

Original Article

Manakin's moving melody: the interplay between courtship dance display and vocalization as a predictor of hybridization in manakins (Aves: Pipridae)

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ABSTRACT

Behavioural changes can play an essential role in the development of reproductive barriers between populations. Yet, the interplay between courtship dance display and vocalization on hybridization probability remains unexplored. In this study, we used manakins (family Pipridae) to compare courtship vocalization similarity, dance similarity, and their multimodal interaction to quantify the importance and interaction between the courtship elements as predictors for hybridization. This Neotropical bird family shows a large diversity of courtship displays, vocalizations (vocal and non-vocal mechanical sounds) and many natural hybridization occurrences. We found that similarity in courtship vocalization might predict hybridization, although this pattern was strongly influenced by divergence time. We also demonstrated that vocalization similarity, dance similarity, and their multimodal interaction are equally valid predictors for hybridization based on Akaike information criterion model comparison, probably owing to the comparable evolutionary pathways. However, hybridization in manakins is probably linked to a combination of other factors besides vocalization and dance similarity, such as plumage ornamentation. Nevertheless, our findings can improve our understanding of hybridization and how courtship dance display and vocalization influence the speciation process.

Keywords: bird song; frequency; mate choice; multimodal signalling; prezygotic isolation; sexual selection; speciation

INTRODUCTION

In essence, the study of the origin of species is the study of how reproductive isolation mechanisms evolve (Coyne and Orr 2004, Uy *et al.* 2018). These reproductive isolation mechanisms can be categorized into prezygotic (i.e. before syngamy) and postzygotic (i.e. after syngamy) barriers (Coyne and Orr 2004, Birkhead and Brillard 2007). Behavioural changes can represent an example of a prezygotic isolating mechanism, which might play an important role in the initial development of reproductive barriers between populations (Uy *et al.* 2018). Sexual selection in birds can drive the divergence in behavioural isolation mechanisms in the form of courtship displays (Ligon *et al.* 2018, Ottenburghs 2025), ornamentation (Barrera-Guzmán *et al.* 2018), and vocalizations (Seddon 2005, Maynard *et al.* 2015, Mason *et al.* 2017). However, the speciation process is not always a straightforward process towards increased reproductive isolation. Speciation might be halted or

reversed when hybridization, the interbreeding of species (Grant and Grant 1992), breaks down reproductive isolation mechanisms (Stankowski and Ravinet 2021). The consequences of hybridization between genetically distinct lineages can result in several outcomes, including interspecific genetic introgression (Rheindt and Edwards 2011, Ottenburghs *et al.* 2017), the displacement and/or the extinction of one or both parental taxa (Ellstrand and Elam 1993), and the fusion of earlier diverged taxa (Grant and Grant 2014, Vallejo-Marín and Hiscock 2016). Moreover, hybridization can result in hybrid offspring and even new hybrid species, depending on the position of the species pair along the speciation continuum, which ranges from no reproductive isolation to complete reproductive isolation (Barrera-Guzmán *et al.* 2018, Ottenburghs 2018, Stankowski and Ravinet 2021).

Evolutionary divergence in mating signals has led to reproductive isolation in numerous bird taxa (Seddon 2005). Birds are an

exceptionally diverse vertebrate clade, in which acoustic signals play an important role in sexual signalling and speciation (Tobias *et al.* 2020, Hay *et al.* 2024). A vocalization characterizes a bird species and has been widely used to study avian evolution and speciation (Slabbekoorn and Smith 2002, Alström *et al.* 2016, Mason *et al.* 2017, Sangster *et al.* 2022, Simões *et al.* 2022). Therefore, vocal mating signals are considered highly important as a behavioural isolation mechanism (Coyne and Orr 2004, Willis *et al.* 2014) and are even considered the most important prezygotic isolation mechanism in many birds (Qvarnström *et al.* 2006).

Besides vocalization, courtship dance displays can play an important role in mate selection and hybridization between displaying birds (Ligon *et al.* 2018, Ottenburghs 2025). However, closely related species are more likely to perform comparable courtship dance displays and vocalizations (Prum 1990, Nali *et al.* 2023), which might facilitate hybridization. For that reason, divergence time needs to be considered when linking the probability of hybridization with behavioural traits (Willis *et al.* 2014, Ottenburghs 2025). In addition, courtship displays typically involve visual and vocal signals simultaneously (Mitoyen *et al.* 2019), and the incidence of hybridization might increase when different species share similar dance and vocalization patterns. Despite the extensive research on avian courtship displays (Ligon *et al.* 2018, Pease *et al.* 2022, Ottenburghs 2025) and vocalization as a behavioural isolation mechanism (Willis *et al.* 2014), the combined influence of dance display and vocalization on hybridization has remained largely unexplored.

In this study, we aim to uncover how the interplay between courtship dance and vocalization similarity affects hybridization patterns. To do so, we focus on a monophyletic group of birds with a large diversity of vocalizations and courtship displays and with many reliable hybridization records. The manakins (Aves: Pipridae) are a clade comprising 55 species of suboscine passerine birds that are primarily restricted to the (sub)tropical forest of Central and South America, with the greatest diversity in the Amazon Basin (Kirwan *et al.* 2011, Bennett *et al.* 2021). In manakins, sexual selection has driven the evolution of complex ornamentation (Doucet *et al.* 2007, Barrera-Guzmán *et al.* 2018), social behaviour (Bennett *et al.* 2021), and diverse courtship displays (Trainer and McDonald 1993, Kirwan *et al.* 2011, Maynard *et al.* 2015). Courtship displays in many manakin species are performed in leks, where males display for females at clustered display sites (Fuxjager and Schlinger 2015). Ottenburghs (2025) found a positive relationship between courtship dance similarity and the probability of manakin hybridization. However, manakin courtship displays include not only visual elements, but also vocal and non-vocal mechanical sounds (Prum 1998, Fuxjager and Schlinger 2015, Alfonso *et al.* 2021), thus involving signals in different sensory modalities (Mitoyen *et al.* 2019). Additionally, many records of hybridizing species of manakins have been reported (Haffer 1970, Stotz 1993, Marini and Hackett 2002, Barrera-Guzmán *et al.* 2018, Sampaio *et al.* 2020). On a species level, 31% (17 of 55) of the manakin species have convincing evidence for hybridization (Ottenburghs 2025), which is higher than the estimated 15%–20% for birds overall (Ottenburghs 2023). All in all, the wide range of vocalizations, the complex courtship behaviour, and the many natural hybridization occurrences make the Pipridae an excellent avian family in which to study the interplay between

courtship dance and vocalization similarity on hybridization patterns.

Specifically, we compiled a dataset of manakin courtship vocalization variables to obtain insights into the effect of courtship vocalization similarity on hybridization patterns, while taking divergence time into account. We also compared manakin courtship dance similarity, courtship vocalization similarity, and their multimodal interaction as predictors of hybridization. Moreover, the regime shaping the evolution underlying a behavioural trait might provide insights into the influence of a trait as a behavioural isolation mechanism. Therefore, we compared different models of evolution for a subset of vocalization variables. We expected to uncover the following patterns. First, we predicted a positive correlation between courtship vocalization similarity and the probability of hybridization, because comparable vocalizations between species might facilitate hybridization (Willis *et al.* 2014). Second, we expected courtship vocalization similarity to be a better predictor of hybridization than dance similarity, owing to the well-established importance of song as a prezygotic isolation mechanism in many birds (Qvarnström *et al.* 2006, Tobias *et al.* 2020), whereas the multimodal interaction between courtship dance and vocalization similarity would be a better predictor of hybridization in comparison to these two factors individually, because courtship displays often involve simultaneous signals in different sensory modalities (Mitoyen *et al.* 2019). The findings of this study can contribute further insights into the drivers of behavioural signal divergence, which is fundamental to our understanding of hybridization and speciation (Seddon 2005).

MATERIALS AND METHODS

We sourced courtship vocalizations representing 53 of 55 manakin species (17 hybridizing and 36 non-hybridizing) from the xeno-canto database (<https://xeno-canto.org/>) and the Macaulay Library at Cornell Lab of Ornithology (<https://www.macaulay-library.org>) (November 2024). *Cryptopipo litae* and *Lepidothrix velutina* were excluded because no usable courtship vocalizations were found for these species. We considered only male courtship vocalizations, which were selected based on vocalization descriptions by Kirwan *et al.* (2011) and Winkler *et al.* (2020). Only recordings with suitable signal-to-noise levels were used, in order to reduce potential errors or biases by choosing the best-quality recordings available for each species (recordings scored as 'A' or 'B' in xeno-canto and more than three stars in Macaulay Library) (Hay *et al.* 2024). Moreover, the location of each recording was checked based on a visual inspection of the distribution ranges of every species from the Birds of the World website (<https://bird-softheworld.org/>). If needed, the package 'av' (Ooms 2022) was used to convert WAV to MP3 files, and the scientific names of the species were checked with the International Ornithology Community (IOC) World Birds Names v.14.2 (Gill *et al.* 2024).

Only one bout of an individual vocalization was analysed from each recording to ensure the independence of our samples. We defined a bout as a vocalization including vocal elements from a single individual bird, separated by a gap of >1 s. Recordings from different geographical locations were assumed to be of a different individual bird (Hay *et al.* 2024). Hann spectrograms with a window size of 512 samples of 548 individuals

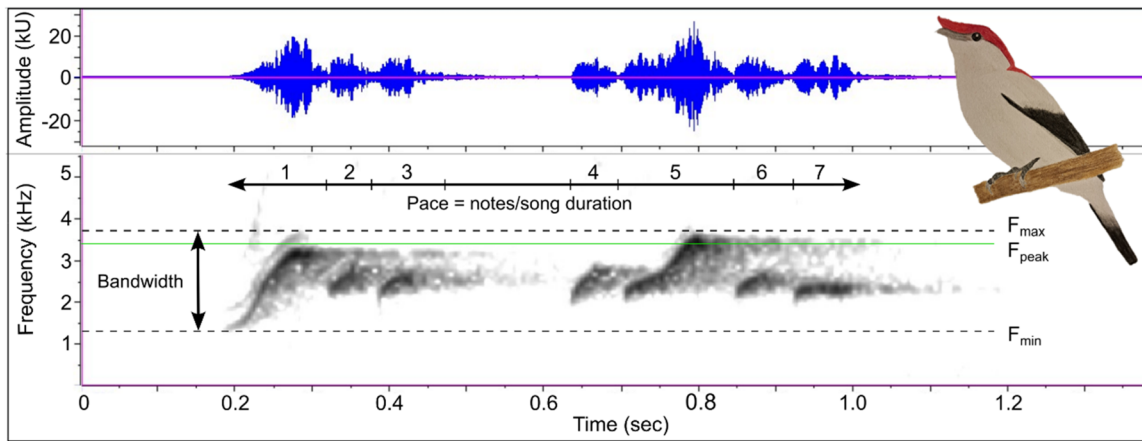


Figure 1. Waveform and spectrogram showing the amplitude (in kilounits) and frequency (in kilohertz) over time (in seconds) for an Araripe manakin (*Chiroxiphia bokermanni*) vocalization (xeno-canto accession number: XC427075). The five song variables considered were the minimum frequency (F_{\min}), maximum frequency (F_{\max}), peak frequency (F_{peak}), pace, and bandwidth (see main text for vocalization variables descriptions). Note that there are no non-vocal mechanical sounds in this vocalization. Image attributions can be found in [Supporting Information, Appendix S1](#). The figure was inspired by [Hay et al. \(2024\)](#). Edited with Inkscape 1.3.2.

from 53 manakin species [1–31 recordings per species (mean = 10.34); [Supplementary Material](#)] were made using RAVEN PRO v.1.6.5 (Cornell Laboratory of Ornithology). Based on previous studies ([Alström et al. 2016](#), [Berv et al. 2021](#), [Mikula et al. 2021](#), [Simões et al. 2022](#), [Hay et al. 2024](#), [Porzio et al. 2024](#)), we selected five acoustic variables for each vocal bout to characterize courtship vocalizations of the manakin species: (i) minimum frequency, the lowest frequency of a bout; (ii) maximum frequency, the highest frequency of a bout; (iii) peak frequency, a measure of frequency where the highest portion of energy is discharged of the total bout ([Boncoraglio and Saino 2007](#)), measured with the peak frequency function available in the measurements of RAVEN PRO v.1.6.5; (iv) pace, the number of notes per second; and (v) bandwidth, the range between the minimum and maximum frequency of a bout ([Fig. 1](#)). These variables reflect the basic acoustic characteristics of a vocalization, capturing the general overview of the vocalization.

In addition to the vocalization characteristics, non-vocal mechanical sounds produced by males of several manakin species were included in the analysis. For example, some manakin males generate non-vocal mechanical sounds by striking their wings above their heads to produce a ‘firecracker-like’ zonation ([Fuxjager and Schlinger 2015](#)). The analysed non-vocal mechanical sounds included: (i) single and double wing snaps (WS); and (ii) roll-snaps (RS), comprising multiple wing snaps that can sometimes create mechanical wing-buzz noises or harmonic oscillations ([Prum 1990, 1998](#), [Bostwick and Prum 2003](#), [Fuxjager and Schlinger 2015](#), [Ariznavarreta et al. 2025](#)). Recorded wing slaps and roll-snaps were added for each species in the dataset as a binary variable (1 = present, 0 = absent; [Supplementary Material](#)). We made the separation of wing slaps and roll-snaps instead of the four different physical mechanisms of mechanical sound production in manakins by [Prum \(1998\)](#) to reduce the overfitting of the non-vocal mechanical sounds.

An overview of reliable hybrid records in the Pipridae family was made by [Ottenburghs \(2025\)](#), including 15 hybrids involving 17 species. Briefly, hybrid records were assessed and considered

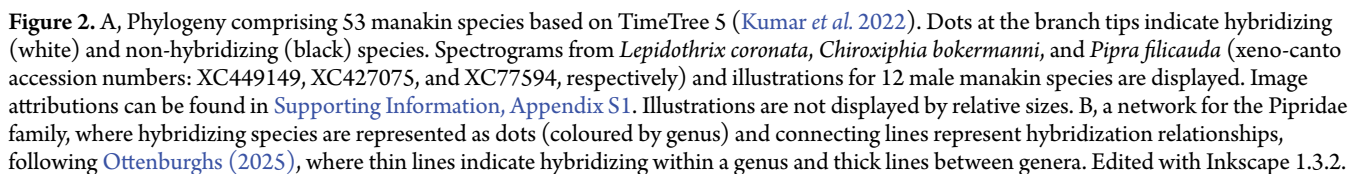
reliable if there was a detailed description of museum specimens or genetic analysis. We used possible species pairs within the Pipridae family to compare courtship vocalizations between hybridizing and non-hybridizing species pairs. Following [Ottenburghs \(2025\)](#), we used only species pairs with a divergence time <25 Mya (obtained from [Harvey et al. 2020](#)), dividing the Ilicurinae clade from the clade including Piprinae and Neopelminae ([Fig. 2A](#)), because it is unlikely that hybridization will occur after a divergence time of >25 Mya. Moreover, we selected only sympatric or parapatric species pairs ([Bennett et al. 2021](#)). We used the distribution ranges of 53 manakins from BirdLife International (datum: WGS1984) and the ‘*st_intersection*’ function from the package ‘sf’ ([Pebesma 2018](#)) to determine whether a species pair was sympatric. We considered a species pair sympatric when the distribution ranges overlapped ([Ottenburghs and Nicolai 2024](#)). The hybridizing species pair with *Chiroxiphia galeata* (formerly classified as *Antilophia galeata*) and *Chiroxiphia caudata* was excluded because no divergence time for this species pair was available in the paper by [Harvey et al. \(2020\)](#).

To obtain dance similarity scores for the species pairs, we followed the approach of [Ottenburghs \(2025\)](#) by counting the number of common display elements for each species pair using the behavioural display matrix from the paper by [Ariznavarreta et al. \(2025\)](#). Based on peer-reviewed literature, a dataset was made with 59 binary present/absent behavioural display characters for 43 manakin species (for details, see [Ariznavarreta et al. 2025](#)).

A phylogenetic tree of the Pipridae family was made using TimeTree 5, a public knowledge base that collects species divergence times derived from molecular sequence data ([Kumar et al. 2022](#)) ([Fig. 2A](#); [Supplementary Material](#)). Moreover, to visualize the hybridization relationships from [Ottenburghs \(2025\)](#), a network was constructed of the hybridizing manakins using the package ‘igraph’ ([Csárdi 2013](#)) ([Fig. 2B](#)).

Statistical analysis

To meet parametric assumptions of normality and homogeneity of variance ([Derryberry et al. 2018](#)) and because logarithmic scales of sound frequency represent the perception of birds



Next, 10 additional binary logistic regression models were conducted, including dance similarity scores as a fixed factor, with

hybridization as the response variable. These models aimed to compare divergence times, courtship dance, and vocalization similarity as predictors of hybridization. We used only species pairs for which courtship dance and vocalization similarity scores were available [amounting to 241 species pairs (13 hybridizing and 228 non-hybridizing); [Supplementary Material](#)]. To assess the interplay between courtship dance and vocalization directly, we also included binary logistic regressions with dance and vocalization similarity as either an interaction effect or as a combined multimodal factor. The combined factor of dance and vocalization similarity was made using a principal component analysis with the ‘prcomp’ function from the package ‘stats’ ([R Core Team 2024](#)). We considered only principal component 2 (PC2; 48.4% of cumulative variation), because the two variables have a positive loading in this component ([Supporting Information, Appendix S2](#)). These loadings suggest that PC2 represents the mutual variance of both variables better than principal component 1, where the opposite loadings represent the contrast between the two variables ([Supporting Information, Appendix S2](#)). The divergence time, courtship dance similarity, vocalization similarity, and the combined factor were compared as predictors for hybridization using AIC value model comparison. Moreover, we calculated Nagelkerke’s R^2 ([Nagelkerke 1991](#)) using the ‘pR2’ function in the package ‘pscl’ ([Jackman et al. 2015](#)) to quantify the contribution of the predictors on hybridization in each model. No collinearity between divergence time, dance similarity, and courtship vocalization was found according to our variance inflation factors (all less than five).

To gain deeper insights into the pattern of trait evolution for manakin courtship vocalization traits, we also evaluated the fit of five evolutionary models [Brownian motion (BM), Ornstein–Uhlenbeck (OU), early burst (EB), kappa (κ), and delta (δ)] for the vocalization traits. Each of these evolutionary models represents a different selective regimen shaping the evolution of a particular trait (for descriptions, see Results). The corrected AIC (AIC_c) values ([Sugiura 1978](#), [Hurvich and Tsai 1989](#)) for five evolutionary models were calculated based on average species values of three courtship vocalization traits (peak frequency, pace, and bandwidth) using the ‘fitContinuous’ function from the package ‘geiger’ ([Harmon et al. 2008](#)). All song variables are, to some extent, correlated with each other. Following [Hay et al. \(2024\)](#), we focused only on peak frequency, pace, and bandwidth. Peak frequency is less sensitive to background noise than the minimum and maximum frequency. Therefore, caution in interpreting the result of the bandwidth needs to be exercised, because this variable was calculated by subtracting the minimum from the maximum frequency ([Hay et al. 2024](#)). The different models were compared using AIC_c values, because AIC_c is more suitable in model selection for relatively small datasets than AIC ([Bedrick and Tsai 1994](#), [Wong and Li 1998](#), [Yessoufou et al. 2012](#)).

All statistical analyses were performed using R v.4.4.1 ([R Core Team 2024](#)).

RESULTS

Overall, courtship vocalization similarity scores were calculated for 378 sympatric and parapatric species pairs (14 hybridizing and 364 non-hybridizing; [Supplementary Materials](#)). Vocalization similarity scores (D^2) varied between 1.01 and 5.63

(mean = 3.83) for the hybridizing species pairs and between 2.24 and 19.00 (mean = 5.16) for the non-hybridizing species pairs. Divergence times based on the study by [Harvey et al. \(2020\)](#) varied between 0.3 and 7.3 Mya (mean = 2.7) for the hybridizing species pairs and between 0.6 and 15.1 Mya (mean = 8.4) for the non-hybridizing species pairs. We calculated dance similarity scores for 241 sympatric and parapatric species pairs (13 hybridizing and 228 non-hybridizing; [Supplementary Materials](#)), which ranged between 0 and 14 (mean = 5.69) for the hybridizing species pairs and between 0 and 13 (mean = 2.06) for the non-hybridizing species pairs.

As predicted, we found a negative relationship between courtship vocalization similarity and hybridization probability (binary logistic regression, $N=378$, z -value = -2.35 , $P=.02$; [Fig. 3A](#); [Table 1](#)). Moreover, there was a negative relationship between divergence time and hybridization probability (binary logistic regression, $N=378$, z -value = -4.83 , $P<.001$; [Fig. 3B](#); [Table 1](#)). When divergence time was included in the model with vocalization similarity, the effect of courtship vocalization similarity on hybridization was mitigated (binary logistic regression, $N=378$, z -value = -1.42 , $P=.16$; [Table 1](#)). Including divergence times in the binary logistic regression model with courtship vocalization similarity showed the best model fit according to the AIC model comparison ([Table 1](#)). However, this model fit was not significantly different from the binary logistic regression model with only divergence times ($\Delta AIC=.83$; [Table 1](#)). Therefore, the hybridization probability increases with courtship vocalization similarity in manakins, although divergence time strongly influences this pattern ([Table 1](#)).

Next, we assessed the importance of the explanatory variables (courtship vocalization similarity, courtship dance similarity, divergence times, and the multimodal factor including courtship dance and vocalization similarity) on hybridization probability by comparing AIC values of 10 different binary logistic regression models. Divergence time alone provided the best model fit according to the AIC model comparison ([Table 2](#)). However, the best-fitting model did not differ significantly from the models with vocalization similarity and divergence time ($\Delta AIC=.44$) and with dance similarity and divergence time ($\Delta AIC=1.90$; [Table 2](#)). In addition, the model including the multimodal factor (PC2) was also not significantly different from the best model fit ($\Delta AIC=1.17$; [Table 2](#)). Nagelkerke’s R^2 values for the four best-fitting models ranged from .38 to .40, whereas the models including only dance and vocal similarity showed low Nagelkerke’s R^2 values (.13 and .09, respectively; [Table 2](#)). Furthermore, the interaction between courtship dance and vocalization similarity was not significant ([Table 2](#); [Fig. 3D](#)). Overall, our analysis showed multiple best-fitting models for hybridization probability, all including divergence time as a fixed factor.

The three courtship vocalization variables (peak frequency, pace, and bandwidth) showed different evolutionary patterns. Both pace and bandwidth followed the OU model according to the AIC_c model comparison, indicating that these traits evolved towards an optimal value ([Table 3](#)). In contrast, the κ model was the best-fitting model for the peak frequency, which suggests that peak frequency shows evolutionary change associated with speciation events ([Table 3](#)). For all three vocalization variables, the support for the best model was significantly different from the other models ($\Delta AIC_c > 2$).

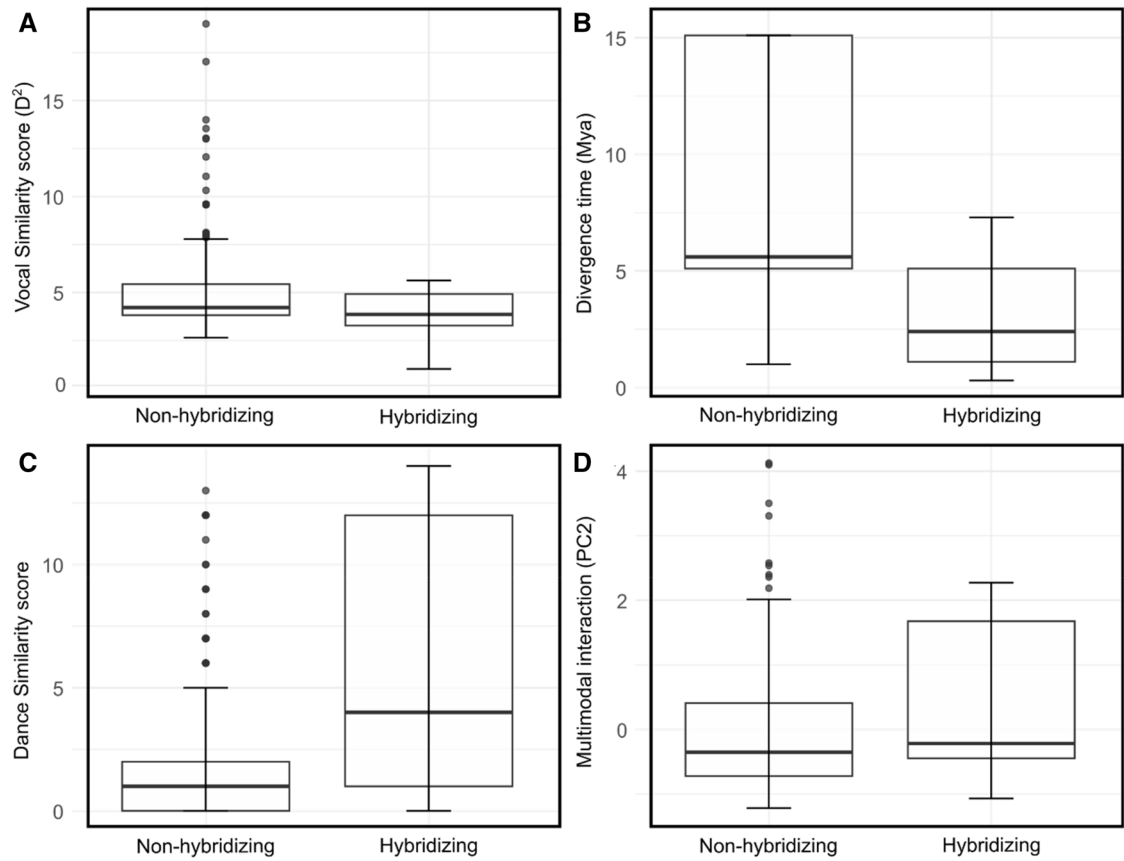


Figure 3. Boxplots showing the relationships between the probability of hybridization over the vocalization similarity score (D^2) (A; $N = 378$), the divergence time (in millions of years ago) (B; $N = 378$), the dance similarity score (C; $N = 241$), and the multimodal factor PC2 including vocalization and dance similarity (D; $N = 241$) between hybridizing and non-hybridizing manakin species pairs. Note the smaller sample size for the dance similarity score and the multimodal factor over the probability of hybridization. The interquartile ranges (boxes) and median (horizontal line in boxes) are displayed. Whiskers show the lowest and highest value within $1.5 \times$ interquartile range, while dots represent outliers. Edited with Inkscape 1.3.2.

Table 1. Binary logistic regression models ($N = 378$) with an Akaike information criterion-based comparison of manakin hybridization probability with courtship vocalization similarity and divergence times as predictors.

Model formula ($N = 378$)	Model coefficients			AIC value
	Factor	z-value	P-value	
Hybrid ~ Vocal Similarity + Divergence time	Vocal Similarity	-1.42	.156	85.62
	Divergence time	-4.16	<.001	
Hybrid ~ Divergence time	Divergence time	-4.83	<.001	86.45
Hybrid ~ Vocal Similarity	Vocal Similarity	-2.35	.018	114.82

The factors ‘Vocal similarity’ and ‘Divergence time’ were not collinear in the models (variance inflation factors <5). Significant P -values (<.05) and AIC values for the best model fit are highlighted in bold. Abbreviation: AIC, Akaike information criterion.

DISCUSSION

We investigated the interplay between courtship dance and vocalization, in relation to divergence time, to assess the predictability of hybridization in manakins. Although strongly influenced by

divergence time, we found that similarity in courtship vocalization can predict the incidence of hybridization. A similar pattern was found between courtship dance similarity and hybridization in manakins, also strongly influenced by the divergence time. Ottenburghs (2025) found the same pattern for courtship dance displays using a different behavioural dataset from the study by Shogren et al. (2022). Nevertheless, the pattern between hybridization and courtship vocalization similarity has not been reported previously in any suboscine passerine family (but for an example in oscines, see Willis et al. 2014). The strong influence of divergence time on the probability of hybridization suggests strong intrinsic postzygotic isolation between more distantly related manakin species (Price and Bouvier 2002). This aspect remains to be investigated with genomic techniques (e.g. by quantifying rates of past introgression or identifying genetic incompatibilities). In the following discussion, we will focus on hybridization between closely related manakin species where prezygotic isolation mechanisms are still relevant.

Most hybridizing manakin species pairs showed high similarity in vocalizations ($D^2 = 1.1\text{--}5.63$) and diverged recently (0.3–7.3 Mya) (Harvey et al. 2020). This pattern was especially apparent in the species pairs within the genera *Manacus*, *Pipra*, and *Lepidothrix*. For instance, the species pairs *Manacus vitellinus* with

Table 2. Binary logistic regression models ($N = 241$) with Akaike information criterion value comparison and Nagelkerke's R^2 values of manakin hybridization probability with courtship vocalization similarity, dance similarity, divergence times, the interaction between courtship dance and vocalization similarity, and the multimodal factor PC2 (including vocalization and dance similarity) as predictors.

Model formula ($N = 241$)	Model coefficients			AIC value	Nagelkerke's R^2
	Factor	z-value	P-value		
Hybrid ~ Divergence time	Divergence time	-4.63	<.001	71.39	.382
Hybrid ~ Vocal similarity + Divergence time	Vocal similarity	-1.06	.291	71.83	.398
	Divergence time	-3.96	<.001		
Hybrid ~ PC2 + Divergence time	PC2	-0.88	.381	72.56	.390
	Divergence time	-4.38	<.001		
Hybrid ~ Dance similarity + Divergence time	Dance similarity	-0.32	.746	73.29	.383
	Divergence time	-3.86	<.001		
Hybrid ~ Vocal similarity + Dance similarity + Divergence time	Vocal similarity	-1.04	.297	73.76	.399
	Dance similarity	-0.27	.788		
	Divergence time	-3.32	<.001		
Hybrid ~ Vocal similarity + Dance similarity	Vocal similarity	-2.01	.044	90.32	.197
	Dance similarity	3.21	.001		
Hybrid ~ Vocal similarity × Dance similarity	Vocal similarity	-0.75	.456	91.47	.207
	Dance similarity	1.50	.134		
	Vocal: Dance	-0.90	.366		
Hybrid ~ Dance similarity	Dance similarity	3.44	<.001	94.51	.127
Hybrid ~ Vocal similarity	Vocal similarity	-2.18	.029	97.91	.087
Hybrid ~ PC2	PC2	1.41	.158	103.43	.021

The factors 'Vocal similarity', 'Dance similarity', and 'Divergence time' were not collinear in the models (variance inflation factors consistently <5). Significant P-values (<.05) and AIC values for the best model fit are highlighted in bold. Abbreviation: AIC, Akaike information criterion.

Table 3. Corrected Akaike information criterion value comparison for five evolutionary models [Brownian motion (BM), Orstein–Uhlenbeck (OU), early burst (EB), kappa (κ), and delta (δ)] fitted to three courtship vocalization variables (peak frequency, pace and bandwidth) in manakins.

Model	Model indicators	Courtship vocalization variables		
		Peak frequency	Pace	Bandwidth
BM	Traits diverge indefinitely following a random walk	61.731	143.551	111.909
OU	Taxa diverge less on long branches than expected, owing to stabilizing force pulling towards the centre	50.552	112.773	95.602
EB	There is an initial burst of trait diversification but less later	64.515	146.335	114.693
κ	Change occurs with each speciation event, but is not proportional to branch length	38.119	131.004	104.436
δ	Brownian rate parameter speeds up or slows down over time	59.849	141.249	110.103

The AIC_c values for the best model fit for each courtship vocalization variable are highlighted in bold, whereas underlined AIC_c values indicate the second-best model fit. Table and model indicator descriptions are adjusted from Yessoufou *et al.* (2012). Abbreviation: AIC_c, corrected Akaike information criterion.

Manacus candei, and *Manacus vitellinus* with *Manacus manacus* (Brumfield and Carling 2010) showed the highest vocalization similarity ($D^2 = 1.01$ and 1.75 , respectively) and diverged recently (1.2 and 0.3 Mya, respectively) (Harvey *et al.* 2020). Moreover, the intergeneric species pair *Pipra aureola* and *Heterocercus linteatus* (Parkes 1961) showed the lowest vocalization similarity among the hybridizing species pairs ($D^2 = 5.63$), which can be attributed to their high divergence time (5.1 Mya) (Harvey *et al.* 2020). Therefore, in parallel with courtship dance similarity (Ottenburghs 2025), courtship vocalization similarity increases the incidence of hybridization between closely related manakin species.

We also compared dance and vocalization similarity as predictors of hybridization in manakins. Multiple best-fitting models for predicting hybridization probability were found based on the AIC

model comparison, contradicting our expectation that vocalization similarity would be a better predictor of hybridization than dance similarity because song functions as an important prezygotic isolation mechanism in birds (Qvarnström *et al.* 2006); but see Pulido-Santacruz *et al.* (2018) for the role of postzygotic isolation mechanisms in tropical bird species. Our results can be explained by the evolutionary patterns underlying the different courtship variables. The pace and bandwidth variables in manakins were best captured by the OU model, indicating an evolution towards an optimal value for these traits. The κ model was the best-fitting model for the peak frequency, suggesting that with each speciation event, the peak frequency changed. These patterns are in line with the acoustic and behavioural traits from the study by Ariznavarreta *et al.* (2025), who tested whether acoustic, colour, and behavioural signals in manakins have evolved

independently or in a correlated manner. As the vocalization variables and courtship dance changed with each speciation process (κ) and evolved towards an optimal value (OU), manakin species might display distinct courtship dances and vocalizations. Consequently, courtship dance and vocalization are likely to act as strong behavioural isolation mechanisms in manakins, which reduces the probability of hybridization. Therefore, neither dance nor vocalization similarity provides a clearly superior indicator of the probability of hybridization.

Surprisingly, the model including the combined factor of vocalization with dance similarity (PC2) was not significantly better than the other models according to our AIC model comparison. Courtship displays are typically multimodal, meaning that they involve simultaneous signals in different sensory modalities (Mitoyen *et al.* 2019). For example, vocal courtship signals in Túngara frogs (*Engystromops pustulosus*) are individually not attractive for the female; however, they become attractive in combination with the visual signal of vocal sac inflation (Taylor and Ryan 2013). Manakin courtship dance display is often accompanied by a variety of sounds, both 'natural' and mechanical vocalizations (Kirwan *et al.* 2011). Moreover, courtship dance similarity (Ottenburghs 2025) and vocalization similarity (this study) might predict hybridization in manakins. However, we found no evidence that the model including the multimodal courtship display was a significantly better predictor for hybridization than models including vocalization and courtship dance similarity individually. Models including only dance and vocalization similarity showed low Nagelkerke's R^2 values (see Table 2), indicating a low contribution of these individual predictors of hybridization. In contrast, all best-fitting models included divergence time as a fixed factor and showed moderate Nagelkerke's R^2 values for the best-fitting models, suggesting that hybridization is explained mainly by divergence time in our models. Hence, the low individual contributions of courtship dance and vocalization similarity and the strong influence of divergence time in predicting the occurrence of hybridization might explain why models including courtship dance and vocalization similarity individually were equally valid as the model including the multimodal courtship display.

The moderate Nagelkerke's R^2 values also imply that hybridization in manakins might be linked to a combination of predictors besides divergence times, dance, and vocalization similarity. For example, sexual selection has favoured the evolution of male plumage ornamentations in manakins that enhance signal efficacy (Doucet *et al.* 2007, Barrera-Guzmán *et al.* 2018). Although plumage ornamentations are common in manakins (Kirwan *et al.* 2011, Kajiki *et al.* 2023), and males across the Pipridae family exhibit multiple predefinitive plumage stages with distinctively male patches (Schaedler *et al.* 2021), the influence of plumage ornamentation on hybridization in manakins remains an open question. Moreover, some manakin species are more abundant or more extensively studied (e.g. the genus *Manacus*) than others, which might have introduced biases in our dataset. Furthermore, species pairs with a single reported hybrid and those undergoing extensive hybridization were treated equally in our binary presence/absence scoring. These potential biases can be reduced in future studies by incorporating conspicuousness or publication bias measurements (Randler 2006) and by using finer-resolution measures for hybridization probability (Willis *et al.* 2014).

Lastly, species-specific analyses might improve our understanding of the factors that influence the probability of hybridization. In addition, the interplay between courtship dance and vocalization on the probability of hybridization should be tested among other monophyletic bird groups to assess the generality of the patterns discovered in this study. Grouse (Phasianidae: Tetraonini) and birds-of-paradise (Paradisaeidae) would be interesting groups in which to test this pattern, because these groups also have elaborate courtship displays, vocalizations, and many natural hybridization occurrences (Quintela *et al.* 2010, Martin 2015, Ottenburghs 2019, Kleven *et al.* 2020, Blom *et al.* 2024). Expanding the analysis of courtship dance and vocalization similarity to other avian groups can improve our understanding of the drivers underlying natural hybridization. Moreover, it can offer insights into how hybridization might have contributed to speciation through the formation of new hybrid taxa (Abbott *et al.* 2013).

CONCLUSION

Although similarity in courtship vocalization appears to predict hybridization in manakins, its predictive power is moderated by divergence time. Nevertheless, this finding has not been reported previously in any suboscine passerine family. In addition, vocalization similarity is not a better predictor for hybridization than courtship dance similarity, probably because they follow similar evolutionary pathways (κ and OU model). Moreover, according to our analysis, the model including the multimodal courtship display was not significantly better than other models, probably owing to the strong correlation between divergence times and the probability of hybridization. Our results also imply that hybridization in manakins might be linked to a combination of factors besides vocalization and dance similarity, possibly plumage ornamentation. Therefore, a comparative study of courtship dance, vocalization, and plumage ornamentation of the complete Pipridae family is needed to provide a comprehensive overview and insights into the isolation mechanisms driving hybridization within this Neotropical bird family. All in all, our results highlight the importance of behavioural traits in relation to divergence time, emphasizing that understanding the evolutionary regimes of these traits might provide valuable insights into avian hybridization and the speciation process.

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overview of the user prompts and model outputs from ChatGPT 4.0 can be found in [Supporting Information, Appendix S3](#).

AUTHOR CONTRIBUTIONS

A.K. (conceptualization, methodology, formal analysis and investigation, writing—original draft preparation, writing—review and editing), J.O. (conceptualization, methodology, writing—review and editing, supervision).

SUPPLEMENTARY DATA

[Supplementary data](#) is available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY STATEMENT

The datasets and R code are available in the [Supporting Information, Supplementary material](#) to replicate this study.

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