrics.

Species	Latin name	Species code	Mass (g)	Wing (mm)	Tail (mm)	Bill (mm)
Brown Violetear	<i>Colibri delphinae</i>	BRVI	7.17	72.2	41.0	16.5
Fawn-breasted Brilliant	<i>Heliodoxa rubinoides</i>	FBBR	8.17	68.7	42.1	22.8
Green-crowned Brilliant	<i>Heliodoxa jacula</i>	GCBR	8.32	68.6	42.9	25.0
Emperor Brilliant	<i>Heliodoxa imperatrix</i>	EMBR	9.57	70.6	60.9	25.3
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	RTHU	6.53	58.2	33.2	21.6
White-necked Jacobin	<i>Florisuga mellivora</i>	WNJA	7.47	66.5	36.1	19.1
Green-crowned Woodnymph	<i>Thalurania colombica</i>	GCBR	5.19	55.1	35.5	19.5
White-whiskered Hermit	<i>Phaethornis yaruqui</i>	WWHE	5.99	59.0	55.6	41.4
Purple-bibbed Whitetip	<i>Urostroke benjamini</i>	PBWT	4.24	48.4	32.1	19.3
Andean Emerald	<i>Amazilia franciae</i>	ANEM	5.38	52.9	30.6	22.4
Purple-throated Woodstar	<i>Calliphlox mitchellii</i>	PTWO	3.5	37.0	18.0	14.9

Note: All morphometric data come from individuals captured at the study site.

## 2.4 | Coloration data

Hummingbirds frequently have color patches that are particularly important for one-on-one interaction and the largest patch gamuts (i.e., achieved color diversity) are on the gorget and the crown (Venable et al., 2022). Given the lack of behaviors involving crown displays in our focal species, we limited our data collection to gorget coloration. We measured reflectance spectra from gorget patches of specimens housed at the Yale Peabody Museum and the American Museum of Natural History using a S2000 Ocean Optics spectrometer and a bifurcated fiber with an Ocean Optics DH-2000-BAL deuterium-halogen light source (Ocean Optics) in a dark room with an integration time of 100 ms according to the methods used in Venable et al. (2022). In cases where we had more than one representative of the species, we chose specimens according to which ones were in the best condition relative to the other individuals in the collection. The plumage patch was measured from a different position three times, as centrally as possible, and then averaged. While averaging multiple measurements might flatten highly saturated peaks with slightly different hues, we opted to take a broader view of coloration in this case. While we used one museum specimen per species as coloration for this metric, the color of this patch is not known to vary geographically for the species tested here (Birds of the World, 2022). All museum specimens were known males so when we refer to color in the text, we are referencing the male phenotype of each species.

To model avian color perception, we used an ultraviolet-inclusive tetrahedron colorspace computer program (TetraColorSpace; Stoddard & Prum, 2008). TetraColorSpace models reflectance spectra as color points within a 3D-tetrahedron colorspace representing all the colors that a bird can see given its presumed visual system. Each colorpoint is plotted a distance  $r$  away from an achromatic origin of equal cone stimulation, which represents chroma (i.e., saturation). The position of the colorpoint relative to the tetrahedron's vertices is defined by two angles,  $\theta$ , and  $\varphi$ , which represent hue. We used a violet-sensitive visual system setting because hummingbirds have a violet-sensitive visual system (Ödeen & Håstad, 2010; Stoddard et al., 2020).

## 2.5 | Statistical analyses

### 2.5.1 | Rankings

To infer dominance ranks we used a randomized Elo-rating method utilizing the “aniDom” package in R (Version 4.1.3, R Development Core Team, 2022; Sánchez-Tójar et al., 2018). Standard Elo-rankings create a rank by sequentially assessing the outcome of an interaction and updating the rank after each interaction based on the probability of the higher ranked individual winning the interaction (i.e., “dominant” in our dataset). This method does not require a complete matrix where all individuals interact with

each other. However, it can introduce temporal bias in studies that span prolonged periods of time (Sánchez-Tójar et al., 2018). Randomized Elo-rankings circumvent this by randomizing each of the interactions and assessing the outcome non-sequentially. Additionally, this is a method frequently utilized when comparing between species rather than within species and is robust against uneven sample sizes. A more detailed explanation can be found in Sánchez-Tójar et al. (2018), where the authors discuss the benefits and drawbacks of popular contemporary tools used to create dominance ranks (Sánchez-Tójar et al., 2018). Furthermore, we confirmed the validity of our Elo rankings by simultaneously running the Bradley-Terry Models, a ranking method not assessed in that review study but one that is nonetheless popular due to its efficiency (Leighton et al., 2018; Miller et al., 2017; Shev et al., 2014). The hierarchies created by Elo rankings and Bradley-Terry Models had complete agreement as to the positions of each species.

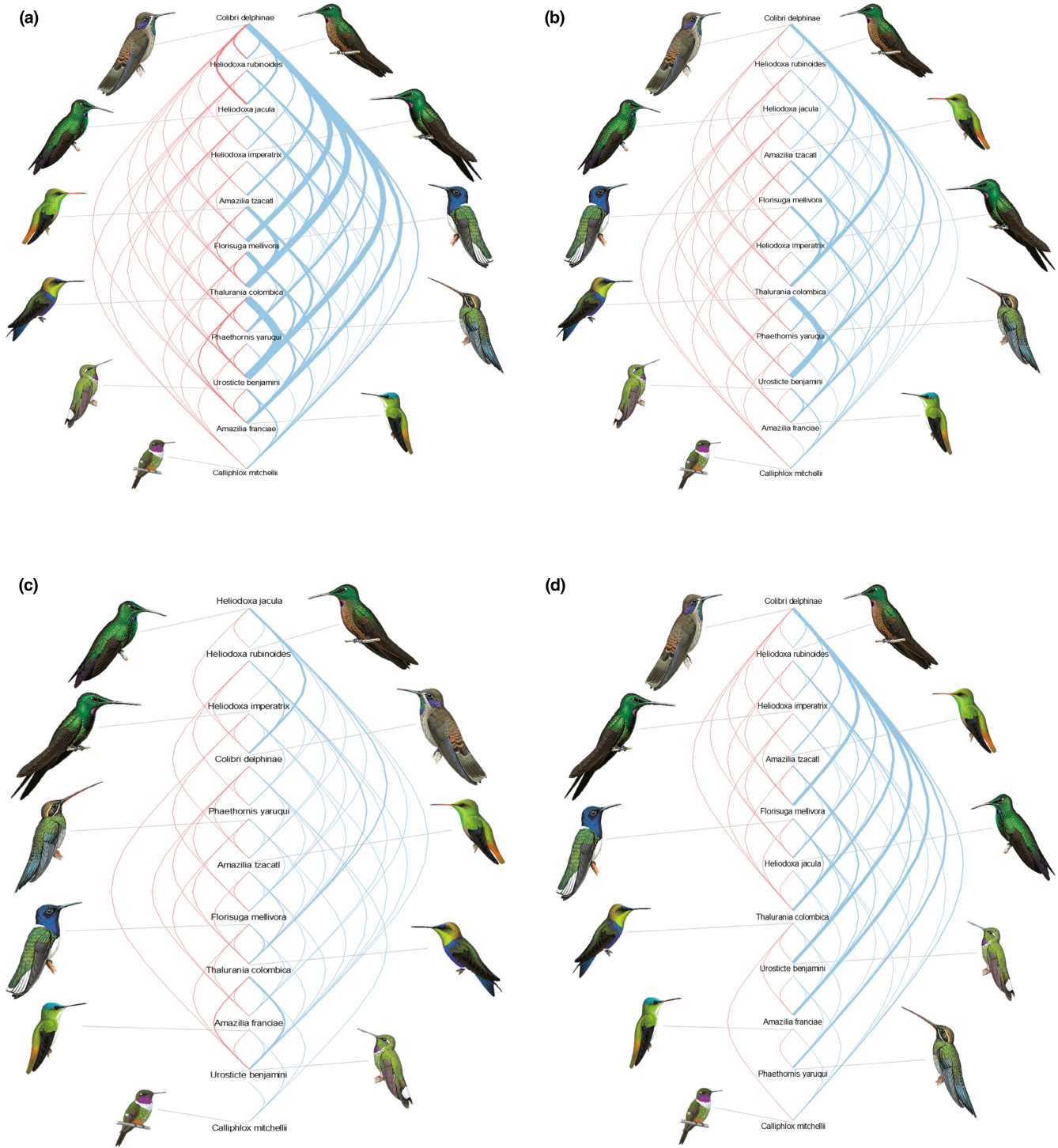
Finally, to minimize and estimate measurement errors stemming from our dataset, we calculated the uncertainty and linearity of our hierarchies utilizing the “aniDom” package in R (Sánchez-Tójar et al., 2018). First, we ensured an appropriate sampling effort by calculating the ratio of interactions to individuals. Then we estimated the level of uncertainty in our hierarchies through Elo-rating repeatability and steepness half-comparisons. We used triangle transitivity to verify and report the linearity of the hierarchies. Due to our desire to cross-validate the Elo rankings with Bradley-Terry Models, these analyses were not blind.

### 2.5.2 | Attribute-ordered dominance ranks

Using the Elo ratings, we generated an attribute-ordered dominance rank for each of the hierarchies following the steps laid out by Hobson et al. (2015) and with the R package *networkTricks* (Miller, 2017). Given our large datasets, this is a good way to display and visualize a large number of interactions between several species. These graphs rank the species according to the Elo ratings, and then visually represent the number of interactions between two individuals with lines. For our networks, the thickness of the line represents the number of interactions between the two species and the color dictates where the more dominant individual won the interaction (blue, right-hand side) or the more subordinate individual won the interaction (red, left-hand side) (Figure 1).

### 2.5.3 | Analysis of dominance related traits

We assessed the correlates of species rank, morphometrics (mass, wing length, tail length, and culmen length), and coloration ( $\theta$ ,  $\varphi$ , and  $r$ ) by using phylogenetic generalized least square (PGLS) regressions to fit a model with dominance as the dependent variable (as represented by the Elo ratings) and the variables of interest as explanatory



**FIGURE 1** A visual representation of every interaction for each of the hierarchies (hummingbird drawings from Birds of the World, 2022). From left to right and top to bottom: (a) overall hierarchy, (b) displacement hierarchy, (c) stand ground hierarchy, (d) chasing hierarchy. The thickness of each line represents the relative number of interactions between the two species and the color dictates whether the more dominant individual won the interaction (blue, right-hand side) or the more subordinate individual won the interaction (red, left-hand side).

variables. The phylogeny used in the PGLS was a maximum clade credibility tree created from the complete set of possible trees obtained from Jetz et al. (2012) and appropriately pruned using the “ape” package in R (Paradis & Schliep, 2019). Based on our hypotheses, 12 separate models were run for each hierarchy. The PGLS regressions

for each dominance hierarchy were then run under a lambda model of evolution using the package “phylolm” (Ho & Ané, 2014), and the best model (according to its AIC value) was selected. Below, we report the AIC values of the best model and the second-best model for comparison.

### 3 | RESULTS

#### 3.1 | Overall hierarchy

First, we present the results of the analysis of the overall hierarchy and then, those corresponding to the disaggregated behaviors: displacement, chasing, and standing ground. The overall Elo rankings showed that, of the species we observed, the Brown Violetear (*Colibri delphinae*) was the most dominant while the Purple-throated Woodstar (*Calliphlox mitchellii*) was the least dominant (Figure 2, Table 2). The best-fit model (AIC value of  $-8.6$  vs.  $15.9$ ,  $r^2 = .99$ , Table 3) for the overall hierarchy showed that for the morphometrics, wing size ( $\beta = -.31$ ,  $p = .003$ ), culmen ( $\beta = -.13$ ,  $p = .04$ ), and the interaction between wing size and tail size ( $\beta = -.004$ ,  $p = .03$ ) correlated positively with dominance, while tail size ( $\beta = .44$ ,  $p = .02$ ) correlated negatively with dominance. As for the coloration,  $\phi$  ( $\beta = -2.01$ ,  $p = .005$ ),  $\theta$  ( $\beta = -.61$ ,  $p = .02$ ), and color saturation ( $\beta = -.63$ ,  $p = .03$ ) all correlated positively with dominance.

#### 3.2 | Displacement hierarchy

The displacement rank was very similar to the overall rank, with only one alteration where the second and third-ranked species switched places (Figure 2, Table 2). The displacement model (AIC value of  $7.2$  vs.  $18.9$ ,  $r^2 = .99$ , Table 3) showed that wing size ( $\beta = -.35$ ,  $p = .007$ ) correlated positively with dominance, while tail size ( $\beta = .45$ ,  $p = .05$ )

correlated negatively with dominance. For coloration,  $\phi$  ( $\beta = -1.94$ ,  $p = .01$ ), and color saturation ( $\beta = -1.17$ ,  $p = .02$ ) correlated positively with dominance.

#### 3.3 | Standing ground hierarchy

For the standing ground hierarchy, the changes compared to the overall hierarchy were more drastic, with only one retaining its place in the standing ground hierarchy (Figure 2, Table 2). This rank showed that the Green-crowned Brilliant (*Heliodoxa jacula*) was the most dominant while the Purple-throated Woodstar was the least dominant, the only species to retain its rank. Another interesting aspect of this hierarchy is that the Brown Violetear which is the most dominant species in every other behavior, drops down to the fourth rank. For the top model (AIC value of  $8.7$  vs.  $18.6$ ,  $r^2 = .99$ , Table 3) of this hierarchy, only the wing size ( $\beta = -.22$ ,  $p = .02$ ) correlated positively with dominance.

#### 3.4 | Chasing hierarchy

The chasing hierarchy had an intermediate level of change, with four species retaining their rank (Figure 2, Table 2). The Green-crowned Brilliant which was the 1st ranked species in the most static behavioral rank (standing ground), and top three in the other two hierarchies, dropped down to the 6th position in the

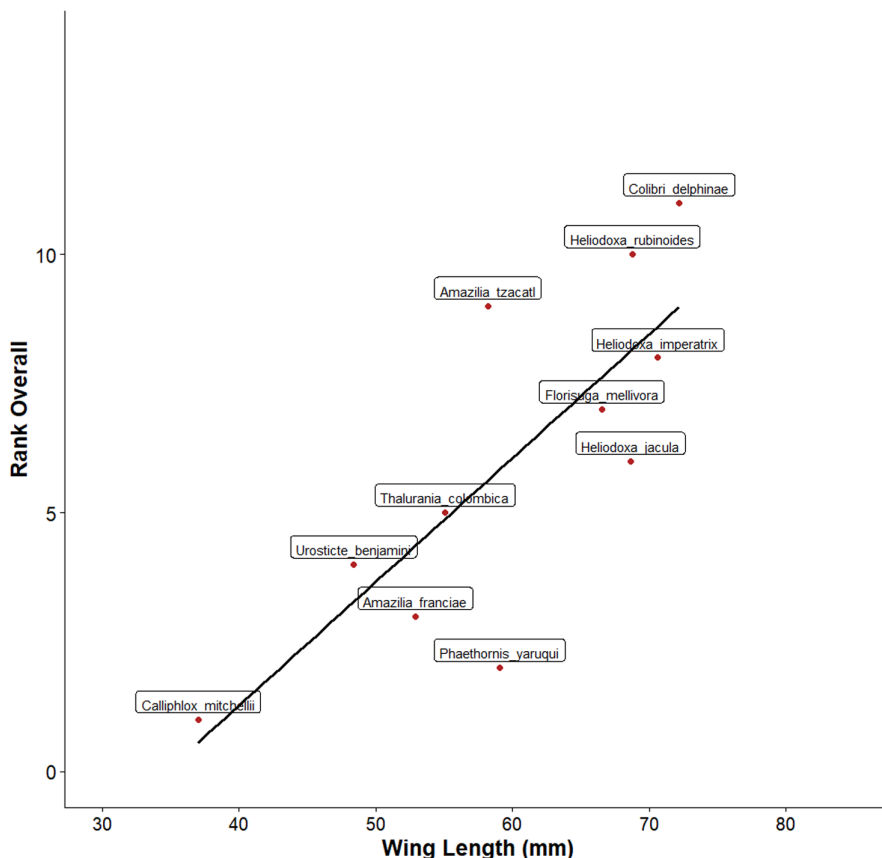


FIGURE 2 The relationship between rank in the overall hierarchy and wing length, the strongest predictor of dominance across all hierarchies.

TABLE 2 The species assessed in this study and their ranking in each of the hierarchies.

Species	Latin name	Overall rank	Displacement rank	Stand ground rank	Chasing rank
Brown Violetear	<i>Colibri delphinae</i>	1	1	4	1
Fawn-breasted Brilliant	<i>Heliodoxa rubinoides</i>	2	3	2	2
Green-crowned Brilliant	<i>Heliodoxa jacula</i>	3	2	1	6
Emperor Brilliant	<i>Heliodoxa imperatrix</i>	4	4	3	4
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	5	5	6	3
White-necked Jacobin	<i>Florisuga mellivora</i>	6	6	7	5
Green-crowned Woodnymph	<i>Thalurania colombica</i>	7	7	8	7
White-whiskered Hermit	<i>Phaethornis yaruqui</i>	8	8	5	10
Purple-bibbed Whitetip	<i>Urosticte benjamini</i>	9	9	10	8
Andean Emerald	<i>Amazilia franciae</i>	10	10	9	9
Purple-throated Woodstar	<i>Calliphlox mitchellii</i>	11	11	11	11

Note: The number "1" denotes the highest rank (most dominant), while the number "11" denotes the lowest rank (least dominant).

most dynamic behavioral rank (chasing). For the chasing model (AIC value of 6.5 vs. 13.3,  $r^2 = .99$ , Table 3) the wing size ( $\beta = -.26$ ,  $p = .02$ ), and interaction between wing and tail size ( $\beta = -.0065$ ,  $p = .04$ ) were both positively correlated with dominance, while tail size ( $\beta = .66$ ,  $p = .03$ ) correlated negatively with dominance. For the coloration data, both  $\phi$  ( $\beta = -2.5$ ,  $p = .01$ ) and  $\theta$  ( $\beta = -1.5$ ,  $p = .02$ ) correlated positively with dominance.

### 3.5 | Reliability of hierarchies

To minimize and estimate measurement errors stemming from our dataset we report the uncertainty and linearity of our hierarchies. Each of the hierarchies has a ratio of interactions to individuals (a metric of sampling effort) that is well above 10–20, the minimum recommended ratio (Table 4; Sánchez-Tójar et al., 2018). The steepness of the hierarchies based on Elo-rating repeatability and half-comparisons suggests that the certainty of all the estimated hierarchies is moderate to high (Table 4). Lastly, the triangle transitivity for the hierarchies shows that they are linear (Table 4).

## 4 | DISCUSSION

We set out to assess how the morphometrics and coloration values for 11 Neotropical hummingbird species foraging at stable feeders are linked to dominance between species, and if these patterns change when looking at different types of dominance behaviors. Similar to recent studies on interspecific dominance interactions, we found that certain metrics of body size correlated with dominance (Francis et al., 2018; Leighton et al., 2023; Márquez-Luna et al., 2018; Rabinowicz et al., 2020). Of all morphometrics, the best predictor of dominance rank seemed to be wing size (Figures 2 and 3). Wing size correlated strongly and positively with dominance rank across all types of interactions. Likewise, tail

length consistently correlated negatively with dominance, except for in the standing ground hierarchy. Long tails may interfere with flight performance and maneuvering during displacement and chasing events while remaining irrelevant during the more static standing ground events.

Since avian vision differs from human vision (Cuthill et al., 2017), this study attempted to look at plumage coloration values that might be more perceptually relevant to hummingbirds. Hummingbird gorgets are commonly used in displays and are diverse and colorful across the lineage (Hogan & Stoddard, 2018; Simpson & McGraw, 2019; Venable et al., 2022). For the overall hierarchy and the displacement hierarchy, the gorget's  $\phi$  (one vector of hue) and color saturation positively correlated with dominance. The use of these avian perceivable signaling cues to predict dominance hierarchies across species is a critical finding for the role of familiarity and signal-reliability within stable hummingbird communities.

Furthermore, we detected a difference in this correlation when looking at chasing and standing ground behaviors. For chasing, the link changed to  $\phi$  and  $\theta$  independently being significant, which could suggest that in faster interactions the quick flashes of some aspect of the gorget hue might play a greater role in signifying status than the color saturation. Regarding standing ground, none of the coloration metrics correlated significantly with dominance. Although an argument could be made that standing ground is the most static interaction and, thus, might allow for the best assessment of coloration hue, the gorget remains relatively hidden as it is turned away from approaching individuals during feeding bouts. Furthermore, winning a standing ground event is the only behavior that could be considered "defensive" rather than "offensive," suggesting a fundamental difference in interaction type and flight form.

Based on observations of standing ground, species that tended to win standing ground events (i.e., all *Heliodoxa* spp.) would usually perch at the feeder rather than hover. Hovering and perching are potential subsets in interaction behaviors that were not recorded during the study but could be interesting to explore in future

TABLE 3 Morphometric and coloration predictors of dominance based on the top models for each of the hierarchies.

	Overall			Displacement			Standing ground			Chasing		
	$\beta$	t-value	p-value	$\beta$	t-value	p-value	$\beta$	t-value	p-value	$\beta$	t-value	p-value
Intercept	18.33	15.43	.0042	21.69	11.19	.0079	20.43	15.32	.0042	11.74	4.97	.038
Wing	-.31	-17.58	.0032	-.35	-12.12	.0067	-.22	-7.46	.018	-.26	-7.48	.017
Culmen	-.13	-4.91	.039	-.22	-3.83	.062	-.10	-1.96	.19	-.095	-1.79	.22
Tail	.44	7.48	.017	.45	4.42	.048	.079	2.20	.16	.66	5.63	.030
Wing*tail	-.0038	-5.28	.034	-.0031	-2.56	.12	NA	NA	NA	-.01	-4.56	.044
Mass	NA	NA	NA	NA	NA	NA	-.54	-3.04	.093	NA	NA	NA
$\theta$	-.61	-6.40	.024	-.22	-1.68	.23	-.22	-1.31	.32	-1.50	-7.98	.015
$\phi$	-2.01	-13.99	.0051	-1.94	-8.59	.013	-.92	-2.97	.097	-2.54	-8.87	.012
$\theta^*\phi$	-.31	-1.18	.36	1.87	3.67	.067	-1.75	-3.06	.092	-1.33	-2.54	.13
r	-.63	-5.47	.032	-1.17	-6.28	.024	-.61	-2.65	.12	.30	1.30	.32

Note: Interacting terms are denoted by an asterisk. Statistically significant results are bolded.

studies. This would be particularly relevant to examine as it pertains to foraging strategies (i.e., trap-lining vs. territorial species; Sargent et al., 2021). The only known trap-lining species in our study, the White-whiskered Hermit (*Phaethornis yaruqui*), was the most dominant in standing-ground interactions and the least dominant in chasing interactions. This pattern is consistent considering that this foraging strategy might require a species to stand its ground for short periods and then move on, with no need to chase another individual and, thus, expending additional energy on a resource it will not otherwise defend. We consider that reporting these potential patterns opens the doors for future studies regarding the role of foraging ecology on interspecific interactions. This aspect seems especially important in the context of delving further into hummingbird signaling traits and behaviors.

Despite a high frequency of interspecific interactions and aggression in hummingbirds, few studies have investigated the role that plumage coloration plays in interspecific dynamics. Rather, studies have tended to focus on sexual selection and female preference for ornamented males (Beltrán et al., 2021; Parra, 2010; Simpson & McGraw, 2018). However, females of some dimorphic species still have bright iridescent plumage patches, and many species are monomorphic with colorful plumage in both sexes. Some studies have hypothesized that ornamentation in females is associated with increased territoriality or dominance (Bleiweiss, 1985; Wolf, 1969), but it is unclear whether these signals could be used by other species. Furthermore, in one hummingbird, *Florisuga mellivora*, 20% of females are ornamented and visually indistinguishable from males (Falk et al., 2021). These ornamented females are thought to be mimics of more aggressive and territorial males, as both con- and hetero-specific individuals avoid aggression toward males (Falk et al., 2021, 2022). These behaviors demonstrate that different species can and do attend to each other's plumage in ways that may affect the evolution of ornamentation. At the same time, one of the few studies looking at patterns of interspecific signaling coloration across avian species recently showed that dominant species typically display more black coloration in regions crucial for aggressive signaling, while carotenoid colors do not consistently signal dominance except in specific taxonomic groups (Kenyon & Martin, 2023). Additionally, white plumage patches may serve contrasting functions: it can indicate dominance in species where black denotes dominance but also can indicate subordination in species potentially utilizing carotenoid-based signals for dominance (Kenyon & Martin, 2023). These combined results provide valuable insights into the role of colors as signals of dominance in competitive species interactions, which may help mediate aggressive encounters among different bird species and reduce the costs associated with co-occurrence, thus facilitating coexistence in natural ecosystems.

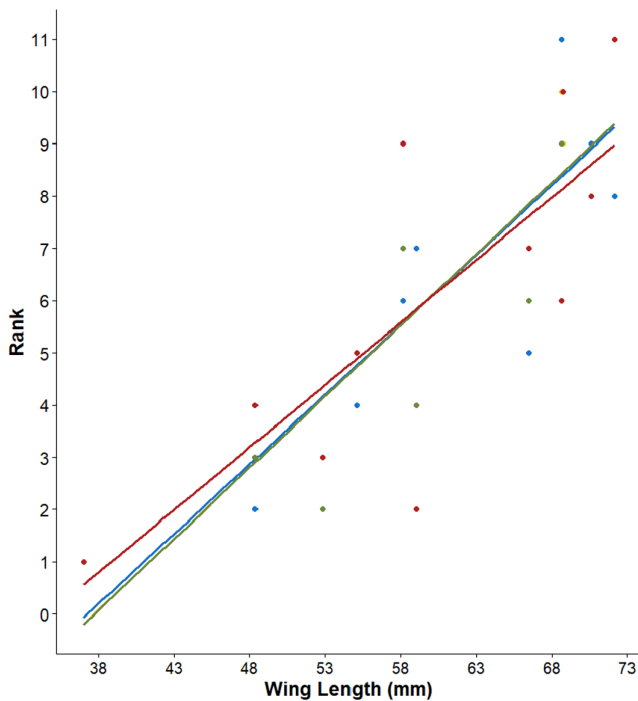
Another aim of the study was to explore the importance of subdividing behavioral interactions. While it might be difficult in some systems (e.g., few interactions, behaviors too similar to reliably distinguish, behaviors too fast), it seems illogical to assume that chasing an individual for several hundred meters has the same implications as refusing to move from a feeding source. Furthermore,



**TABLE 4** The ratio of interactions to individuals (a metric of sampling effort), steepness based on Elo-rating repeatability, steepness based on half-comparisons, triangle transitivity, and related *p*-value for each of the hierarchies.

Hierarchy	Interaction ratio	Steepness (Elo-rating repeatability)	Steepness (half comparison)	Triangle transitivity	<i>p</i> -value
Overall	149.5	.806	.77 (.54-.94)	.97	<.001
Displacement	69.7	.796	.73 (.40-.93)	.80	<.001
Standing ground	27.3	.788	.61 (.25-.90)	.65	.009
Chasing	52.4	.893	.82 (.62-.95)	.92	<.001

Note: For the half comparisons, the mean is shown with the 2.5% and 97.5% quantiles in parentheses. The ratio of interactions to individuals is a metric of sampling effort. The two measures of steepness estimate uncertainty in the hierarchies, while the triangle transitivity calculates the degree of linearity.



**FIGURE 3** All hierarchies are plotted by rank and wing length. The overall hierarchy is in green, the displacement hierarchy is in yellow, the chasing hierarchy is in red, and the standing ground hierarchy is in blue.

in the hummingbirds, it seems that body size becomes a poorer predictor of dominance as genetic distance increases (Martin & Ghalambor, 2014), which might be explained by shifts in physiology that allow hummingbirds contrasting competitive abilities (Dakin et al., 2018). Therefore, subdividing behavioral interactions at stable feeding sources could highlight these different dimensions of competitive abilities. Specifically, we found that there were changes based on each behavior and that the type of interaction affected a species' likelihood of winning that interaction. While the overall hierarchy and displacement hierarchy were very similar, the standing ground hierarchy proved to be very different and showed some interesting patterns of differing competitive abilities. For example, the Brown Violetear, which is the most dominant in every other hierarchy, fell to 4th place. While not assessed in this study, violetears

have serrations on their bills which have been proposed as a weapon during fights (Rico-Guevara et al., 2019). In conjunction, these results might suggest that the bill serration is beneficial in some interactions but not in others (i.e., attacking vs. defending). Contrary to the Brown Violetear, the Green-crowned Brilliant's rose dramatically from chasing (6th) to standing ground (1st), suggesting that it might be better suited to defending a resource than it is to drive competitors from it.

Whereas our study system of artificial feeders allowed us to collect behavioral data rapidly, copiously, and efficiently, these behaviors might not necessarily be extrapolated to natural foraging settings. Firstly, the community observed at these artificial feeders is not completely representative of the local natural community (Ramírez-Burbano et al., 2022). Regarding our focal taxa, there were several hummingbirds observed in the area that did not attend the artificial feeders. First, in some cases, it was because of a morphological limitation (their bill was too short for the feeder; *Discosura conversii*) or for other unknown reasons (*Doryfera ludovicæ*, *Heliiothryx barroti*) (pers. observs.). Second, natural resource distributions and accesses are far more complex than those of the artificial feeders, and hummingbirds behave accordingly. The distribution and quality of nectar sources in the wild vary both spatially and temporally, which can dictate an individual's behavioral response. In some cases, aggressive territorial behaviors by some dominant hummingbird species are only adopted when certain thresholds of nectar quantity are crossed, and this costly behavior is abandoned when nectar reward is not high enough (Justino et al., 2012). Thus, a stable-feeding sources could create unnatural behavioral responses, or maintain behaviors for longer than would happen at natural nectar sites. While our findings from artificial nectar feeders should not be extrapolated to all natural environments, they could allow us to efficiently provide a base prediction for the behavioral and social dynamics of these hummingbird species at natural resources. Furthermore, understanding the effect of feeding wild birds is increasingly important as it is currently a multi-billion-dollar hobby (U.S. Department of the Interior et al., 2011), is increasing in popularity (U.S. Department of the Interior et al., 2011, 2016), and its implications on wildlife are still poorly understood (Dzielski et al., 2021; Galbraith et al., 2015; Jones & James Reynolds, 2008; Plummer et al., 2015). Given the key role of hummingbirds as pollinators, understanding how an increase in

artificial feeders (e.g., through the increase in Neotropical eco-tourism) affects the surrounding ecosystem is important. For example, Maglianesi et al. (2015) highlighted that when nectar feeders with an unlimited supply of nectar were made available, floral preferences of hummingbirds changed in relation to what was observed in their interactions with flowers. Plants that have co-evolved with hummingbirds (e.g., *Ensifera ensifera* and *Passiflora* spp.; Lindberg & Olesen, 2001) and depend on them as their sole pollinators might be especially impacted.

There are some additional limitations with the data used in this study, especially with regard to the coloration data. First, individual hummingbirds were not uniquely identifiable by us, so it is likely that observations within the same species were repeatedly taken from some of the same individuals. Second, only male specimens were used for the coloration data, but we chose not to divide the behavioral data based on sexual phenotype. Dividing the behavioral data according to sex in a hierarchy with monochromatic and dichromatic species was problematic because sex could only be distinguished in dichromatic species. Even in sexually dichromatic species, the sexes of both juveniles and adults are not always easily distinguishable (Diamant et al., 2021). However, we explored the role of sexual phenotype by subsetting the dichromatic species and examining whether sexual phenotype predicted dominance. One-way ANOVAs for each hierarchy do not suggest that sex is significant for any of the hierarchies (Table S1). Two-way ANOVAs (with sex and species as the independent variables) suggest that sex appears significant for the displacement hierarchy ( $F = 7.63, p = .03$ ; Table S2) but not for any other hierarchy. While not within the scope of this paper, this could be a fruitful avenue for exploring the selective pressures driving plumage coloration and competition (Kenyon & Martin, 2023). Finally, vocalizations, sonations, and other acoustic displays and communication signals may be critical for establishing and mediating dominance hierarchies within and between species (Duque & Carruth, 2022; Leighton & Birmingham, 2021). Our equipment and recordings did not generate high enough acoustic quality to include such an analysis in our study; we recommend that future hummingbird dominance studies explore the possibility of such multimodal signaling and its role in interspecific competitive behaviors (Partan, 2013; Peckre et al., 2019; Smith et al., 2011).

Our study shows the structure of an interspecific hummingbird foraging guild, highlights the morphological and color metrics associated with dominance, and stresses the importance of recording detailed behavioral interactions. Competition for resources drives intra- and interspecific interactions in ecological systems, and natural selection should favor communication systems that reduce physical confrontations. While several traits, including body size, sex, age, relatedness, and ornamentation, have been identified as important factors determining intraspecific dominance, less is known about interspecific communication of competitive ability. A focus on interspecific interactions is essential to gaining insight into the evolution of signaling cues in complex ecological communities. Further research in this area will expand our understanding of communication systems and their role in shaping ecological relationships.

## AUTHOR CONTRIBUTIONS

**Facundo Fernandez-Duque:** Conceptualization; investigation; data curation; formal analysis; writing – original draft; writing – review and editing. **Eliot T. Miller:** Formal analysis; visualization; writing – review and editing. **Matias Fernandez-Duque:** Conceptualization; methodology; investigation; writing – review and editing. **Jay Falk:** Conceptualization; methodology; writing – original draft; writing – review and editing. **Gabriela Venable:** Software; writing – review and editing. **Sophie Rabinowicz:** Conceptualization; methodology; writing – review and editing. **C. Dustin Becker:** Data curation; resources; writing – review and editing. **Mark E. Hauber:** Conceptualization; methodology; writing – original draft; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

All datasets for this study are available on Figshare (<https://figshare.com/s/f2f1287a84e2c8aa9a3c>). DOI: 10.6084/m9.figshare.23913000.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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