†Present address: Department of Biology,
University of Rochester, Rochester, NY 14627,
USA.

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Dancing drives evolution of sexual size dimorphism in manakins

Elsie H. Shogren[1,†], Marina Anciães[2], Julia Barske[3], César Cestari[4],
Emily H. DuVal[5], Milene G. Gaiotti[6], Erik I. Johnson[7,8], Rebecca T. Kimball[9],
Miguel A. Marini[6], T. Brandt Ryder[10], Micah N. Scholer[11], Judit Ungvári[12],
Stewart A. White[13] and W. Alice Boyle[1]

[1]Division of Biology, Kansas State University, Manhattan, KS 66506, USA
[2]Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas CEP
69.067-375, Brazil
[3]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA
[4]Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG, CEP 38405-320, Brazil
[5]Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA
[6]Departamento de Zoologia, Universidade de Brasília, Brasília 701910-900, Brazil
[7]National Audubon Society, Baton Rouge, LA 70808, USA
[8]Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia, Manaus,
Amazonas CPE 69.067-375, Brazil
[9]Department of Biology, University of Florida, Gainesville, FL 32611, USA
[10]Bird Conservancy of the Rockies, Brighton, CO 80603, USA
[11]Biodiversity Research Centre and Department of Zoology, University of British Columbia, Vancouver,
British Columbia, Canada V6T 1Z4
[12]George Mason University, Fairfax, VA 22030, USA
[13]School of Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK

iD EHS, 0000-0002-8619-3549; MA, 0000-0003-2796-3395; CC, 0000-0002-6237-7618;
EHD, 0000-0002-8227-7200; MGG, 0000-0003-4162-471X; EIJ, 0000-0002-8893-6289;
RTK, 0000-0001-5449-5481; MAM, 0000-0002-7300-7321; TBR, 0000-0002-5517-6607;
MNS, 0000-0001-5495-3649; JU, 0000-0002-5180-8048; SAW, 0000-0003-3777-3181;
WAB, 0000-0002-2880-142X

Body size mediates life history, physiology and inter- and intra-specific inter-
actions. Within species, sexes frequently differ in size, reflecting divergent
selective pressures and/or constraints. Both sexual selection and differences
in environmentally mediated reproductive constraints can drive sexual size
dimorphism, but empirically testing causes of dimorphism is challenging.
Manakins (Pipridae), a family of Neotropical birds comprising approximately
50 species, exhibit a broad range of size dimorphism from male- to female-
biased and are distributed across gradients of precipitation and elevation.
Males perform courtship displays ranging from simple hops to complex aero-
batic manoeuvres. We tested associations between sexual size dimorphism
and (a) agility and (b) environment, analysing morphological, behavioural
and environmental data for 22 manakin species in a phylogenetic framework.
Sexual dimorphism in mass was most strongly related to agility, with males
being lighter than females in species performing more aerial display beha-
viours. However, wing and tarsus length dimorphism were more strongly
associated with environmental variables, suggesting that different sources of
selection act on different aspects of body size. These results highlight the
strength of sexual selection in shaping morphology—even atypical patterns
of dimorphism—while demonstrating the importance of constraints and eco-
logical consequences of body size evolution.

1. Introduction

Body size is fundamental to an animal's life history, physiology and ecology, influ-
encing everything from the speed of cellular reactions to the environments in
which it can live [1–3]. Shifts in body size within lineages are often associated
with differences in habitat, foraging strategy and distribution [4,5]. Nevertheless,

size can vary dramatically even within species. Niche-partitioning within a species may lead to sexual size dimorphism just as it shapes interspecific differences; males and females differing in size and adopting divergent foraging strategies can experience reduced competition for food [6,7]. Alternatively, fecundity selection can lead to sexual size dimorphism when larger females produce more or higher quality offspring, or better tolerate environmental conditions influencing sex-linked behaviours [8,9]. Despite these strong sources of natural selection, sexual selection can also drive sexual size dimorphism [10]. In birds and mammals, sexual selection is typically associated with males being larger than females [11,12]. Selection for male-biased size dimorphism may be due to direct competition for access to mates and advantages conferred by being larger and heavier [10,11]. Alternatively, females may choose males based on size-related traits [13,14]. When sexual selection is strong, males are typically larger than females; the reverse is rare but does occur in species under selection for speed or agility, where larger males experience elevated energetic constraints [12,15,16].

The morphological, behavioural and reproductive diversity of birds is ideal for testing whether environment or mating success is more strongly associated with interspecific variation in sexual size dimorphism. When mating systems and foraging strategies are similar among closely related taxa, the direction of sexual size dimorphism is usually also consistent (either male-biased or female-biased ([16], but see [17])). Neotropical manakins (family Pipridae) are an intriguing exception, comprising species in which males are the larger sex, and species in which females are larger. While testing evolutionary drivers of sexual size dimorphism does not require both male- and female-biased size dimorphism, manakins provide an opportunity to do so.

Neotropical manakins are a family of approximately 50 species of small-bodied (9–25 g) suboscine passerines. Manakins are mainly frugivorous and live exclusively in forests [18,19]. Many inhabit hot lowland forests, but some species range to greater than 2000 m above sea level. They also live in habitats varying dramatically in rainfall, from dry savannah woodlands to pluvial montane forest. Manakin research has predominantly focused on the species-specific mating displays performed by males [20–22]. Most species have lek mating systems [23] in which males perform at clustered display sites [19,20], providing no parental care, and deriving all reproductive success from their ability to attract and copulate with females [24,25]. Reproductive skew among males is driven by female choice; sexual selection has resulted in the evolution of striking behaviours, cooperative male alliances and maintenance of display sites [26–28]. The displays themselves are diverse, ranging from exaggerated postures accentuating certain plumage patches to high-speed aerial dives and flips too rapid for humans to see [20,29]. Some displays involve mechanical 'sonations' produced through rapid movements while perched or mid-flight [30]. In some species, socially dominant males are accompanied by subordinates in coordinated displays. In such cases, males generally adhere to strict social hierarchies and only dominant males have opportunities to mate [27,31,32]. Previous studies of sexual size dimorphism in the family demonstrated that manakins follow Rensch's rule of allometry, with male manakins tending to be smaller than females in small species and larger than females in large species [33,34]. Furthermore, wing length and body

Table 1. Hypotheses and predictions for sexual size dimorphism in response to predictors. Hypotheses are detailed in the text. Predictions for direction of sexual size dimorphism are denoted with the abbreviation M or F (for male or female respectively) and greater or less than symbols to show relative size of each sex (i.e. M < F indicates prediction that males will be smaller than females). Note that predictions are not made for all axes of sexual size dimorphism and all hypotheses (denoted with '—' in the table).

hypotheses	direction of predictor	axes of sexual size dimorphism		
		mass	wing	tarsus
sexual selection: display	↑ agility	M < F	M < F	M > F
	↓ agility	M > F	M > F	M ≈ F
abiotic selection: temperature	hotter	M > F	—	—
	colder	M > F	—	—
abiotic selection: rainfall	rainier	M > F	M > F	—
	drier	M > F	M > F	—

mass are not correlated in males, although they are in females, suggesting that the direction of selection on size may vary by sex and/or trait [33]. Thus, the causes of variation in manakin sexual size dimorphism remain unknown, especially because previous analyses did not account for shared evolutionary history.

The importance of display for male fitness suggests that sexual selection may drive patterns of size dimorphism. Although sexual selection typically results in larger males than females, some behavioural traits can result in advantages accruing to smaller males [10]. For example, smaller birds can be more manoeuvrable owing to their higher power-to-mass ratio, which may be advantageous for acrobatic display performance [35]. Consistent with this, female golden-collared manakins (*Manacus vitellinus*) preferentially mate with males that perform certain display behaviours more rapidly [36]. Thus, if sexual selection for agility drives size dimorphism in manakins, we predicted that males would be lighter than females in species with more aerial, acrobatic displays (table 1).

As small endotherms, manakins are also subject to abiotic selection driven by precipitation and temperature. In the tropics, temperature varies little over the year locally, but declines with increasing elevation [37,38]. Environmental conditions may impose sex-specific constraints due to differences in reproductive behaviours; males perform energetically demanding displays, whereas female reproductive behaviour is far more sedentary (e.g. incubation and brooding). Cold tolerance is positively associated with body size because surface area to mass ratios increase with decreasing body size; the smallest birds must expend the most energy per unit mass to maintain homeothermy [39]. Thus, in colder environments, we predicted that females would be larger than males owing to stronger selection for thermogenic efficiency during incubation and brooding (table 1) [40]. Displaying males, by contrast, may still benefit from smaller sizes because conductance is also negatively associated with body size [41,42], and smaller males should be better able to dissipate excess heat generated during displays, particularly under wet conditions [43]. However, in hot environments,

abiotic selection on body size differences may shift [44]. Because internal temperatures are size-dependent [45], body temperatures of small-bodied endotherms are more likely to be closer to upper lethal limits [46]. If displaying elevates body temperatures, we hypothesized that larger males may be able to display under hotter conditions than smaller males because they have a greater capacity for evaporative water loss (table 1) [47,48]. Females, however, should be less constrained by hot temperature than males in low-elevation environments as they do not perform energetically costly displays.

The seasonality and quantity of rainfall are increasingly recognized as potent selective forces in the tropics, influencing energetics, survival and reproductive behaviour, particularly in small birds [49–51]. In at least one manakin (*Corapipo altera*), birds fast during heavy rains [52], and fasting endurance depends upon the size of energy stores relative to demand. Because metabolic rate does not increase with body size as quickly as does capacity for energy storage, fasting endurance increases with body size [39,53]. The frugivorous diet of manakins necessitates frequent foraging, making energetic and fasting constraints particularly acute [54]. Male manakins may be subject to more restrictive foraging constraints than females because they spend much of their time displaying and tending display sites [55,56], and have far smaller home ranges than females [57]. Thus, we predicted that fasting endurance could affect size dimorphism via selection for larger males in rainy environments (table 1).

Body mass provides a direct and relevant measure of avian sexual size dimorphism because mass critically influences wing loading and therefore, the cost of aerial manoeuvrability. Furthermore, 70% of birds' body mass can consist of muscle responsible for thermogenesis [58–60], and body mass correlates with fat storage capacity [61,62]. However, mass fluctuates daily, seasonally and over lifetimes [63,64]. Consequently, we also analysed dimorphism in wing and tarsus length as they are less plastic. Such structural measures may be subject to different sources of natural and sexual selection compared with body mass, however. Because wing length affects efficiency for different types of flight behaviour, we predicted that males of species performing more aerobatic displays would have shorter wings than females, allowing higher wing-beat frequencies and lower wing inertia [65]. The abiotic environment may also influence wing length if forest structure selects for manoeuvrability at slow flight speeds in dense vegetation. Indeed, previous research in this family documented that species displaying in more closed habitats had broader, rounder wings than species displaying in more open environments [66]. Because fine-scale metrics of vegetation structure at spatial scales relevant for this study were unavailable, we used climatic data associated with locality information to test for association between wing-length dimorphism and the environment. Tarsus length is a standard skeletal measure of size, and in manakins may be under sexual selection owing to leaping display elements in some species [20]. Although simple predictions regarding tarsus length and display ability depend upon trade-offs with other morphological traits [67], male tarsi may be longer relative to female in species performing more aerobatic displays, given that longer legs have the potential to increase the force generated during take-off [68]. Thus, to understand how sexual selection for aerial display and abiotic factors influence sexual size dimorphism, we collected body mass, wing and tarsus length data for just under half the species of Pipridae, and related morphology to environment and indices of display agility in phylogenetically explicit analyses.

2. Methods

We conducted all analyses in R, v. 4.0.5 [69].

(a) Morphology

We collected measurements of mass (grams), and tarsus (millimetres) and wing length (millimetres) from individuals in definitive plumage and/or sexed by brood patch or molecular methods for as many manakin species as possible (electronic supplementary material, table S1) [70]. Most individuals were measured during the breeding season when males display. We excluded data from the few females suspected to be carrying an egg in their oviduct because their weight far exceeded normal mass. We calculated the mean value of each metric for each sex, regressing raw and natural-log (ln)-transformed values of wing and tarsus against species mean mass to assess scaling relationships (electronic supplementary material, figures S1 and S2). We then calculated trait- and species-specific indices of sexual size dimorphism that scale symmetrically around zero [71,72]. When males were larger, this index was calculated as (larger sex ÷ smaller sex) − 1. When females were larger, the index was calculated as −1 × ((larger sex ÷ smaller sex) − 1). Thus, species with male-biased dimorphism have positive index values whereas species with female-biased dimorphism have negative index values.

First, we assessed the degree and interspecific variability of sexual size dimorphism among the three morphological metrics. To assess the effect of intra-specific variation on sexual size dimorphism metrics we used the package *boot* [73,74] to calculate 1000 bootstrapped replicates of mean male and female morphological values for each species. Using those, we calculated 1000 sexual size dimorphism indices and 95% confidence intervals for each species (electronic supplementary material, figures S4 and S5). Narrow confidence intervals indicated little variation within species in the values upon which dimorphism indices were based, so we proceeded with sexual size dimorphism indices calculated from means.

(b) Agility

We developed a metric of display agility for each species using comprehensive, peer-reviewed descriptions of display behaviour (electronic supplementary material, table S2). We followed a procedure similar to [29] for scoring display, calculating agility scores by allocating a point for each unique aerial behavioural element included in a species' display repertoire. We considered leaps, stylized flight patterns and high-speed dives to constitute aerial elements. Behaviours during which males remained perched—e.g. bowing or fluttering their wings—were scored as zero and did not contribute to the agility score. This method assumes each included aerial behaviour requires equivalent agility and is necessarily a coarse estimate; however, it provides a first approximation suitable for testing our hypotheses. Furthermore, when males performed aerial display elements in coordination with other males, or when they produced sonations while performing aerial movements, we assumed these required additional agility [20,29,75]. Therefore, we added an additional point for each of these coordinated or acoustic aerial behaviours before summing points to calculate each species' agility score. Because courtship displays can vary depending on context (e.g. only males present, female present, successful copulation), and thus require substantial researcher effort to fully characterize,
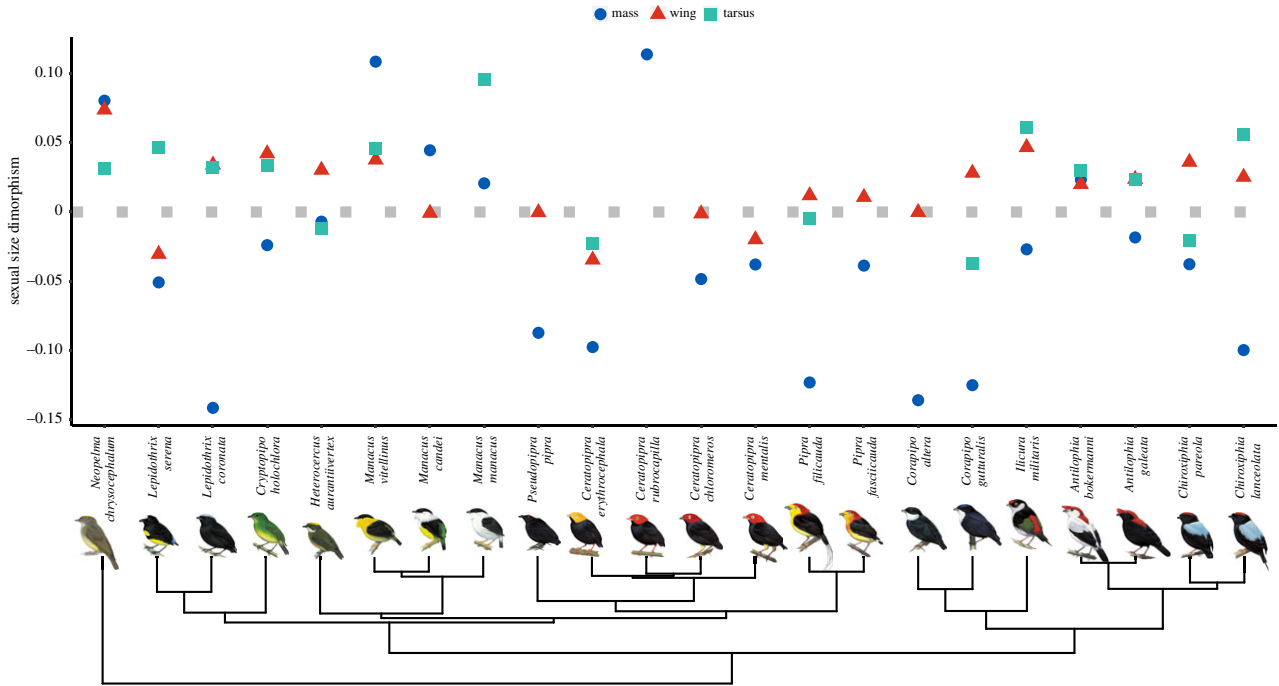
Figure 1. Sexual size dimorphism index for mass, and wing and tarsus across 22 species analysed. Above the dashed 0 line males are larger than females, below the line males are smaller than females. Male manakin illustrations reproduced with the permission of Lynx Edicions. (Online version in colour.)

we restricted our analyses to species with extensive and well-documented observation. Given that display behaviour can change ontogenetically and with social context [76], we did not investigate intra-individual variation in behaviour. Furthermore, while one or two species have been the subject of in-depth behavioural studies in more than one location, most species-level data come from single, well-studied populations. Thus, we did not examine intra-specific variation in behaviour.

(c) Phylogeny
To account for evolutionary relatedness [77], we used a phylogeny [78] constructed using maximum likelihood based on 2237 ultra-conserved element loci [79] which included 51 of 53 manakin species. We made branch lengths of the entire phylogeny ultrametric using non-parametric rate smoothing [80] implemented in TreeEdit v. 1.0 [81], and extracted from that tree the taxa for which we had adequate behavioural data (figure 1).

(d) Environmental variables
To characterize the climatic niche of each species, we used locality data from natural history specimen records [18]. We imported localities into ArcGIS [82] and obtained environmental values (averaged from 1970 to 2000) for each point from WorldClim bioclimatic surfaces [83]. We extracted 13 variables hypothesized to influence thermoregulation and/or fasting endurance: annual precipitation, precipitation seasonality (coefficient of variation of monthly totals), precipitation during the wettest, driest, warmest and coldest months, annual mean temperature, diurnal temperature range, annual temperature range, maximum and minimum temperatures, and elevation. We averaged locality-specific values for each variable by species and included absolute maximum elevation to account for potentially the strongest constraints on thermoregulation and fasting endurance. The conditions a bird experiences at any time in the year can constitute a source of selection and the majority of manakin research occurs at breeding locations; therefore, we did not restrict our sample of morphological and environmental variables spatially or temporally. Because we lack a clear mechanistic understanding of how abiotic variables may influence fitness and therefore selection on

morphology, we included environmental characteristics heuristically, reducing the dimensionality of the environmental variables for each species. This allowed us to effectively test relationships with response variables and to characterize environments according to the axes of climatic variation best distinguishing them. To do this, we used the phylogeny to perform a phylogenetic principal components analysis in *phytools* [84], deriving two principal components (electronic supplementary material, table S3) used in subsequent analyses.

(e) Rensch's rule
We determined if manakin dimorphism follows Rensch's rule, calculating phylogenetic independent contrasts from ln-transformed mean values of male and female mass, wing length and tarsus length using the *APE* package [34,85,86]. We removed outliers, defined as points beyond $1.5 \times$ the interquartile range, and then performed major axis regression of female contrasts against male contrasts, forcing the origin through zero using the *smatr* package [87,88]. The positive relationship between body size and size dimorphism when males are the larger sex and negative relationship between those variables when males are smaller exemplifies Rensch's rule and predicts that evolutionary divergence in male size is greater than in female size for sister taxa; thus we used a paired *t*-test of male and female phylogenetically independent contrasts following [16]. As an additional test of the association between body size and magnitude of dimorphism in wing and tarsus length, we regressed indices of sexual size dimorphism for tarsus and wing length against species' average mass and assessed the Pearson's product–moment correlation.

(f) PGLS model construction and selection
To test core predictions regarding agility or environmental variation driving patterns of sexual size dimorphism, we performed phylogenetic generalized least-squares (PGLS) regression using the *APE* package [86,89,90]. We constructed a candidate model set including single factors of agility score and two phylogenetic principal components of environmental variables. We also evaluated models including additive and interactive combinations of agility score and environmental principal components. We

evaluated model sets using five different response variables: dimorphism in mass, dimorphism in wing length, dimorphism in tarsus length, female mass and male mass. Our sample sizes did not allow us to effectively calculate a maximum-likelihood estimate of phylogenetic signal (Pagel's lambda, λ; [91,92]). To choose the most appropriate underlying evolutionary framework for analysing each response variable, we used a model selection approach, considering both Brownian motion (explicitly correcting for evolutionary distance between taxa) and Pagel's lambda set to 0 (i.e. no phylogenetic signal). Thus, for each combination of response and predictor variables, we constructed a model in which phylogenetic signal was maximized and a model with no phylogenetic signal. We then used Akaike's information criteria corrected for small sample sizes (AICc) in the package *MuMIn* to determine which evolutionary framework provided the best fit for the data [93]. Finally, we compared models with the same evolutionary framework and response variable to determine which predictors best fitted the data, considering ΔAICc values of less than 2 competitive, and assessing support for those models using Akaike weights [93]. To illustrate the relationship between mass sexual size dimorphism and agility score given phylogenetic relatedness, we also built a phylomorphospace plot in *phytools* [84].

3. Results

(a) Morphology and agility
We analysed morphological data for 3051 individuals representing 22 species in 12 different genera (electronic supplementary material, table S1). Our median sample size was 32 males and 31 females (male range: 2–615, female range: 2–334). We gathered mass data for all 22 species, wing measurements for 20 species and tarsus measurements for 15 species (electronic supplementary material, table S1). Agility scores ranged from 0 (in species not known to perform aerial display, e.g. *Cryptopipo holochlora*) to 14 (in *Chiroxiphia lanceolata*, a species in which males perform complex and coordinated multi-male aerial display manoeuvres; electronic supplementary material, table S2). Among species, correlations between mass and wing length were stronger for females than males (electronic supplementary material, figure S1), and the strength of the correlation between mass and tarsus length was low for both sexes (electronic supplementary material, figure S2). Indices of mass sexual size dimorphism ranged from –0.14 to +0.12. Wing dimorphism values ranged from –0.03 to +0.07 and tarsus dimorphism ranged from –0.04 to +0.10 (electronic supplementary material, figure S3). In 10 species, females were heavier than males, but had smaller wing or tarsus measurements, indicating that different metrics capture somewhat independent types of size variation (electronic supplementary material, table S1). Bootstrap calculations of dimorphism indices did not generate large 95% confidence intervals for mass (electronic supplementary material, figure S4), wing length or tarsus length (electronic supplementary material, figure S5).

(b) Rensch's rule
The slope of the relationship between phylogenetic independent contrasts of ln-transformed male and female values was less than 1 for all morphological traits, suggesting that as body size increases, male-biased size dimorphism is slightly more pronounced, as predicted by Rensch's rule. However, the 95% confidence interval from major axis regression overlapped 1 for all traits (electronic supplementary material, figure S6), and paired t-test of male and female contrasts revealed no differences (mass: $\beta = 0.89$, 95% CI: 0.73–1.08, $p = 0.63$; wing: $\beta = 0.71$, 95% CI: 0.19–1.78, $p = 0.88$; tarsus: $\beta = 0.88$, 95% CI: 0.73–1.06, $p = 0.43$). Species' average mass was unrelated to dimorphism indices of wing and tarsus (electronic supplementary material, figure S7).

(c) Environmental variables
The first two principal components collectively explained 72% of the variance in 13 environmental variables (electronic supplementary material, table S3). Variables loading positively on the first component (PC1; 44% of variance) described temperature range (diurnal and annual variability) and elevation, whereas precipitation in the coldest month and minimum temperature loaded negatively. Seasonality of precipitation loaded positively on the second component (PC2; 28% of variance), whereas the remaining precipitation variables loaded negatively.

(d) PGLS model results
The strength of phylogenetic signal (i.e. whether setting Pagel's lambda equal to 0 or to 1 better fitted the data) varied by response variable. Sexual dimorphism in mass and tarsus length best fitted models with no phylogenetic signal. Similarly, a phylomorphospace plot of mass sexual size dimorphism and agility score showed little evidence of phylogenetic constraint (electronic supplementary material, figure S8). Conversely, analysis of male and female mass as separate response variables showed stronger phylogenetic signals; the data fitted models with Pagel's lambda set to 1 best.

Sexual size dimorphism in mass was best explained by the single main effect of agility score, which accounted for 56% of the model weight (table 2). Consistent with the sexual selection hypothesis, males were generally smaller than females in species having more aerial display behaviours ($\beta = -0.011$, 95% CI: –0.019, –0.003; figure 2).

The difference between sexes in wing length was negatively associated with PC2 (table 2); males had longer wings than females in less seasonal and wetter environments, but shorter wings in drier and more seasonal environments ($\beta = -0.006$, 95% CI: –0.010, –0.001; electronic supplementary material, figure S9). All other wing size dimorphism models were greater than 2.5AICc below the top model (electronic supplementary material, figure S10).

Tarsus dimorphism was not correlated with the variables we tested, being equally well explained by each of the single-effect models (agility score, PC1 and PC2; table 2, electronic supplementary material, figure S10).

Finally, both males and females were heavier in colder, high elevation environments with broader diurnal and annual temperature ranges (table 2).

Results of all models are reported in electronic supplementary material, table S4.

4. Discussion
Manakins are subject to strong sexual selection, with female choice and male–male competition directly and dramatically influencing reproductive success of males. The variability of sexual size dimorphism across the clade is surprising; other
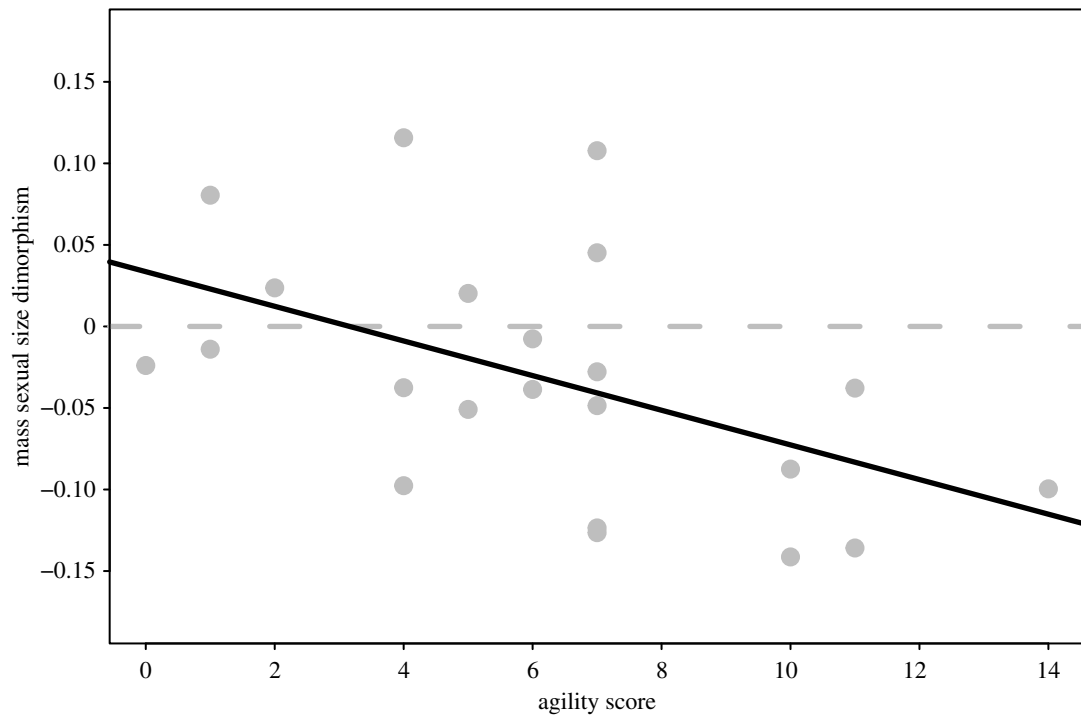
Figure 2. Relationship between species mass sexual size dimorphism and agility score. Points are not phylogenetically corrected, and the solid line is extracted from the top-performing phylogenetic generalized least-squares model, with lambda = 0. Points above the dashed line at 0 are for species in which males are heavier than females and points below the dashed line are for species in which males are lighter than females.

Table 2. Model results for each response variable, including all models within 2ΔAICc units of the top model. response, variable used as response in model selection. λ, Pagel's lambda for response variable. See electronic supplementary material, table S3 for complete set of models for both Brownian motion ($\lambda = 1$) and no phylogenetic signal ($\lambda = 0$). model, predictor variables of respective model. ΔAICc, number of AICc units from top model. weight, relative model weight. β, slope of relationship between response and predictor variable(s). 95% CI, 95% confidence interval of slope. s.s.d., sexual size dimorphism. Predictor variables are abbreviated as follows: agility, agility score; PC1, phylogenetic principal component 1 (environmental variation in temperature, elevation); PC2, phylogenetic principal component 2 (environmental variation in precipitation).

response	λ	model	ΔAICc	weight	β	95% CI
mass s.s.d.	0	agility	0.00	0.560	−0.0106	−0.0190, −0.0026
wing s.s.d.	1	PC2	0.00	0.545	−0.0055	−0.0116, −0.0009
tarsus s.s.d.	0	PC1	0.00	0.367	0.0044	−0.0029, 0.0116
		PC2	0.63	0.269	0.0044	−0.0052, 0.0140
		agility	1.50	0.174	−0.0004	−0.0055, 0.0046
female mass	1	PC1	0.00	0.440	0.4092	−0.0234, 0.8417
		PC1 + PC2	1.95	0.166	PC1: 0.4092	−0.0239, 0.8422
					PC2: 0.2684	−0.8088, 0.2720
male mass	1	PC1	0.00	0.425	0.3727	−0.1063, 0.8517

than in hummingbirds [16], such variation in patterns of dimorphism is rare. In most lekking or sexually selected avian species, males are larger than females and display often further accentuates male size (e.g. sage grouse, turkeys, peacocks; [23]). We tested whether sexual selection for agility or environmental constraints explained three metrics of size dimorphism in manakins. Agility score was the best predictor of sexual dimorphism in mass; males on average were lighter than females in species performing displays with more aerial elements, consistent with mate choice ultimately selecting for relatively smaller, more agile males. Dimorphism in wing length and tarsus length varied much less than did mass, and tarsus dimorphism was not strongly associated

with either agility or environment. However, dimorphism in wings varied with climate; in wetter environments, males had longer wings than females, consistent with multiple-sources of selection affecting different components of size dimorphism independently. Even though males of some larger species (e.g. *Chiroxiphia lanceolata*) were smaller than females, the overall pattern is consistent with Rensch's rule; in general, males were larger than females in large species, and smaller than females in small species.

Given the importance of courtship display in mate choice for this system, the association between sexual selection and sexual size dimorphism is unsurprising. However, the direction of selection on male body size and its relation to aerial

display behaviours is unusual. Previous work with hummingbirds, another group with aerial courtship display and both male- and female-biased size dimorphism, suggests that sexual selection via male–male competition drives selection for male-larger species, whereas resource constraints and absolute energetic costs of courtship may be responsible for relative size in species in which males are smaller than females [16]. Our analysis of metrics reflecting courtship behaviours reveals that size dimorphism can also be explained by the nature of the display. Observing relatively smaller males in species performing more aerobatic manoeuvres is consistent with higher power-to-mass ratios in smaller individuals increasing their acceleration and manoeuvrability [35].

The influence of environmental variation on dimorphism in wing length informs our understanding of abiotic sources of selection in tropical forests. Rainy environments were associated with male-biased dimorphism in wing length. This result is surprising, as we expected the opposite: that males with shorter wings would be better able to manoeuvre during displays in the presumably more dense vegetation of rainier forests [66]. Although environmental conditions do vary by species, all manakins inhabit tropical forest, and though vegetation density likely differs, foraging on fruit does not require the same agility needed by a sallying insectivore. Determining the underlying ecological selective pressures leading to this pattern of dimorphism is beyond the scope of our study, but several hypotheses exist. Longer male wing length may result from fasting endurance constraints; longer wings may allow more efficient flights to forage and replenish energy stores during or following rainfall. Alternatively, because wetter lowland forests have more clearly defined forest strata and complete canopies, the sub-canopy zone may be more open, requiring less manoeuvrability in flight. Finally, six or more species of manakin migrate altitudinally during the non-breeding season [94]; in at least one, males are more likely to migrate than females [52]. Perhaps, like Swainson's thrushes with more pointed wings and lower wing-loading, males expend less energy during such migrations [95]. Distinguishing among these explanations would benefit from the broader taxonomic sampling possible in a study not constrained by the availability of detailed behavioural observations.

The costs associated with reproduction differ for males and females in any species. It follows, therefore, that selection on body size would also operate in sometimes opposing ways depending on sex. However, males and females function in the same environment, so physiology and ecology may limit the scope of within-species variation. Our analysis sheds light on the potential for such evolutionary constraints. Models of dimorphism were largely free from phylogenetic constraints, whereas raw morphological characters (male and female mass) indicated a strong historical signal. Separate analyses of male and female mass also exhibited similar relationships with environmental variation; for both sexes, species were heavier in colder, high elevation environments, consistent with Bergmann's rule. Thus, our data suggest that body size generally has been subject to natural selection and an evolutionary history of thermoregulatory constraints, and that the relative sizes of males and females have evolved more flexibly and independently within lineages in response to sexual selection.

Despite sampling broadly across the Pipridae family, our inferences are subject to some caveats. First, given that the hypotheses relating to thermoregulation and fasting represent immediate physiological challenges, we assumed that the current environment reflects historical sources of abiotic selection. Second, owing to the availability of high-speed video for some but not all species, the accuracy of our agility score likely varies by species because some display manoeuvres occur too quickly for human eyes to detect. Additionally, our point-score system equates multiple different types of display behaviours, and scoring may not reflect the relative difficulty of all behaviours. Furthermore, it is likely that our agility score and its underlying assumption of additive selective pressures does not reflect the only way in which evolution of additional aerobatic behaviours could influence sexual size dimorphism. Finally, because the collection of data necessary to compile this behavioural dataset required enormous effort, our taxonomic sampling is not complete. Crucially, however, each of these limitations would tend to reduce rather than magnify the biological signal in results. Thus, although confidence intervals for some responses overlap zero, relationships between mass dimorphism and agility score suggest that our findings are robust, and our methods represent a standardized, reproducible approach that could be expanded upon as new behavioural data become available. We recognize, however, that alternative analytical approaches (e.g. mixed models or analysis of effect sizes) could also be used to answer similar questions in this and other datasets.

This study leveraged a large, field-collected morphological dataset and detailed behavioural information from a charismatic group of Neotropical birds to understand the evolution of sexual size dimorphism. We advance on the previous understanding of size dimorphism in manakins by incorporating a phylogenetic comparative framework, considering multiple axes of size dimorphism, and testing whether variation in environment constrains evolution of sexual sizedimorphism [96,97]. The alternative-hypothesis-testing framework demonstrates that although associations between courtship displays and sexual dimorphism in mass reveal the importance of sexual selection in the morphological evolution of this clade, other aspects of morphology have been more strongly shaped by environmental constraints. Typically, differences between sexes are attributed to male–male competition, female choice, or fecundity selection without considering alternative drivers of dimorphism. That patterns of dimorphism vary by trait even within species (i.e. some males are lighter than females, while being the same size or slightly larger in tarsus and wing length; figure 1) implies that sexual selection does not consistently drive sexual size dimorphism in the same direction. In manakins, mass seems to be under stronger sexual selection than other aspects of morphology; using structural size (e.g. tarsus length, wing length) or a composite metric of size to infer the strength of sexual selection would thus lead to erroneous conclusions. Degree of sexual size dimorphism should therefore only be used as a proxy for the strength of sexual selection when the selective forces shaping size dimorphism are understood.

Our findings provide insight into the selective forces shaping body size, a trait with far-reaching implications for a species' ecology and evolution. Even when sexual selection is the main driver of male reproductive success, body size evolution is still subject to environmental constraints that influence morphology in unexpected ways. Considering the multiple evolutionary forces at play within and across taxa is critical to understanding how organisms evolve under changing selective regimes and how body size itself may shape and be shaped by life-history strategies.

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