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Courtship dance similarity, but not complexity, may explain patterns of hybridization in manakins (Aves: Pipridae)

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ABSTRACT

Differences in behaviour can play an important role in the emergence of species and the maintenance of species boundaries. In birds, behavioural isolation mechanisms range from simple vocalizations to elaborate courtship displays. The breakdown of these isolation mechanisms could result in the production of viable hybrid offspring. In general, we might expect a negative relationship between the complexity of a behavioural isolation mechanism and the incidence of hybridization. I tested this prediction in manakins, a Neotropical bird family that shows a large variety of courtship displays. I compiled a database of reliable hybrid records and quantified the complexity of species-specific courtship displays. Binary logistic regressions indicated that courtship similarity was a better predictor of hybridization probability than courtship complexity. However, this pattern was strongly influenced by phylogenetic relatedness, in that closely related species exhibited similar courtship displays that were already being performed by their common ancestor. The main limitation of this study concerns the incomplete dataset. I could assess the courtship complexity for only 22 manakin species; consequently, not all hybrid combinations could be included in the analyses. Nonetheless, these findings provide important insights into the role of courtship displays in explaining patterns of hybridization.

Keywords: behaviour; female choice; hybridization; introgression; reproductive isolation; sexual selection; speciation

INTRODUCTION

Behavioural differences can come into play at various stages in the speciation process, from the origin of new species (Uy *et al.* 2018) to the strengthening of species boundaries through reinforcement (Calabrese and Pfennig 2019). In birds, behavioural isolation mechanisms come in a variety of forms, such as the production of specific songs (Slabbekoorn and Smith 2002, Mason *et al.* 2017), the building of elaborate structures (Zyskowski and Prum 1999, Uy and Borgia 2000), and the performance of complex courtship displays (Ligon *et al.* 2018). The strength of a specific behavioural isolation mechanism is often dependent on the divergence time between the interacting species. Incipient species might not yet have evolved complete reproductive isolation (Campagna *et al.* 2011, Uy *et al.* 2018), and older species might experience the breakdown of strong isolation mechanisms in particular circumstances, such as a scarcity of conspecifics (Hubbs 1955). Depending on the position of a species pair along the speciation continuum, ranging from a panmictic population to two distinct species, incomplete reproductive isolation can result in the production of viable hybrid offspring (Stankowski and Ravinet 2021, Ottenburghs 2023) or even the emergence of hybrid species (Barrera-Guzmán *et al.* 2018, Ottenburghs 2018).

In general, we would expect a negative relationship between the complexity of a behavioural isolation mechanism and the incidence of hybridization. For example, more elaborate courtship displays might lower the probability that a female mates with a heterospecific male, because she does not recognize the male as a potential mate (Paterson 1985, Alatalo *et al.* 1994). However, closely related species might show similar courtship behaviour that was already being performed by their common ancestor (Prum 1990, Nováková and Robovský 2021). Consequently, the phylogenetic context needs to be taken into account, and courtship similarity might be a better predictor of hybridization probability (Nali *et al.* 2023). Moreover, certain elements of a courtship display might be exchanged between distantly related species through social learning, potentially influencing female choice (Varela *et al.* 2018). Hence, the relationship between courtship display complexity and hybridization probability might be more complicated than a simple negative correlation.

Manakins (family Pipridae) are an excellent study system in which to explore the interplay between courtship behaviour

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and hybridization patterns. These Neotropical birds show a large variety of courtship displays that are usually performed in a lek (Prum 1990, Fuxjager and Schlinger 2015). The displays range from 'exaggerated postures accentuating certain plumage patches to high-speed aerial dives and flips too rapid for humans to see' (Shogren *et al.* 2022). In addition, several manakin hybrids have been described, both within and between genera (Parkes 1961, Graves 1993, Marini and Hackett 2002). In this study, I combine information on courtship displays and reliable hybrid records to investigate the interplay between these two phenomena. As explained above, I expect to find two main patterns: (i) a negative relationship between courtship display complexity and hybridization probability; and (ii) a positive relationship between courtship display similarity and hybridization probability. The results from this study can provide insights into the role of sexual selection in the hybridization dynamics of manakins.

MATERIALS AND METHODS

I compiled a database of reliable hybrid records based on three main sources: the Serge Dumont Bird Hybrids Database (http://www.bird-hybrids.com/), the *Handbook of Avian Hybrids of the World* (McCarthy 2006), and species descriptions on the Birds of the World website (Billerman *et al.* 2022). For each hybrid record, I tracked down the original reference to assess its reliability. Only hybrid records based on detailed descriptions of museum specimens or genetic analyses were considered as reliable.

For 22 species, I quantified the complexity of their courtship display using the agility scores of Shogren *et al.* (2022). In short, these researchers allocated one point for each unique aerial behavioural element in the display repertoire of a manakin. An additional point was added when males performed certain display elements in coordination with other males or when they produced sounds while performing the movements. Next, I counted the number of common display elements for each pairwise combination of manakin species, resulting in a similarity score for each species pair. All scores were based on peer-reviewed descriptions of display behaviour. Intraspecific variation in courtship behaviour was not taken into account. With only a few exceptions, most species-level data were obtained from single, well-studied populations (for details, see Shogren *et al.* 2022). Finally, it is important to keep in mind that these agility scores are only a proxy for courtship complexity, because Shogren *et al.* (2022) did not consider non-aerial courtship display elements in their calculations.

To assess the relationship between display complexity and hybridization probability, I used the R package *phylolm* (Tung Ho and Ané 2014) to perform a phylogenetic binary logistic regression with hybridization (1 = yes, 0 = no) as a function of the agility score per species. This approach performs a binary logistic regression while taking into account the phylogenetic relationships between the manakin species (as depicted in Fig. 1).

The relationship between display similarity and hybridization probability was assessed through a binary logistic regression with hybridization (1 = yes, 0 = no) as a function of the

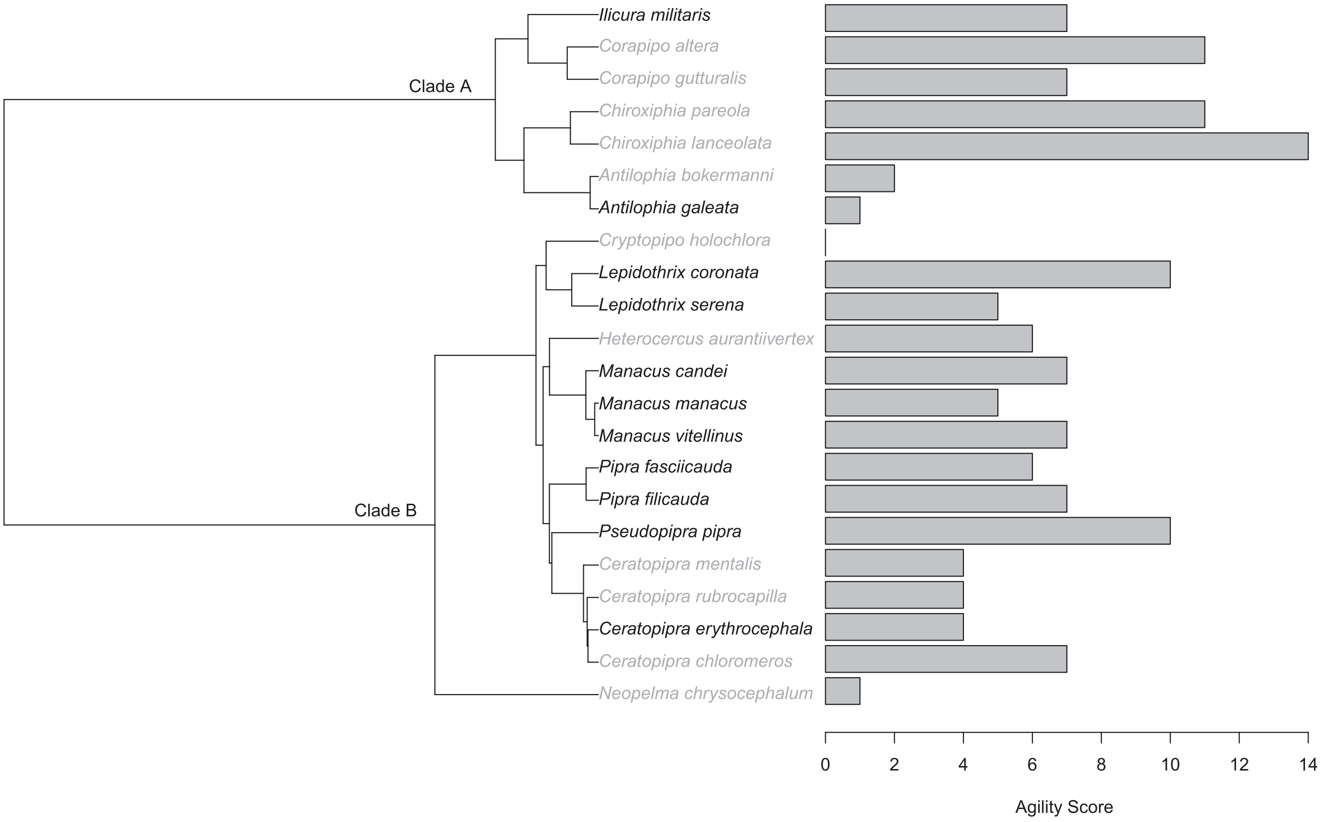

Figure 1. A phylogenetic overview of the dataset based on TIMETREE (Kumar *et al.* 2022), showing two main clades (A and B), with hybridizing species highlighted in black. The bar graph shows the agility score per species (based on the study by Shogren *et al.* 2022).

similarity score for each species combination. To reduce the number of species combinations in this analysis, I considered only comparisons between sympatric or parapatric species (based on visual inspection of distribution maps in *Handbook of Birds of the World*) that belong to the same clade (A or B; Fig. 1). The species in these two clades diverged ~25 Mya (Harvey *et al.* 2020) and are thus unlikely to hybridize. To take into account phylogenetic relatedness, the binary logistic regression was also run with pairwise divergence times as a fixed factor (either alone or in combination with display similarity). Divergence times were based on the phylogeny of Harvey *et al.* (2020). The resulting linear models were compared based on Akaike information criterion (AIC) values. If a model was more than two AIC units lower than another, I considered it significantly better than that model. All analyses were conducted in R v.4.2.1 (R Core Team 2021).

RESULTS

I found convincing evidence for 15 manakin hybrids, involving 16 species (out of 55 species, 29%; Table 1). Reliable records of hybrids were based on detailed morphological descriptions of museum samples (Parkes 1961, Haffer 1970, Graves 1993, Stotz 1993, Rezende *et al.* 2013) or genetic analyses revealing admixed individuals (Parsons *et al.* 1993, Marini and Hackett 2002, Sampaio *et al.* 2020, Barrera-Guzmán *et al.* 2022, Moncrieff *et al.* 2022). Most hybridization events occurred between species of the same genus, but six cases concerned intergeneric hybrids. I also came across a few unreliable records, highlighting the importance of assessing the original sources. McCarthy (2006) listed two hybrids involving *Manacus aurantiacus* (with *M. candei* and with *M. vitellinus*). However, these species combinations are unlikely because the distributions of *M. aurantiacus* and the other two species are allopatric (Brumfield and Carling 2010, Bennett *et al.* 2021). A putative intergeneric hybrid between *Manacus manacus* and *Pipra filicauda* was questioned by Parkes (1961), who noted that the collected specimen 'may well have been hybrid between *Teleonema* [now classified as *Pipra*] *filicauda* and a race of *Pipra aureola* or *P. fasciicauda*'. Given the unreliable evidence, these three cases were not included in the final dataset.

Agility scores were available for 11 hybridizing species and 11 non-hybridizing species (Fig. 1). This score varied between 1 and 10 (mean = 6.4) for the hybridizing species and between 0 and 14 (mean = 6) for the non-hybridizing species. There was no significant relationship between the agility scores and hybridization probability on a species level (phylogenetic binary logistic regression, z-value = −0.36, P = 0.72; Fig. 2A). Next, I calculated similarity scores (i.e. the number of common display elements) for 72 pairwise species combinations that are sympatric or parapatric and belong to the same clade (A and B in Fig. 1). The similarity scores varied between zero and five (mean = 1.17) for the hybridizing species pairs, and between zero and five (mean = 1.01) for the non-hybridizing species pairs. There was a positive relationship between similarity scores and hybridization probability (binary logistic regression, z-value = 2.69, P = 0.007; Fig. 2B). However, the effect of courtship similarity on hybridization probability was weakened when including divergence times in the model (binary logistic regression, z-value = 1.52, P = 0.13; see Table 2). Indeed, there was a negative relationship between divergence times and hybridization probability (binary logistic regression, z-value = −3.16, P = 0.002; Fig. 2C). The divergence times varied between 0.3 and 5.1 Mya (mean = 2.4) for hybridizing species pairs and between 1 and 15.1 Mya (mean = 6.4) for non-hybridizing species pairs (based on Harvey *et al.* 2020). Model comparisons based on AIC values showed that the inclusion of divergence times (alone or in combination with courtship similarity) resulted in the best model fit (Table 2). Hence, the probability of hybridization increases with courtship display similarity, but this pattern is strongly influenced by phylogenetic relatedness.

Table 1. An overview of records of hybrids in the family Pipridae with reliable evidence. Divergence times are based on the study by Harvey *et al.* (2020).

Species 1	Species 2	Divergence time (Mya)	References
Chiroxiphia caudata	*Antilophia galeata*		(Rezende *et al.* 2013)
Chiroxiphia caudata	*Ilicura militaris*		(Marini and Hackett 2002)
Lepidothrix coronata	*Lepidothrix serena*	2.5	(Haffer 1970, Stotz 1993)
Lepidothrix coronata	*Lepidothrix suavissima*	2.5	(Haffer 1970, Stotz 1993, Moncrieff *et al.* 2022)
Lepidothrix serena	*Lepidothrix suavissima*		(Haffer 1970, Stotz 1993)
Lepidothrix iris	*Lepidothrix nattereri*	0.5	(Barrera-Guzmán *et al.* 2018)
Heterocercus linteatus	*Pipra aureola*	5.1	(Parkes 1961)
Manacus candei	*Manacus vitellinus*	1.1	(Parsons *et al.* 1993, Brumfield and Carling 2010)
Manacus manacus	*Manacus vitellinus*	0.3	(Brumfield and Carling 2010)
Manacus manacus	*Pipra aureola*	5.1	(Parkes 1961)
Manacus manacus	*Ceratopipra erythrocephala*	5.1	(Parkes 1961)
Pipra aureola	*Pipra fasciicauda*	1	(Sampaio *et al.* 2020, Barrera-Guzmán *et al.* 2022)
Pipra aureola	*Pipra filicauda*	1.1	(Haffer 1970, Barrera-Guzmán *et al.* 2022)
Pipra fasciicauda	*Pipra filicauda*	1.1	(Barrera-Guzmán *et al.* 2022)
Pipra filicauda	*Pseudopipra pipra*	4.5	(Graves 1993)

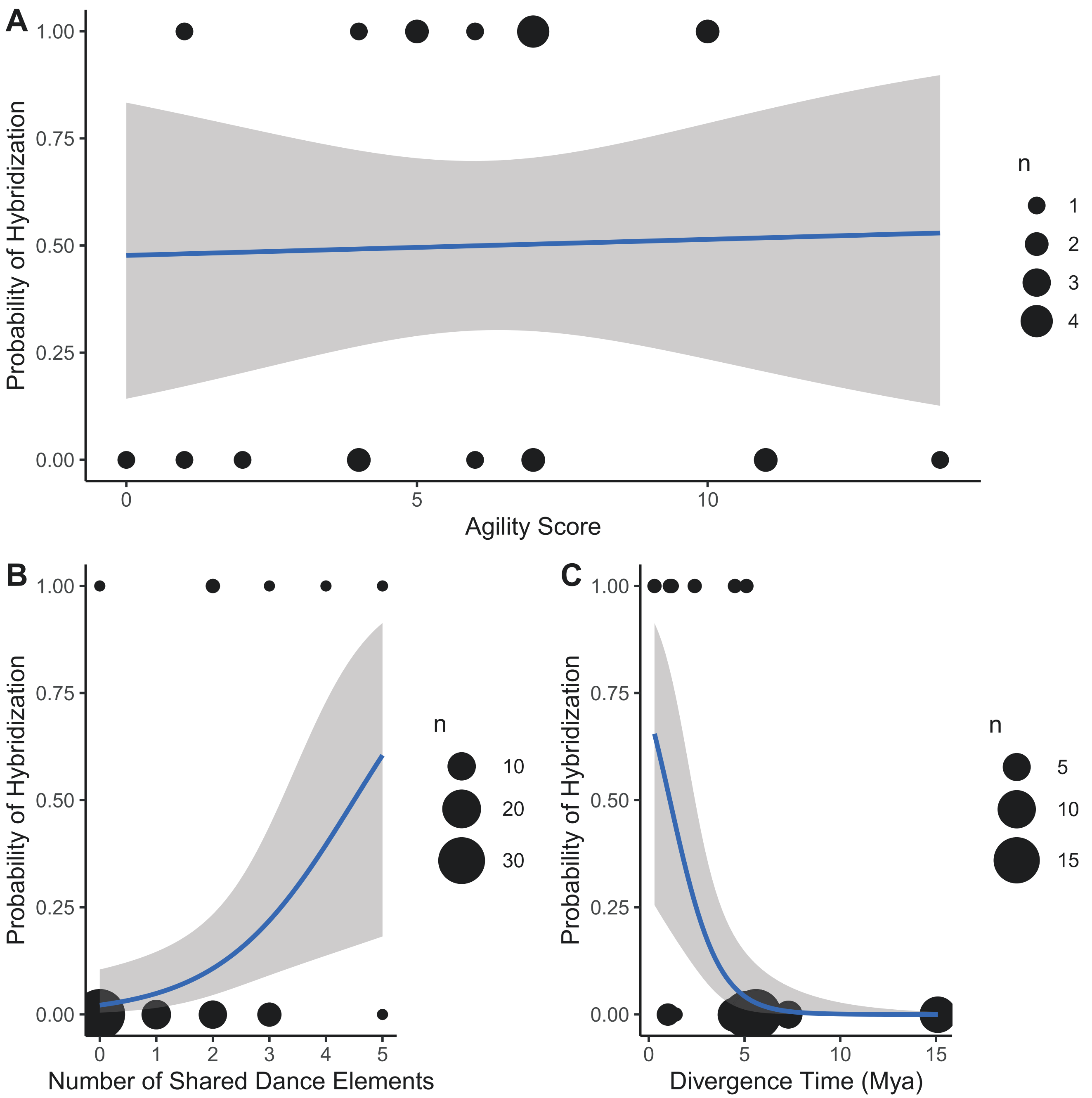

Figure 2. Relationships between the probability of hybridization in manakins and the agility score per species (A), the number of shared dance elements in a species pair (B), and divergence times between species pairs (C).

DISCUSSION

Complex courtship displays could function as a behavioural barrier between species (Uy *et al.* 2018). However, focusing solely on courtship complexity does not take into account the phylogenetic context (Prum 1990, Nováková and Robovský 2021). Closely related species might perform complex courtship displays that are sufficiently similar that females might select a partner from the 'wrong' species. Indeed, my analyses showed that, in manakins, courtship similarity is a better predictor of hybridization probability than courtship complexity. However, the similarity of courtship displays is strongly shaped by phylogenetic relatedness.

Most hybridizing species pairs in the dataset were recently diverged species with similar courtship displays. For example, the three *Manacus* species diverged between 0.3 and 1.1 Mya (Harvey *et al.* 2020) and showed agility scores within a narrow range, between five and seven points (Shogren *et al.* 2022). Likewise, *Pipra fasciicauda* and *P. filicauda*, which diverged ~1.1 Mya (Harvey *et al.* 2020), differed in only one point when comparing their agility scores (scores of six and seven, respectively, Shogren *et al.* 2022). The similarity of courtship displays was also reflected in the high number of shared dance elements in these genera (see Fig. 2B). Hence, similar courtship displays increase the probability of hybridization between closely related species.

Table 2. Akaike information criterion (AIC)-based comparison of binary logistic regression models of hybridization probability as a function of courtship similarity and/or divergence times. Models that differ by more than two AIC units were considered significantly different from each other. Significant factors within each model ($P < .05$) are highlighted in bold.

Model formula	Model coefficients			AIC value
	Factor	*z*-value	*P*-value	
Hybridization ~ similarity + divergence time[a]	Similarity	1.52	.130	31.722
	Divergence time	−2.44	**.015**	
Hybridization ~ divergence time	Divergence time	−3.16	**.002**	32.089
Hybridization ~ similarity	Similarity	2.69	**.007**	36.804

[a] The factors 'similarity' and 'divergence time' were not collinear in the model, as shown by variance inflation factors below five.

An interesting exception to this pattern of courtship display similarity between closely related species concerns hybridization between *Lepidothrix coronata* and *L. serena* (Haffer 1970, Stotz 1993). The agility scores between these two species were different (scores of 10 and 5, respectively, Shogren *et al.* 2022), which could be explained by their longer divergence time of 2.5 Mya (Harvey *et al.* 2020). Moreover, hybridization in the genus *Lepidothrix* seems to be a relatively rare phenomenon (but see Barrera-Guzmán *et al.* 2018). In his description of a hybrid specimen (which was then included in the genus *Pipra*, but now classified as *Lepidothrix*), Stotz (1993) noted that 'within the *P. serena* superspecies (including *P. coronata*, *P. serena*, *P. iris*, *P. coeruleocapilla*, *P. isidorei*, *P. nattereri*, and *P. vilasboasi*) the lack of hybridization among adjacent species is striking'. The rarity of hybridization in *Lepidothrix* contrasts with the situation in *Manacus* and *Pipra* where several hybrid zones have been described (Brumfield and Carling 2010, Barrera-Guzmán *et al.* 2022).

Rare hybridization events can be explained by Hubb's principle, which states that 'Great scarcity of one species coupled with the abundance of another often leads to hybridization: the individuals of the sparse species seem to have difficulty in finding their proper mates' (Hubbs 1955). For example, hybridization between *Ilicura militaris* and *Chiroxiphia caudata* occurred at the edge of their geographical ranges, where individuals might have difficulty finding a conspecific mate (Marini and Hackett 2002). Likewise, the hybridization event between the parapatric species *Lepidothrix coronata* and *L. serena* in Brazil could have been the outcome of an *L. serena* individual that wandered downslope and into the range of *L. coronata* (Stotz 1993, Moncrieff *et al.* 2022). With no conspecifics around, the wandering individual might have settled for a partner from another species. Under the assumption that female birds are more attracted to complex and novel courtship behaviours (DuVal *et al.* 2023), we could speculate that hybridization occurred between a female *L. serena* and a male *L. coronata* (i.e. the species with highest agility score). Unfortunately, Stotz (1993) could not deduce the sex of the parental species in his description of the hybrid specimen. Moreover, I could not find clear sex biases in other cases of hybridization between manakin species with known agility scores. This aspect of female choice could be studied through observational studies in hybrid zones (e.g. Barske *et al.* 2023).

The role of female choice in the hybridization dynamics between manakin species remains to be explored in more detail. My approach entailed assessing the overall complexity and similarity of courtship displays without assessing the impact of individual dance elements. Female choice might be focused on particular dance elements in the courtship displays (Barske *et al.* 2011). In addition, I did not take other traits into account, such as plumage patterns or vocalizations. Although some authors have suggested that plumage is a neutral trait irrelevant to male mating success in some manakin species (Butlin and Neems 1994), it would still be interesting to explore the role of plumage patterns in manakin hybridization (Schaedler *et al.* 2021). Likewise, the relationship between manakin vocalizations (produced either by calling or by wing-beating) and hybridization probability remains an open question.

The main limitation of the present analyses concerns the incomplete dataset. I could obtain an agility score for only 22 manakin species; consequently, not all hybrid combinations were included in the binary logistic regression. The courtship displays of other manakin species will need to be described and quantified (following the approach of Shogren *et al.* 2022). In addition, some manakin groups (e.g. the genus *Manacus*) have been studied in more detail, potentially resulting in undescribed hybrids and/or gaps in the available display ethograms of other genera. Finally, the generality of the pattern uncovered in this study (i.e. courtship similarity is more important than courtship complexity in predicting hybridization) remains to be tested in other bird groups with elaborate courtship displays and high levels of hybridization, such as cranes (Nováková and Robovský 2021) and grebes (Konter 2011). The relationship between courtship similarity and hybridization also raises questions about the speciation process, namely how differences in courtship display are linked to the early stages of speciation (Anciães and Prum 2008, Anciães *et al.* 2009). Extending the analyses of courtship displays to other sections of the avian tree of life can thus provide important insights into patterns of hybridization and speciation.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

All data are incorporated into the article and its Supplementary material.

REFERENCES

Alatalo RV, Gustafsson L, Lundberg A. Male coloration and species recognition in sympatric flycatchers. *Proceedings of the Royal Society B: Biological Sciences* 1994;**256**:113–8. https://doi.org/10.1098/rspb.1994.0057

Anciães M, Durães R, Cerqueira MC *et al.* Diversidade de piprídeos (Aves: Pipridae) amazônicos: seleção sexual, ecologia e evolução. *Oecologia Brasiliensis* 2009;**13**:165–82.

Anciães M, Prum RO. Manakin display and visiting behaviour: a comparative test of sensory drive. *Animal Behaviour* 2008;**75**:783–90. https://doi.org/10.1016/j.anbehav.2007.06.013

Barrera-Guzmán AO, Aleixo A, Faccio M *et al.* Gene flow, genomic homogenization and the timeline to speciation in Amazonian manakins. *Molecular Ecology* 2022;**31**:4050–66. https://doi.org/10.1111/mec.16562

Barrera-Guzmán AO, Aleixo A, Shawkey MD *et al.* Hybrid speciation leads to novel male secondary sexual ornamentation of an Amazonian bird. *Proceedings of the National Academy of Sciences of the United States of America* 2018;**115**:E218–25. https://doi.org/10.1073/pnas.1717319115

Barske J, Fuxjager MJ, Ciofi C *et al.* Beyond plumage: acrobatic courtship displays show intermediate patterns in manakin hybrids. *Animal Behaviour* 2023;**198**:195–205. https://doi.org/10.1016/j.anbehav.2023.01.020

Barske J, Schlinger BA, Wikelski M *et al.* Female choice for male motor skills. *Proceedings Biological Sciences* 2011;**278**:3523–8. https://doi.org/10.1098/rspb.2011.0382

Bennett KFP, Lim HC, Braun MJ. Sexual selection and introgression in avian hybrid zones: spotlight on *Manacus*. *Integrative and Comparative Biology* 2021;**61**:1291–309. https://doi.org/10.1093/icb/icab135

Billerman SM, Keeney BK, Rodewald PG *et al. Birds of the World*. Ithaca: Cornell Laboratory of Ornithology, 2022.

Brumfield RT, Carling MD. The influence of hybrid zones on species tree inference in manakins. In: Knowles LL, Kubatko LS (ed.), *Estimating Species Trees: Practical and Theoretical Aspects*. Hoboken, NJ: John Wiley & Sons, 2010, 115–27.

Butlin RK, Neems RM. Hybrid zones and sexual selection. *Science* 1994;**265**:122. https://doi.org/10.1126/science.265.5168.122

Calabrese GM, Pfennig KS. Reinforcement and the proliferation of species. *Journal of Heredity* 2019;**111**:138–46. https://doi.org/10.1093/jhered/esz073

Campagna L, Benites P, Lougheed SC *et al.* Rapid phenotypic evolution during incipient speciation in a continental avian radiation. *Proceedings of the Royal Society B: Biological Sciences* 2011;**279**:1847–56. https://doi.org/10.1098/rspb.2011.2170

DuVal EH, Fitzpatrick CL, Hobson EA *et al.* Inferred attractiveness: a generalized mechanism for sexual selection that can maintain variation in traits and preferences over time. *PLoS Biology* 2023;**21**:e3002269. https://doi.org/10.1371/journal.pbio.3002269

Fuxjager MJ, Schlinger BA. Perspectives on the evolution of animal dancing: a case study of manakins. *Current Opinion in Behavioral Sciences* 2015;**6**:7–12. https://doi.org/10.1016/j.cobeha.2015.06.007

Graves GR. A new hybrid manakin (*Dixiphia pipra* × *Pipra filicauda*) (Aves, Pipridae) from the Andean foothills of eastern Ecuador. *Proceedings of the Biological Society of Washington* 1993;**106**:436–41.

Haffer J. Art-Entstehung bei einigen Waldvögeln Amazoniens. *Journal für Ornithologie* 1970;**111**:285–331. https://doi.org/10.1007/bf01653396

Harvey MG, Bravo GA, Claramunt S *et al.* The evolution of a tropical biodiversity hotspot. *Science* 2020;**370**:1343–8. https://doi.org/10.1126/science.aaz6970

Hubbs CL. Hybridization between fish species in nature. *Systematic Biology* 1955;**4**:1–20. https://doi.org/10.2307/sysbio/4.1.1

Konter A. Interbreeding of *Aechmophorus* grebes. *The Wilson Journal of Ornithology* 2011;**123**:132–6. https://doi.org/10.1676/10-091.1

Kumar S, Suleski M, Craig JM *et al.* TimeTree 5: an expanded resource for species divergence times. *Molecular Biology and Evolution* 2022;**39**:msac174. https://doi.org/10.1093/molbev/msac174

Ligon RA, Diaz CD, Morano JL *et al.* Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. *PLoS Biology* 2018;**16**:e2006962. https://doi.org/10.1371/journal.pbio.2006962

Marini MA, Hackett SJ. A multifaceted approach to the characterization of an intergeneric hybrid manakin (Pipridae) from Brazil. *The Auk* 2002;**119**:1114–20. https://doi.org/10.1642/0004-8038(2002)119[1114:amattc]2.0.co;2

Mason NA, Burns KJ, Tobias JA *et al.* Song evolution, speciation, and vocal learning in passerine birds. *Evolution* 2017;**71**:786–96. https://doi.org/10.1111/evo.13159

McCarthy E. *Handbook of Avian Hybrids of the World*. New York: Oxford University Press, 2006.

Moncrieff AE, Faircloth BC, Brumfield RT. Systematics of *Lepidothrix* manakins (Aves: Passeriformes: Pipridae) using RADcap markers. *Molecular Phylogenetics and Evolution* 2022;**173**:107525. https://doi.org/10.1016/j.ympev.2022.107525

Nali RC, Zamudio KR, Prado CPA. Hybridization despite elaborate courtship behavior and female choice in Neotropical tree frogs. *Integrative Zoology* 2023;**18**:208–24. https://doi.org/10.1111/1749-4877.12628

Nováková N, Robovský J. Behaviour of cranes (family Gruidae) mirrors their phylogenetic relationships. *Avian Research* 2021;**12**:40. https://doi.org/10.1186/S40657-021-00275-4

Ottenburghs J. Exploring the hybrid speciation continuum in birds. *Ecology and Evolution* 2018;**8**:13027–34. https://doi.org/10.1002/ece3.4558

Ottenburghs J. How common is hybridization in birds? *Journal für Ornithologie* 2023;**164**:913–20. https://doi.org/10.1007/s10336-023-02080-w

Parkes KC. Intergeneric hybrids in the family Pipridae. *The Condor* 1961;**63**:345–50. https://doi.org/10.2307/1365294

Parsons T, Olson S, Braun M. Unidirectional spread of secondary sexual plumage traits across an avian hybrid zone. *Science* 1993;**260**:1643–6. https://doi.org/10.1126/science.256.5054.193

Paterson HEH. The recognition concept of species. In: Vrba ES (ed.), *Species and Speciation. Transvaal Museum Monograph*. Pretoria, 1985, 21–9.

Prum RO. Phylogenetic analysis of the evolution of display behavior in the Neotropical manakins (Aves: Pipridae). *Ethology* 1990;**84**:202–31. https://doi.org/10.1111/j.1439-0310.1990.tb00798.x

R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R foundation for Statistical Computing, 2021. https://www.R-project.org/.

Rezende MA, Vasconcelos MF, Nogueira W *et al.* Novas ocorrências de híbridos entre *Chiroxiphia caudata* e *Antilophia galeata* em Minas Gerais, Brasil, com a primeira descrição de uma fêmea híbrida e comentários sobre os riscos da hibridação. *Atualidades Ornitológicas* 2013;**174**:33–9.

Sampaio L, Ferraz DO, da Costa ACM *et al*. Analyses of plumage coloration and genetic variation confirm the hybridization of *Pipra fasciicauda* and *Pipra aureola* in the Brazilian Amazon basin. *Journal of Ornithology* 2020;**161**:503–8. https://doi.org/10.1007/s10336-020-01744-1

Schaedler LM, Taylor LU, Prum RO *et al*. Constraint and function in the predefinitive plumages of manakins (Aves: Pipridae). *Integrative and Comparative Biology* 2021;**61**:1363–77. https://doi.org/10.1093/icb/icab063

Shogren EH, Anciães M, Barske J *et al*. Dancing drives evolution of sexual size dimorphism in manakins. *Proceedings of the Royal Society B: Biological Sciences* 2022;**289**:20212540. https://doi.org/10.1098/rspb.2021.2540

Slabbekoorn H, Smith TB. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 2002;**357**:493–503. https://doi.org/10.1098/rstb.2001.1056

Stankowski S, Ravinet M. Defining the speciation continuum. *Evolution* 2021;**75**:1256–73. https://doi.org/10.1111/evo.14215

Stotz DF. A hybrid manakin (*Pipra*) from Roraima, Brazil, and a phylogenetic perspective on hybridization in the Pipridae. *The Wilson Bulletin* 1993;**105**:348–51. https://doi.org/10.2307/4163293

Tung Ho L, Ané C. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology* 2014;**63**:397–408. https://doi.org/10.1093/sysbio/syu005

Uy JAC, Borgia G. Sexual selection drives rapid divergence in bowerbird display traits. *Evolution* 2000;**54**:273–8. https://doi.org/10.1111/j.0014-3820.2000.tb00027.x

Uy JAC, Irwin DE, Webster MS. Behavioral isolation and incipient speciation in birds. *Annual Review of Ecology, Evolution, and Systematics* 2018;**49**:1–24. https://doi.org/10.1146/annurev-ecolsys-110617-062646

Varela SAM, Matos M, Schlupp I. The role of mate-choice copying in speciation and hybridization. *Biological Reviews* 2018;**93**:1304–22. https://doi.org/10.1111/brv.12397

Zyskowski K, Prum RO. Phylogenetic analysis of the nest architecture of Neotropical ovenbirds (Furnariidae). *The Auk* 1999;**116**:891–911. https://doi.org/10.2307/4089670