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Intersexual social dominance mimicry drives female hummingbird polymorphism

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Female-limited polymorphisms, where females have multiple forms but males have only one, have been described in a variety of animals, yet are difficult to explain because selection typically is expected to decrease rather than maintain diversity. In the white-necked jacobin (*Florisuga mellivora*), all males and approximately 20% of females express an ornamented plumage type (androchromic), while other females are non-ornamented (heterochromic). Androchrome females benefit from reduced social harassment, but it remains unclear why both morphs persist. Female morphs may represent balanced alternative behavioural strategies, but an alternative hypothesis is that androchrome females are mimicking males. Here, we test a critical prediction of these hypotheses by measuring morphological, physiological and behavioural traits that relate to resource-holding potential (RHP), or competitive ability. In all these traits, we find little difference between female types, but higher RHP in males. These results, together with previous findings in this species, indicate that androchrome females increase access to food resources through mimicry of more aggressive males. Importantly, the mimicry hypothesis provides a clear theoretical pathway for polymorphism maintenance through frequency-dependent selection. Social dominance mimicry, long suspected to operate between species, can therefore also operate within species, leading to polymorphism and perhaps similarities between sexes more generally.

1. Introduction

The persistence of polymorphisms, or discrete phenotypic variation, has been the subject of an enduring debate in evolutionary biology because most forms of natural selection and genetic drift are expected to reduce rather than maintain diversity over time [1–4]. Sex-limited polymorphisms, where one sex exhibits multiple forms, but the other does not, are of particular interest because adaptive explanations for the polymorphism's persistence must also account for the difference between the sexes. The study of such sex-limited polymorphisms has traditionally focused on male-limited polymorphism and the ways in which sexual selection maintains a diversity of breeding phenotypes [5,6]. Although female-limited polymorphism has been studied in an increasing diversity of taxa [7–10], much like female ornamentation, the adaptive hypotheses used to explain female-limited polymorphism are diverse and relatively untested compared to those in males [6,11].

Negative frequency-dependent selection, a type of balancing selection [1], has been shown to maintain several examples of sex-limited polymorphism. Theoretically, if a morph's fitness is high when it is rare but low when common, it can remain in the population at equilibrium with alternative morphs [12,13]. Negative frequency-dependent selection is a characteristic of many common situations found in nature, such as mimicry, apostatic selection and alternative behavioural strategies [14]. For example, polymorphic female *Ischnura* damselflies have been shown to be under negative frequency-dependent selection to avoid male mating attempts [15,16], either by mimicking males [17], or by reducing the ability to identify females [18,19]. In polymorphic male bluegill sunfish, two behavioural mating strategies are maintained by negative frequency dependence because each alternative strategy has higher relative fitness when rare [20].

Many species of hummingbirds exhibit female-limited polymorphisms, and a recent study suggests the phenomenon may be widespread across the hummingbird clade [21]. In at least one hummingbird species, the white-necked jacobin (*Florisuga mellivora*), female-limited polymorphism appears to have evolved through competition for food resources via non-sexual social selection [22]. All males and approximately 20% of adult female white-necked jacobins are ornamented, containing an iridescent blue head, white neck and white tail (androchromic plumage type). Female and male androchromes are nearly indistinguishable in the field. Other females are drab in coloration, with a green dorsum, speckled throat and dark tail (heterochromic plumage type, see electronic supplement material and [22] for detailed descriptions and illustrations). Androchromes of unknown sex initiate chases more often than heterochrome females, and both con- and heterospecific hummingbirds avoid aggression toward both androchrome females and males compared to heterochrome females [22]. Androchrome females have increased access to food resources, likely because they experience reduced aggression in comparison to heterochrome females. Thus, there appears to be an advantage to androchrome plumage through a perceived association with aggression. However, it remains untested whether competitive ability is actually signalled by androchrome plumage in both sexes.

Understanding competitive ability relates directly to hypotheses for how the polymorphism is maintained. Given previous findings, two explanations are plausible. First, androchromes of both sexes may have evolved a suite of morphological, physiological and behavioural adaptations that facilitate a territorial feeding strategy signalled by their conspicuous plumage, whereas heterochrome females use a non-territorial strategy [23]. In other words, the two female types exhibit alternative behavioural strategies, and androchrome plumage in both males and females is associated with more aggressive behaviour and higher competitive ability. Other individuals avoid androchromes because this plumage type is a direct signal of these potentially dangerous behaviours. Critically, under this hypothesis, we expect androchrome individuals of both sexes to have similar resource-holding potential (RHP) that is greater than that of heterochrome females. This hypothesis is supported in many examples of species-wide and male polymorphism where alternative phenotypes are not only visually distinct but morphologically, physiologically and behaviourally divergent as well (e.g. [24–26]; reviewed in [5,6]). Alternative behavioural strategies are typically maintained because one strategy competes against the other most effectively when rare, though the specific parameters influencing these dynamics are diverse [6,27,28].

Alternatively, androchrome females may mimic male coloration but are otherwise more like heterochrome females in morphology, physiology and behaviour. According to this hypothesis, males have evolved more aggressive behaviour and territorial feeding strategies, and their ornamentation is a signal of high RHP and its associated adaptations. Androchrome females mimic males by having similar plumage coloration but do not employ a similar feeding strategy, nor the associated morphological or physiological adaptations to facilitate that behaviour. Instead, androchrome females benefit because other hummingbirds cannot easily distinguish them from more aggressive males, yet these females do not pay the costs of higher RHP such as energetically expensive muscle mass and risky aerial combat. Diminishing benefit with increasing frequency of mimics is inherent in deceptive mimicry systems [13,29,30], offering a potential avenue for polymorphism maintenance. A critical distinguishing prediction of this hypothesis is that androchrome and heterochrome females should have similar morphologies, physiologies and behaviours (i.e. similar RHP) that differ from those of males. This hypothesis is related to the 'competitive mimicry' hypotheses proposed to explain phenotype convergence [31–33], especially where members of one group mimic a more socially dominant competitor to gain access to ecological resources.

Here, we seek to distinguish between these alternative hypotheses by testing a critical difference in their predictions: whether RHP (as measured by morphology, physiology and behaviour) is best predicted by plumage type (indicating alternative behavioural strategies across females), or by genetic sex (indicating mimicry of males by some females). First, we used a weight-lifting assay to assess burst power, which is a measure of flight performance in hummingbirds [34,35]. Burst power is the maximum energetic output during hummingbird flight [35,36] and is related to agility and the ability to perform aerial manoeuvres that are used in direct competition and territoriality such as chasing and aerial fighting [34,35,37,38]. Second, we measured wing loading (i.e. the ratio of body weight to wing area) via wing shape measures, which are associated with aspects of manoeuvrability such as in-flight rotations, turns and acceleration [34,39], in addition to other wing parameters. Third, we compared overall body size, as larger size is associated with dominance across hummingbird species [40,41] and other taxa [42]. Finally, we observed whether androchrome female feeding behaviour is more like that of males or that of heterochrome females by monitoring birds fitted with radio frequency identification (RFID) tags in a network of feeders with RFID-detecting antennae. Ultimately, comparing morphology, physiology and behaviour across both sexes and plumage types can elucidate the mechanisms by which discrete variation in females is maintained.

2. Methods

(a) Morphology, ageing and sexing

We captured 436 white-necked jacobins from August 2015 to May 2019 in and around Gamboa, Panama (9°7′12″, −79° 42′0″). All birds were photographed and identified as either androchromic, heterochromic, or mixed by JFF while in hand.

We verified this classification strategy with the procedure described in [22]. Briefly, we extracted colour values from photographs of 208 white-necked jacobins and used unsupervised clustering methods to show two clusters of colour in this species. This objective classification of photos matched in-hand identifications of androchromes and heterochromes in 100% of cases. We therefore included all birds with in-hand identification in these analyses except those identified as 'mixed' which could not be consistently classified but made up only 1.3% of all captures. Throughout this paper, we refer to 'bird type' as a three-factor plumage/sex variable which includes heterochrome females, androchrome females and androchrome males.

At the time of each capture, we collected morphological measurements: mass (± 0.01 g digital scale), length of culmen, length from nare to bill tip, tarsus (± 0.1 mm manual calipers), right closed wing length f (± 0.05 cm hand ruler [43]), right wing width c_m, (± 0.05 cm hand ruler [43]) and tail length (± 0.5 mm ruler). In addition to these measurements taken during capture, we also photographed the spread right-side wing on graphing paper of 137 individuals for more detailed wing parameter measurements. Using these photographs, we measured wing length, width and area using ImageJ [44], and used these to calculate the shape ratio (length/width), aspect ratio ($2 \times \text{length}^2/\text{area}$) and wing taper (length × width/area) following guidelines in [45].

We used bill corrugation to distinguish juveniles from adults, as young hummingbirds have more bill corrugation than do older birds, [46–48]. Previous analyses in this species have found that most adult females can have up to 40% of the bill corrugated [22], so we considered birds with 40% or more corrugation to be juveniles in their first year. For genetic sexing, we collected 5–15 µl of blood from the tarsal vein into 2% SDS lysis buffer. Samples were stored at room temperature and shipped to the Cornell Lab of Ornithology, where all DNA samples were extracted using Qiagen DNeasy Blood & Tissue Kits. We sexed individuals using either 2550F/2718R primers or 1237L/1272H primers to amplify fragments of the sex chromosomes on agarose gels or an Applied Biosystems 3730xl sequencer, respectively [22].

(b) Burst power

We measured burst power of 210 captured birds in a 38 × 38 × 60 cm mesh enclosure covered on all sides except the top with an opaque grey fabric and placed an LED light (Ledlenser SE07R) above the enclosure to attract the bird upwards. A rubber loop connected to a string of coloured weights was loosely draped over the bird's neck (see Data Accessibility for the mass of each bead). Birds were encouraged to fly by releasing them approximately 3 cm from the cage base. Once in flight, the birds lift progressively more weights, and we recorded videos of the maximum number of weights lifted. We targeted 5–7 lift flights for each bird and were able to extract data accurately from the videos for 2–10 lifts per bird. We removed trials with less than four lifts, resulting in an average of 6.3 lifts per bird (± 1.4 s.d.). For each lift, we took the mass of the bird and added this to the mass lifted to calculate the total mass lifted. We averaged all lifts for a mean burst power measurement for each capture. The number of lifts per bird was not associated with mean burst power ($p = 0.55$). Before analysing the data, we removed individuals with 40% or more corrugation to remove juveniles, resulting in 167 individuals (52 heterochrome females, 10 androchrome females and 105 androchrome males). We then compared heterochromic females, androchromic females and males by calculating means and bootstrapped 95% confidence intervals for each bird type with 5000 resamples. Contrasts between types were then evaluated using permutation tests to calculate p-values with 5000 permutations ($p < 0.025$ or greater than 0.975 are significant at alpha = 0.05).

(c) Wing load

Wing loading is the total sustained mass in flight per area of both spread wings [49]. The mass of each bird was measured with a digital scale (± 0.005 g). We approximated wing area by multiplying the length of the closed wing by the wing width (see Methods: morphology, ageing and sexing). We verified the accuracy of this technique by comparing this estimate of wing area to measured wing area using detailed measurements from 144 photographs of spread wings. Estimates were significantly predictive of measured wing load ($p < 0.0001$, correlation = 0.659, residual s.e. = 0.00025). Therefore, we proceeded to use the wing area approximations in analysis of wing load (though see table 1 for wing load calculations based on detailed area measures). As with burst power, we removed juveniles, resulting in 282 individuals (78 heterochrome females, 20 androchrome females and 184 androchrome males) and evaluated differences between the three bird types by calculating mean and bootstrapped 95% CI with 5000 resamples, and calculated p-values using permutation tests with 5000 permutations ($p < 0.025$ or greater than 0.975 are significant at alpha = 0.05).

(d) Body size

We incorporated all seven morphological measurements taken in the field into a principal components analysis to interpret and visualize morphological variation in this species. To test whether bird types differed from each other, we performed three discriminant function analyses with the MASS package in R [50,51] to test whether any axes of morphological variation could distinguish between heterochrome and androchrome females, androchrome females and males, and heterochrome females and males. For each of these pairwise comparisons, we generated jackknifed predictions of bird type with our observed data. Overall prediction accuracy was calculated as the weighted mean of the prediction accuracy for each bird type. We then permuted the bird type 5000 times to generate an estimation of the null accuracy of jackknifed predictions under randomized association of type and morphology measurements. We calculated p-values as the proportion of permutations that exceeded the accuracy of the observed dataset. In a final comparison, we repeated this analysis to compare whether genetic sex could be predicted by morphology.

(e) Feeding strategy

To assess the behaviour of individual white-necked jacobins, we used a RFID system to log feeding behaviour across the town of Gamboa, Panama, as described in [22]. Briefly, white-necked jacobins were sub-dermally tagged with PIT tags between the shoulders, and we detected tagged birds in the wild using RFID loggers attached to hummingbird feeders [52]. If a tag was detected, the ID was logged with date and time to the second. We began PIT tagging white-necked jacobins in December of 2017, and we tagged most subsequent captures until the experiment ended in May 2019. All tagged birds were genetically sexed as described above. Feeders were placed a minimum of 50 m apart with no line of sight between any two feeders, and we attempted to keep spacing even when changing the number of feeders. We filled feeders with sugar and water solution in high- and low-sugar concentrations (1 : 3 and 1 : 6 parts sucrose : water solutions). However, a previous study on this same dataset [22] found that visitation to high- versus low-sugar feeders did not differ between the males, heterochrome females or androchrome females. Therefore, we did not incorporate feeder sugar levels into our analyses of behavioural strategies since our purpose in this study was to find aspects of feeding behaviour that distinguish bird types. Thirty-eight heterochrome females, 15 androchrome females and 104 males visited a feeder

Table 1. Comparison of wing measures of white-necked jacobin plumage types. Hf = heterochrome female, Af = androchrome female, Am = Androchrome male. We photographed the spread right wing of 116 white-necked jacobins (Hf, $n = 31$; Af, $n = 8$; Am, $n = 77$) on 0.5 cm graph paper and measured the length, width and area. Wing load, aspect ratio, shape ratio and taper were calculated as in [45]. Ninety-five per cent confidence intervals were calculated with bootstrapping, and *p*-values were calculated by permutations of all three bird types. *p*-values < 0.025 and greater than 0.975 are significant (italics) at alpha = 0.05.

measurement	bird type	mean	95% CI	Hf-Af contrast *p*-value	Am-Hf contrast *p*-value	Am-Af contrast *p*-value
wing area (cm^2)	Hf	11.61	(11.34, 11.86)	0.81	*<0.0002*	*<0.0002*
	Af	11.94	(11.52, 12.45)			
	Am	12.70	(12.51, 12.90)			
length (cm)	Hf	6.97	(6.89, 7.57)	0.7	*<0.0002*	*<0.0002*
	Af	7.04	(6.91, 7.04)			
	Am	7.33	(7.27, 7.39)			
width (cm)	Hf	2.25	(2.22, 2.28)	0.82	*<0.0002*	*<0.0002*
	Af	2.30	(2.27, 2.32)			
	Am	2.47	(2.44, 2.49)			
wing load (kg m^{-2})	Hf	3.00	(2.85, 3.07)	0.84	0.48	0.06
	Af	2.78	(2.68, 2.89)			
	Am	3.00	(2.89, 3.04)			
aspect ratio	Hf	8.53	(8.45, 8.62)	0.32	0.10	0.10
	Af	8.47	(8.30, 8.62)			
	Am	8.62	(8.54, 8.71)			
shape ratio	Hf	3.13	(3.09, 3.18)	0.26	*>0.9998*	0.94
	Af	3.09	(3.01, 3.17)			
	Am	3.00	(2.96, 3.04)			
taper	Hf	0.363	(0.344, 0.383)	0.60	*<0.0002*	*<0.0002*
	Af	0.369	(0.334, 0.401)			
	Am	0.439	(0.425, 0.452)			

at least once during the two seasons. Androchrome females may switch to heterochrome plumage during moult. Therefore, we removed the data from 2019 from two androchrome females that were tagged in 2018, but not recaptured in 2019 because we could not verify their plumage type. Another two androchrome females from 2018 were recaptured in 2019 and we verified that they had moulted to heterochromic plumage. Therefore, we changed their plumage type to heterochromic in the 2019 dataset.

A major difference between non-territorial and territorial feeding strategies is in space usage [53]. Specifically, territoriality involves frequent feeds from a small region of space, while non-territorial strategies are more dispersed. We therefore compared daily feed frequency to daily space usage, using the number of feeding stations visited as a proxy for space use. For non-territorial birds, we expect a positive relationship between feed frequency and number of stations visited. By contrast, territorial behaviour should be associated with low number of stations visited but high feed frequency [53]. A preliminary analysis of all individuals found a nonlinear, hump-shaped relationship—the number of stations visited appeared to increase from low- to mid-level feed frequencies, but then decreased from mid- to high-level feed frequencies, suggesting that both non-territorial and territorial strategies exist in the population. Both juveniles and adults showed a similar relationship between feed frequency and stations visited, so we combined both for future analyses. We modelled this relationship with the daily number of stations visited as a response to the total daily feeds. We then evaluated this model with and without a quadratic representation for total daily feeds as a second predictor variable. Models were compared with and without the quadratic component using a likelihood ratio test to test whether a quadratic relationship better describes the relationship than a linear relationship. Last, we repeated these same steps for each of the three bird types to observe whether all three exhibited similarly shaped relationships.

3. Results

(a) Burst power, wing load, wing shape and body size

Androchrome and heterochrome females had similar burst power (figure 1*a*: androchrome female mean = 18.4 g, 95% CI = 17.7, 19.1 g; heterochrome female mean = 19.1 g, 95% CI = 17.87, 20.2 g; difference in mean $p = 0.75$) whereas males (mean = 22.0 g, 95% CI = 21.5, 22.5 g) had higher burst power than both heterochrome females ($p < 0.002$) and androchrome females ($p = 0.03$). Androchrome female wing load (figure 1*b*: mean = 4.66, 95% CI = 4.50, 4.83) was not significantly different from either heterochrome females (mean = 4.72, 95% CI = 4.62, 4.82; $p = 0.30$) or males (mean = 4.56, 95% CI = 4.50, 4.62; $p = 0.14$). Males had significantly lower wing load than heterochrome females ($p = 0.002$), but the effect size was small (figure 1*b*). We also found overlap

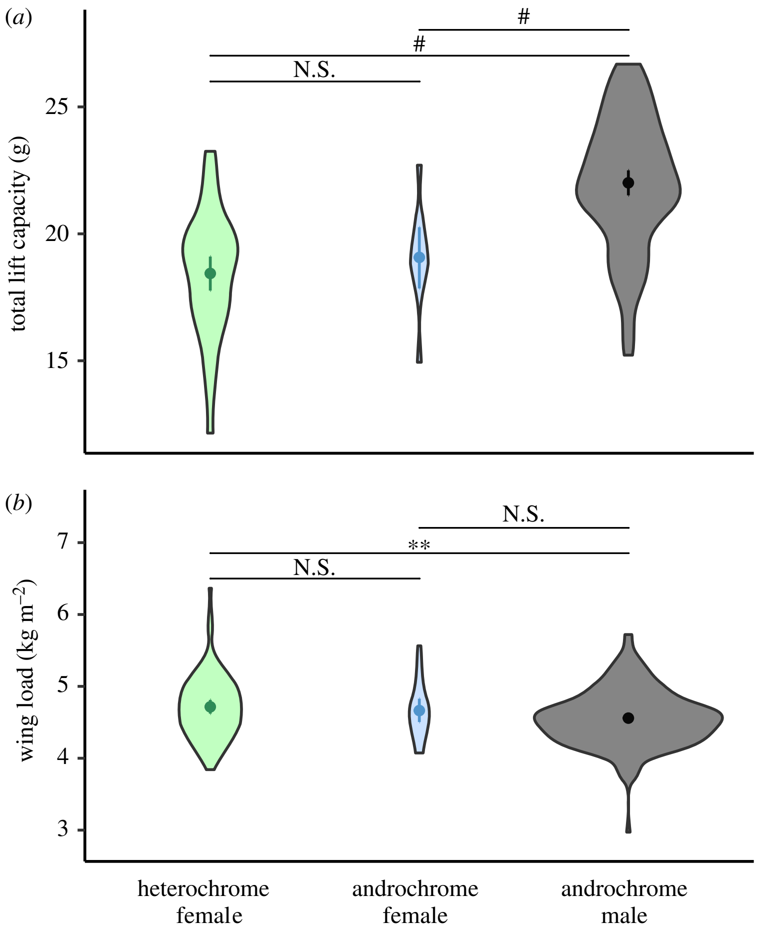

Figure 1. Burst power and wing loading in heterochrome females, androchrome females and androchrome males. Points and lines represent means and bootstrapped 95% CI. Shaded areas represent the distribution of individual data points. *p*-values for differences in means are indicated by N.S., $p > 0.05$; **$0.01 > p > 0.001$; $p < 0.0001$. Juveniles were excluded from both graphs. (*a*) Females of both plumage types were similar in burst power, but males lifted significantly more than both female types. (*b*) Similar wing loading measures were found between female plumage types, and between androchrome females and males. Heterochrome females had slightly but significantly lower wing load than androchrome males. (Online version in colour.)

in all measures and calculations of wing size/shape between the two female types (table 1). By contrast, males had larger wing length, width, wing area and taper than both female types. Wing load and aspect ratio calculations were similar across all three bird types, and male shape ratio was different from heterochrome but not from androchrome females.

Discriminant function analysis comparing the two female types showed that morphology predicted female type with an overall 79.6% accuracy, but this was not better than null expectations under permuted datasets ($p = 0.68$) indicating that female types cannot be distinguished by morphology. Males and androchrome females could be distinguished with an overall 95.5% accuracy, and heterochrome females and males were distinguished with 93.4% accuracy, both of which exceeded the accuracy of permuted datasets ($p < 0.002$ both comparisons). The overall prediction accuracy of genetic sex based on morphology was 93.2%, which was also greater than null expectations from permuted datasets ($p < 0.002$). Similarly, principal component analysis of morphology clearly showed an overlap between female types, but that males and females can be distinguished (figure 2).

Together, our results suggest that female plumage type cannot be distinguished by any traits associated with RHP that we measured, including burst power, wing loading, overall body size or wing shape. By contrast, males differed from both female types in all of these traits except some measures of wing morphology (wing load, shape ratio and aspect ratio).

(b) Feeding strategy

The model of the relationship between the number of stations visited and feed frequency for all individuals was improved by inclusion of a negative quadratic term (ΔAIC = −57.9, $\beta = -0.003$, electronic supplementary material, table S1). We then fit the same model parameters to the same data but subset by bird type. Model fit of heterochrome females was not improved with the addition of a quadratic term (ΔAIC = +1.5, electronic supplementary material, table S1; figure 3). Androchrome females showed a marginal positive quadratic relationship (ΔAIC = −3.1, $\beta = +0.025$, electronic supplementary material, table S1; figure 3), opposite the direction we found across all three groups. The male model was also improved with the addition of a quadratic term, but here the relationship was negative (ΔAIC = −34.1, $\beta = -0.002$, electronic supplementary material, table S1; figure 3), reflecting decreased space use at the lowest and highest feeding frequencies. In summary, both female types show evidence for increasing space use as feed frequency increases, but only males showed reduced space use at their highest feed frequencies, a pattern consistent with territorial feeding strategy. This difference between the sexes appears

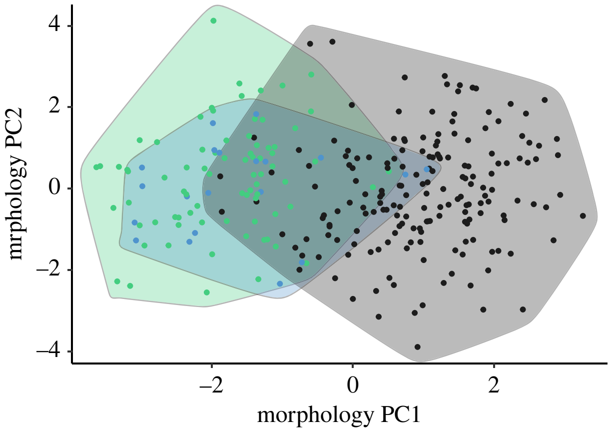

Figure 2. Principal components for seven measures of body size in white-necked jacobins. The first and second PC axes are depicted here, which explain 38.5% and 25.4% of the total variation. Green points and shading represent heterochrome female morphology, while blue and grey represent androchrome females and androchrome males, respectively. Both female types overlap, while most males are distinct from either female type. (Online version in colour.)

to be driven by a much more limited range of mean daily feeding visits for females compared to males (figure 3). Indeed, the maximum mean feeder visit rate for any female was 19.2 visits per day, less than half the maximum found in males, 55.8 visits per day.

4. Discussion

Directional selection and genetic drift tend to reduce variation over time, but polymorphisms can persist through several adaptive mechanisms [1]. Alternative behavioural strategies have been implicated as a form of balancing selection that can maintain polymorphism through negative frequency-dependent fitness [5,6,27]. In these cases, suites of morphological and physiological traits are often linked to divergent behavioural strategies. In white-crowned sparrows, for example, a plumage colour polymorphism is linked to differences in aggression through hormonal and neural correlates [54]. Alternative behavioural strategies have been described in a diversity of taxa and are often involved in male–male competition for access to mating opportunities leading to male polymorphism [6], for example, the α-, β- and γ-male morphs in a marine isopod that each use a different mating strategy [55]. Similar alternative behavioural strategies could in theory evolve in other contexts such as competition for social rank, breeding resources or limited food energetic resources. As such, it has been proposed that female polymorphism in hummingbirds could be explained by the coexistence of multiple feeding strategies [23]. Ornamentation is often associate with territoriality in hummingbirds, whether found on females or males [56,57]. Therefore, colourful plumage could be used as a signal for high RHP not only across species and sex, but within sex as well.

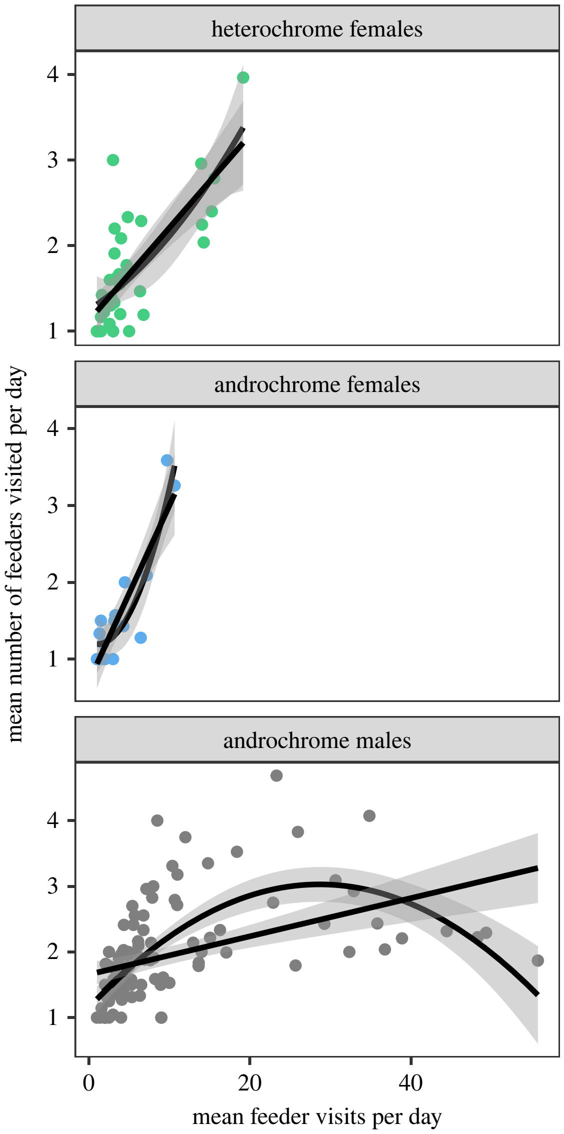

Figure 3. A comparison of space use (mean number of feeders visited) and feed frequency (mean feeder visits) as a measure of feeding strategy. Best-fit linear and quadratic relationships are shown in each graph. If both non-territorial and territorial strategies are used, we expect a negative quadratic component (upside-down U) to this relationship, which was only found in androchrome males. Females of both types only exhibited a positive relationship, indicating a lack of detected territoriality. Individuals of all three types therefore can be observed using a non-territorial feeding strategy, but some males show patterns consistent with territoriality. (Online version in colour.)

In contrast with this hypothesis, we found that even though androchrome females and males have similar coloration, they differ in morphology, physiology and behaviour. Furthermore, we did not find any difference between the two female types in measures that are known to be associated with divergent feeding strategies in hummingbirds, including burst power, body size, wing load and wing shape [34,53]. Therefore, our results are inconsistent with the prediction that both androchrome females and males are co-dominant over heterochromes [23]. Based on our measurements, sex—not plumage type—can predict the outcome of an antagonistic interaction should one occur. In a previous study, androchrome female mounts experienced less aggression than heterochrome females, they accessed food resourced at higher rates, and androchromes of unknown sex were more aggressive toward other hummingbirds [22]. Here, we find that some males are more territorial than females and that their morphology and physiology are adapted to this behavioural strategy. Taken together with previous findings [22], our results suggest that the benefit to androchrome females derives from mimicry of more socially aggressive males rather than through alternative behavioural strategies where androchrome coloration would be a direct signal of aggression in both sexes.

Hummingbirds differ widely in their propensity to engage in aggression and exclusionary competition at food resources, both within and between species [53,58]. While in some species, both sexes compete for flower resources [56,57], in others males are more prone to aggressive behaviour around food [59]. The reasons for these behavioural differences have not been explicitly tested, but it has been hypothesized that males defend food resources to attract mates [60], and perhaps nesting females must maintain spatial flexibility. In white-necked jacobins, androchrome of unknown sex are on average more aggressive than heterochrome females [22]. However, based on the results here, it is likely that most observed chases are from males, not androchrome females. Despite this, if other hummingbirds cannot easily distinguish female androchromes from males, then androchrome females can reap the benefit of appearing like an aggressive male through mimicry without the potential costs of behaving like one.

The evidence in favour of mimicry is critical for understanding how this polymorphism is maintained because deceptive mimicry is inherently frequency dependent [13,30]. In classic Batesian mimicry, palatable mimics reduce predation because predators cannot distinguish palatable and distasteful or toxic prey. Mimics should experience the least predation when mimicry is rare because most predator experience will be with distasteful prey. A similar dynamic may be at play in hummingbird females, but with social harassment in place of distastefulness. Males may act as more aggressive models with high RHP that deter competitors through interference competition, and androchrome females resemble males to reap the benefits of reduced competition (e.g. greater access to food) without consistently engaging in potentially harmful aggressive behaviours, or having to produce costly morphologies (e.g. increased muscle mass). However, the greater the frequency of male-mimicking females, the lower the association between plumage type and high RHP, perhaps to the point that heterochrome females are advantaged. Deceptive mimicry therefore provides a clear framework for understanding how female polymorphisms might persist through *intersexual social dominance mimicry* in this and other hummingbird species with female polymorphism [21].

On a related note, juveniles in this species, all of which have androchromic plumage regardless of sex [22], may also be engaging in social dominance mimicry. While the focus of this study was to compare birds at the adult stage, we found that juvenile males indeed have a lower muscle capacity than adult males ($\beta = 1.95$, s.e. = 0.52, $p = 0.0002$), with females showing a similar pattern ($\beta = 1.33$, s.e. = 0.71, $p = 0.06$). We speculate that the conspicuity of androchrome plumage is also advantageous to juveniles through mimicry. Most females moult into heterochrome plumage as adults perhaps due to the increased predation risk of nesting, which is undertaken only by adult females.

Future work will likely add complexity and nuance to this intersexual social dominance mimicry hypothesis. As described above, negative frequency-dependent selection is an inherent aspect of social dominance mimicry. However, this study does not show direct evidence of frequency-dependent selection, which will be important for future experiments to test. It should be noted, however, that negative frequency dependence is not solely a property of deceptive mimicry, and that alternative behavioural strategies are also maintained through negative frequency dependence. Although we found multiple lines of evidence that the female morphs are similar, it is likely that differences will be discovered in other contexts. This would not necessarily contradict the social dominance mimicry hypothesis, but it would add greater ecological context that could affect frequencies of either morph at equilibria [61]. For example, female-limited polymorphism in damselflies is thought to be maintained by intersexual mimicry to avoid mating attention, but female colour morphs nevertheless differ from each other in multiple ways (e.g. temperature sensitivity [61], tolerance to parasites [62] and UV damage [63]).

While differences in hummingbird feeding strategies have long been hypothesized [53], this study is the first to attempt to identify different strategies with many individuals through a passive tracking technique in the wild. By comparing the number of feeders visited with feed frequency, we found a distinct hump-shaped relationship. The initial increase on the left side of this relationship is likely due to lower detection rates for some individuals. Gamboa and the surrounding area has many potential locations for hummingbirds to feed, most of which we were unable to track. If an individual feeds primarily from these alternative locations, then we expect to detect fewer of their feedings, and our ability to identify their strategy is weak. This may be the primary reason that we see increasing space usage from low- to mid-range feeding frequency, because detection at a high number of stations is difficult if detection is low. However, the observed reduction in space use from mid- to high-range feed frequency cannot be explained through lower detection because feeder use is increasing. Therefore, while we cannot confidently identify strategies of the lowest detected individuals, we are more confident that the high space use with mid-range feed frequency, and the low space use with high-range feed frequency represent a spectrum between different feeding strategies. As another caveat, we note that we cannot be certain the birds engaged in any direct competition with other individuals at the feeders with the available data. However, a high number of feeds with lower space is consistent with expectations under exclusionary competition for resources and is distinct from a feeding strategy with higher space use [53]. Furthermore, the spectrum of behaviours we describe here is well documented in hummingbirds [53,64], and exclusionary competition is conspicuously evident by watching white-necked jacobins interact at both natural and artificial food sources in the wild.

Our lack of evidence for differences in feeding strategy between female types does not exclude the possibility that androchrome females can show increased access to food resources. In fact, we previously found that androchrome females had longer duration feedings than heterochrome females [22], which is compatible with our analysis here: even if androchrome females do not exhibit distinct feeding strategies, if mimicry allows them to be harassed less often, they should be able to access food for longer durations. We also previously found that female types differed in feed frequency, but not when excluding days in which birds did not visit our RFID feeders [22]. This lack of a difference is reflected in our analysis here, where we only included days in which individuals were detected at least once. We focus on days where we are confident the birds were present since this is necessary to detect a feeding strategy. Days in which no feeds were detected may be an artefact of the experiment if the birds have completely left the study area. It is also possible, however, that daily presence in the dataset is biologically relevant, reflecting a true difference in female morph strategy. Although challenging with the small size of hummingbirds, combining our RFID with other tracking techniques like automated telemetry may ultimately be necessary to definitively compare feeding and movement strategies [53].

To our knowledge, intersexual social dominance mimicry has not previously been proposed to explain female-limited polymorphism, but a similar form of intersexual mimicry has been studied extensively in damselflies and other taxa. In some damselflies, female-limited polymorphism is thought to play a role in reducing sexual attention from males through intersexual mimicry [65,66]. Mimicry in this case is therefore directed to males of the same species. In contrast, since access to food resources can be limited by any ecological competitor, a female white-necked jacobin appearing like a male may deter aggression from numerous sources: both females and males of the same species, as well as other species if contact is common. Indeed, other species avoided aggressive behaviour toward androchrome mounts of both males and females [22], suggesting that male mimicry by females is effective at deterring social aggression from both this and other species.

A more general phenomena of social dominance mimicry to access ecological resources has been hypothesized in other avian taxa, but discussion typically involves interspecies rather than intersexual mimicry [31–33,67]. For example, some woodpeckers are suspected to have evolved similar plumage coloration to more socially dominant species that occupy similar geographical regions [31,67,68]. There has been debate as to whether interspecies social dominance mimicry involves the deception of the socially dominant models [32,67,69–71], or other third-party species [31,68]. In white-necked jacobins, androchromes, heterochromes, as well as heterospecific individuals avoided androchromes [22], providing support for both hypotheses (albeit at the intersexual level). We note that, compared to interspecies mimicry, intersexual mimicry may be relatively easy to evolve since males and females share much of their genome and adaptive transfer of traits across sexes is common [72]. Intriguingly, intersexual mimicry could even result in sexual monomorphism if the benefits to mimicry are great enough such that androchrome female fitness surpasses that of heterochromes at all frequency levels. Females of some sexually monomorphic avian species have been shown to evolve their ornamentation in association with increased competition for mates or reproductive resources [73]. As an alternative hypothesis, monomorphism through intersexual mimicry has been proposed [74] but has received little empirical attention. Interestingly, many hummingbird species are monomorphically ornamented, providing a rich ground for further testing this hypothesis.

Within-sex polymorphism can provide unique perspectives on both identifying the types of selection that can lead to variation, but also in studying the differences in behaviour between sexes. The morphological, physiological and behavioural results in this study support an intersexual social dominance mimicry hypothesis, adding to a diversity of explanations for female-limited polymorphism in animals. As adaptive hypotheses are considered in other taxa, understanding the connections between cases of female-limited polymorphism should lend itself to a broader understanding of polymorphism, sexual variation and ornamentation in general.

Ethics. All experimental procedures were approved by Institutional Animal Care and Use Committees (IACUC) at both Cornell University (2009-0105) and the Smithsonian Tropical Research Institute (2015-0618-2018-A1, 2016-0120-2019, 2017-0116-2020). Collections were permitted by the Panamanian Ministry of the Environment under SE/A-84-14, SE/A-11-16, SE/A-15-17, SE/A-100-17 and SE/APHBO-7-18. Blood samples were exported from Panama to the USA under CITES permits SEX/A-101-15, SEX/A-111-16, SEX/A-73-17, SEX/A-47-2018, SEX/A-36-19 and USDA Import Permit 52686.

Data accessibility. Data and code are available at Zenodo: https://doi.org/10.5281/zenodo.6975352 [75].

Electronic supplementary material is available online [76].

Authors' contributions. J.J.F.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, writing—original draft and writing—review and editing; D.R.R.: conceptualization and writing—review and editing; A.R.-G.: funding acquisition and writing—review and editing; M.S.W.: conceptualization and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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References

1. Hedrick PW. 2007 Balancing selection. *Curr. Biol.* **17**, R230–R231. (doi:10.1016/j.cub.2007.01.012)
2. Hedrick PW, Ginevan ME, Ewing EP. 1976 Genetic polymorphism in heterogeneous environments. *Annu. Rev. Ecol. Syst.* **7**, 1–32. (doi:10.1146/annurev.es.07.110176.000245)
3. Levene H. 1953 Genetic equilibrium when more than one ecological niche is available. *Am. Nat.* **87**, 331–333. (doi:10.1086/281792)
4. Wallace AR. 1865 I. On the phenomena of variation and geographical distribution as illustrated by the Papilionidæ of the Malayan Region. *Trans. Linn. Soc. Lond.* **1**, 1–71. (doi:10.1111/j.1096-3642.1865.tb00178.x)
5. Gross MR. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 92–98. (doi:10.1016/0169-5347(96)81050-0)

6. Oliveira RF, Taborsky M, Brockmann HJ. 2008 *Alternative reproductive tactics: an integrative approach*. Cambridge, UK: Cambridge University Press.
7. Ajuria Ibarra H, Reader T. 2014 Female-limited colour polymorphism in the crab spider *Synema globosum* (Araneae: Thomisidae). *Biol. J. Linn. Soc.* **113**, 368–383. (doi:10.1111/bij.12338)
8. Dijkstra PD, Seehausen O, Groothuis TGG. 2008 Intrasexual competition among females and the stabilization of a conspicuous colour polymorphism in a Lake Victoria cichlid fish. *Proc. R. Soc. B* **275**, 519–526. (doi:10.1098/rspb.2007.1441)
9. Moon RM, Kamath A. 2019 Re-examining escape behaviour and habitat use as correlates of dorsal pattern variation in female brown anole lizards, *Anolis sagrei* (Squamata: Dactyloidae). *J. Linn. Soc.* **126**, 783–795. (doi:10.1093/biolinnean/blz006)
10. Reinhardt K, Harney E, Naylor R, Gorb S, Siva-jothy MT. 2007 Female-limited polymorphism in the copulatory organ of a traumatically inseminating insect. *Am. Nat.* **170**, 931–935. (doi:10.1086/522844)
11. Alonzo SH. 2008 Conflict between the sexes and alternative reproductive tactics. In *Alternative reproductive tactics: an integrative approach* (eds Rui F Oliveira, Michael Taborsky, H Jane Brockmann), pp. 435–450. Cambridge, UK: Cambridge University Press.
12. Smith JM. 1982 *Evolution and the theory of games*. New York, NY: Cambridge University Press.
13. Fisher RA. 1930 *The genetical theory of natural selection*. New York, NY: Oxford University Press.
14. Ayala FJ, Campbell CA. 1974 Frequency-dependent selection. *Annu. Rev. Ecol. Syst.* **5**, 115–138. (doi:10.1146/annurev.es.05.110174.000555)
15. Svensson EI, Abbott J, Härdling R. 2005 Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *Am. Nat.* **165**, 567–576. (doi:10.1086/429278)
16. Willink B, Duryea MC, Svensson EI. 2019 Macroevolutionary origin and adaptive function of a polymorphic female signal involved in sexual conflict. *Am. Nat.* **194**, 707–724. (doi:10.1086/705294)
17. Rivera AC, Sánchez-Guillén RA. 2007 Male-like females of a damselfly are not preferred by males even if they are the majority morph. *Anim. Behav.* **74**, 247–252. (doi:10.1016/j.anbehav.2006.06.023)
18. Van Gossum H, Stoks R, De Bruyn L. 2001 Frequency-dependent male mate harassment and intra-specific variation in its avoidance by females of the damselfly *Ischnura elegans*. *Behav. Ecol. Sociobiol.* **51**, 69–75. (doi:10.1007/s002650100418)
19. Takahashi Y, Yoshimura J, Morita S, Watanabe M. 2010 Negative frequency-dependent selection in female color polymorphism of a damselfly. *Evolution* **64**, 3620–3628. (doi:10.1111/j.1558-5646.2010.01083.x)
20. Gross MR, Harvey PH, Partridge L, Southwood SR. 1991 Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Phil. Trans. R. Soc. Lond. B* **332**, 59–66. (doi:10.1098/rstb.1991.0033)
21. Diamant ES, Falk JJ, Rubenstein DR. 2021 Male-like female morphs in hummingbirds: the evolution of a widespread sex-limited plumage polymorphism. *Proc. R. Soc. B* **288**, 20203004. (doi:10.1098/rspb.2020.3004)
22. Falk JJ, Webster MS, Rubenstein DR. 2021 Male-like ornamentation in female hummingbirds results from social harassment rather than sexual selection. *Curr. Biol.* **31**, 4381–4387. (doi:10.1016/j.cub.2021.07.043)
23. Bleiweiss R. 1985 Iridescent polychromatism in a female hummingbird: is it related to feeding strategies. *The Auk* **102**, 701–713. (doi:10.1017/CBO9781107415324.004)
24. Brock KM, Chelini MC, Ayton C, Madden IE, Ramos C, Blois JL, Pafilis P, Edwards DL. 2022 Colour morph predicts social behaviour and contest outcomes in a polymorphic lizard (Podarcis erhardii). *Anim. Behav.* **191**, 91–103. (doi:10.1016/j.anbehav.2022.06.017)
25. Kokko H, Griffith SC, Pryke SR. 2014 The hawk–dove game in a sexually reproducing species explains a colourful polymorphism of an endangered bird. *Proc. R. Soc. B* **281**, 20141794. (doi:10.1098/rspb.2014.1794)
26. Dijkstra PD, Lindström J, Metcalfe NB, Hemelrijk CK, Brendel M, Seehausen O, Groothuis TGG. 2010 Frequency-dependent social dominance in a color polymorphic cichlid fish. *Evolution* **64**, 2797–2807. (doi:10.1111/j.1558-5646.2010.01046.x)
27. Shuster SM, Wade MJ. 2003 *Mating systems and strategies*. Princeton, NJ: Princeton University Press.
28. Shuster SM. 2010 Alternative mating strategies. In *Evolutionary behavioral ecology* (eds DF Westneat, CW Fox), pp. 434–450. New York, NY: Oxford University Press.
29. Kunte K. 2009 Female-limited mimetic polymorphism: a review of theories and a critique of sexual selection as balancing selection. *Anim. Behav.* **78**, 1029–1036. (doi:10.1016/j.anbehav.2009.08.013)
30. Pfennig DW, Harcombe WR, Pfennig KS. 2001 Frequency-dependent Batesian mimicry. *Nature* **410**, 323. (doi:10.1038/35066628)
31. Miller ET, Leighton GM, Freeman BG, Lees AC, Ligon RA. 2019 Ecological and geographical overlap drive plumage evolution and mimicry in woodpeckers. *Nat. Commun.* **10**, 1–10. (doi:10.1038/s41467-018-07882-8)
32. Prum RO. 2014 Interspecific social dominance mimicry in birds. *Zool. J. Linn. Soc.* **172**, 910–941. (doi:10.1111/zoj.12192)
33. Rainey MM, Grether GF. 2007 Competitive mimicry: synthesis of a neglected class of mimetic relationships. *Ecology* **88**, 2440–2448. (doi:10.1890/06-1717.1)
34. Dakin R, Segre PS, Straw AD, Altshuler DL. 2018 Morphology, muscle capacity, skill, and maneuvering ability in hummingbirds. *Science* **359**, 653–657. (doi:10.1126/science.aao7104)
35. Segre PS, Dakin R, Zordan VB, Dickinson MH, Straw AD, Altshuler DL. 2015 Burst muscle performance predicts the speed, acceleration, and turning performance of Anna's hummingbirds. *eLife* **4**, 11159. (doi:10.7554/eLife.11159)
36. Chai P, Millard D. 1997 Flight and size constraints: hovering performance of large hummingbirds under maximal loading. *J. Exp. Biol.* **200**, 2757–2763. (doi:10.1242/jeb.200.21.2757)
37. Altshuler DL. 2006 Flight performance and competitive displacement of hummingbirds across elevational gradients. *Am. Nat.* **167**, 216–229. (doi:10.1086/498622)
38. Sholtis KM, Shelton RM, Hedrick TL. 2015 Field flight dynamics of hummingbirds during territory encroachment and defense. *PLoS ONE* **10**, e0125659. (doi:10.1371/journal.pone.0125659)
39. Feinsinger P, Chaplin SB. 1975 On the relationship between wing disc loading and foraging strategy in hummingbirds. *Am. Nat.* **109**, 217. (doi:10.1086/282988)
40. Bribiesca R, Herrera-Alsina L, Ruiz-Sanchez E, Sánchez-González LA, Schondube JE. 2019 Body mass as a supertrait linked to abundance and behavioral dominance in hummingbirds: a phylogenetic approach. *Ecol. Evol.* **9**, 1623–1637. (doi:10.1002/ece3.4785)
41. López-Segoviano G, Bribiesca R, Arizmendi MDC. 2018 The role of size and dominance in the feeding behaviour of coexisting hummingbirds. *Ibis* **160**, 283–292. (doi:10.1111/ibi.12543)
42. Martin PR, Ghalambor CK. 2014 When David beats goliath: the advantage of large size in interspecific aggressive contests declines over evolutionary time. *PLoS ONE* **9**, e108741. (doi:10.1371/journal.pone.0108741)
43. Stiles FG, Altshuler DL. 2004 Conflicting terminology for wing measurements in ornithology and aerodynamics. *The Auk* **121**, 973–976. (doi:10.1093/auk/121.3.973)
44. Schneider CA, Rasband WS, Eliceiri KW. 2012 NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671–675. (doi:10.1038/nmeth.2089)
45. Stiles FG, Altshuler DL, Dudley R. 2005 Wing morphology and flight behavior of some North American hummingbird species. *The Auk* **122**, 872–886. (doi:10.1093/auk/122.3.872)
46. Johnson EI, Wolfe JD. 2018 *Molt in neotropical birds*. Boca Raton, FL: CRC Press.
47. Ortiz-Crespo FI. 1972 A new method to separate immature and adult hummingbirds. *The Auk* **89**, 851–857. (doi:10.2307/4084114)
48. Yanega GM, Pyle P, Geupel GR. 1997 The timing and reliability of bill corrugations for ageing hummingbirds. *West. Birds* **28**, 13–18.
49. Ellington CP. 1984 The aerodynamics of hovering insect flight. II. Morphological parameters. *Phil. Trans. R. Soc. Lond. B* **305**, 17–40. (doi:10.1098/rstb.1984.0050)
50. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org.
51. Venables WN, Ripley BD. 2002 *Modern applied statistics with S*. New York, NY: Springer. See http://www.stats.ox.ac.uk/pub/MASS4.
52. Bridge ES, Bonter DN. 2011 A low-cost radio frequency identification device for ornithological

research. *J. Field Ornithol.* **82**, 52–59. (doi:10.1111/j.1557-9263.2010.00307.x)

53. Sargent AJ, Groom DJE, Rico-Guevara A. 2021 Locomotion and energetics of divergent foraging strategies in hummingbirds: a review. *Integr. Comp. Biol.* **61**, 736–748. (doi:10.1093/icb/icab124)
54. Maney DL, Erwin KL, Goode CT. 2005 Neuroendocrine correlates of behavioral polymorphism in white-throated sparrows. *Horm. Behav.* **48**, 196–206. (doi:10.1016/j.yhbeh.2005.03.004)
55. Shuster SM, Wade MJ. 1991 Equal mating success among male reproductive strategies in a marine isopod. *Nature* **350**, 608–610. (doi:10.1038/350608a0)
56. Wolf LL. 1969 Female territoriality in a tropical hummingbird. *The Auk* **86**, 490–504. (doi:10.2307/4083410)
57. Wolf LL. 1975 Female territoriality in the purple-throated carib. *The Auk* **92**, 511–522. (doi:10.2307/4084604)
58. Skutch AF. 1973 *The life of the hummingbird*. New York, NY: Vineyard Books.
59. Kodric-Brown A, Brown JH. 1978 Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. *Ecology* **59**, 285–296. (doi:10.1080/03610738108259811)
60. Emlen ST, Oring LW. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223. (doi:10.1126/science.327542)
61. Svensson EI, Willink B, Duryea MC, Lancaster LT. 2020 Temperature drives pre-reproductive selection and shapes the biogeography of a female polymorphism. *Ecol. Lett.* **23**, 149–159. (doi:10.1111/ele.13417)
62. Willink B, Svensson EI. 2017 Intra- and intersexual differences in parasite resistance and female fitness tolerance in a polymorphic insect. *Proc. R. Soc. B* **284**, 20162407. (doi:10.1098/rspb.2016.2407)
63. Cooper IA. 2010 Ecology of sexual dimorphism and clinal variation of coloration in a damselfly. *Am. Naturalist* **176**, 556–572. (doi:10.1086/656491)
64. Rico-Guevara A, Hurme K, Elting R, Russell A. 2021 Bene'fit' assessment in pollination coevolution: mechanistic perspectives on hummingbird bill–flower matching. *Integr. Comp. Biol.* **61**, 681–695. (doi:10.1093/icb/icab111)
65. Fincke OM. 2004 Polymorphic signals of harassed female odonates and the males that learn them support a novel frequency-dependent model. *Anim. Behav.* **67**, 833–845. (doi:10.1016/j.anbehav.2003.04.017)
66. Robertson HM. 1985 Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.* **33**, 805–809. (doi:10.1016/S0003-3472(85)80013-0)
67. Prum RO, Samuelson L. 2012 The hairy-downy game: a model of interspecific social dominance mimicry. *J. Theor. Biol.* **313**, 42–60. (doi:10.1016/j.jtbi.2012.07.019)
68. Leighton GM, Lees AC, Miller ET. 2018 The hairy–downy game revisited: an empirical test of the interspecific social dominance mimicry hypothesis. *Anim. Behav.* **137**, 141–148. (doi:10.1016/j.anbehav.2018.01.012)
69. Prum RO, Samuelson L. 2016 Mimicry cycles, traps, and chains: the coevolution of toucan and kiskadee mimicry. *Am. Nat.* **187**, 753–764. (doi:10.1086/686093)
70. Jønsson KA, Delhey K, Sangster G, Ericson PGP, Irestedt M. 2016 The evolution of mimicry of friarbirds by orioles (Aves: Passeriformes) in Australo-Pacific archipelagos. *Proc. R. Soc. B* **283**, 20160409. (doi:10.1098/rspb.2016.0409)
71. Diamond JM. 1982 Mimicry of friarbirds by orioles. *The Auk* **99**, 187–196. (doi:10.1093/auk/99.2.187)
72. West-Eberhard MJ. 2003 *Developmental plasticity and evolution*, pp. 260–295. Oxford, UK: Oxford University Press.
73. Rubenstein DR, Lovette IJ. 2009 Reproductive skew and selection on female ornamentation in social species. *Nature* **462**, 786–789. (doi:10.1038/nature08614)
74. Trail PW. 1990 Why should lek breeders be monomorphic? *Evolution* **44**, 1837–1852. (doi:10.1111/J.1558-5646.1990.TB05254.X)
75. Falk JJ, Rubenstein DR, Rico-Guevara A, Webster MS. 2022 Intersexual social dominance mimicry drives female hummingbird polymorphism. Zenodo. (https://doi.org/10.5281/zenodo.6975352)
76. Falk JJ, Rubenstein DR, Rico-Guevara A, Webster MS. 2022 Intersexual social dominance mimicry drives female hummingbird polymorphism. Figshare. (doi:10.6084/m9.figshare.c.6166889)