



Research

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Sociality and migration predict hybridization across birds

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Hybridization represents a natural experiment that can provide insight into processes of speciation and diversification. Though considerable research has focused on hybrid zone dynamics, macroevolutionary investigations of the factors that influence hybridization are few. Here, we compile a database of avian hybrids and perform comparative analyses to determine whether several social and life-history variables influence broad patterns of hybridization. We perform three main analyses: phylogenetic logistic regression to examine variables that are associated with the presence of hybridization, phylogenetic Poisson regression of only those species exhibiting hybridization to determine which variables are associated with the extent of hybridization, and a phylogenetic logistic regression on a subset of data to assess potential pseudoreplication. After testing several social and life-history variables, we found that social bond duration is associated with the presence and extent of hybridization. Specifically, lengthy social bonds are negatively associated with the presence and extent of hybridization. In addition to social bond length, migration is positively linked with a greater likelihood of hybridization. The broad-scale correlations between species-specific traits and hybridization across diverse avian lineages suggest commonalities in the fine-scale processes involved in mating with heterospecifics, which in turn has implications for how we think about, study and understand hybridization processes and their influence on evolutionary trajectories.

1. Introduction

The spectacular diversity of life, in terms of number of species, is often cited as the main driver of Darwin's curiosity about the natural world [1]. To categorize and group individuals into species, a multitude of species concepts have been advanced [2]. Some of these species concepts are defined based on reproductive barriers [3–5], and thus cases where putative species produce hybrids are of particular interest. Indeed, a multitude of recent research has examined hybrids and hybrid zones to understand how speciation might proceed with gene flow [6–10]. These studies have often investigated the consequences of hybridization among a targeted set of species [11]; however, while recent studies have investigated evolutionary processes between two or a few species, the question of whether and how species-specific traits affect the likelihood of hybridization remains largely unanswered. If species are more likely to hybridize due to certain life-history traits, and these specific species are used to understand speciation and evolution, it is possible that our inferences regarding evolution from hybridizing species do not provide an entirely comprehensive perspective.

At a relatively focused scale, hybridization has been used to understand fundamental evolutionary processes such as speciation and adaptation. Hybrids and hybrid zones have been used to understand evolutionary divergence [12], including some of the earliest states of divergence [13]. Along with divergence, genomic analysis of hybrids and parent species has allowed

researchers to demarcate the specific genes involved in establishing species boundaries. For instance, blue-winged warblers (*Vermivora cyanoptera*) and golden-winged warblers (*Vermivora chrysoptera*) only consistently differ in six genomic regions, all of which are associated with plumage genes [14]. Similarly, in Lake Victoria cichlids, ancient hybridization led to considerable variation in an opsin gene; this opsin gene was the same one implicated in speciation in these species [15]. Hybridization therefore provides a practical window into the genomic architecture of speciation. In addition to providing insight into speciation, hybridization has also been used to document local and ecological adaptation [13,16]. Hybridization also seems causally related to interspecific behaviours. For instance, the presence of hybridization is also a driver of interspecific territoriality and species interactions [17]. In sum, hybridization among species has been used to glean insight into multiple biological processes. While the multitude of studies that have examined the processes of hybridization have provided novel and important insight into several biological phenomena, whether the likelihood or extent of hybridization is influenced by species-specific traits on a macroevolutionary scale remains unclear.

The presence and extent of hybridization in species could evolve due to any number of traits. For example, species may evolve increased recognition of heterospecifics, and consequently reduced likelihood of hybridization, if the two species share a high overlap in ecological resources [18,19]. However, we propose that several other traits may influence the likelihood of hybridization. For instance, social species may show reduced hybridization as an indirect effect if the presence of multiple group members, or stable social bonds and multiple assessments, collectively reduce the joint likelihood of making an error and accepting a heterospecific. One justification for these suppositions relies on assumptions about the probability of interspecific recognition mistakes. We specify that the probability of a species recognition mistake for an individual is α (akin to nestmate recognition error in [20]). In species that aggregate in lekking groups, we argue that females assessing multiple male individuals in the group would be less likely to make a mistake and mate with a heterospecific. Similarly, in species with long-term social bonds individuals will have multiple opportunities to assess a mate. As a result, the probability of an interspecific acceptance would be α^N where N represents the number of individuals in the group or the number of times an individual is assessed. If the probability of individual species recognition mistakes is low—as predicted by theory [21] and seen in practice [22]—then long-term bonds, or breeding groups, may reduce hybridization as α^N will rapidly approach zero.

To determine if the macroevolution of hybridization is associated with species-specific traits a large comparative analysis is required. Consequently, we developed a database of bird hybridization and associated species traits that could influence the likelihood of hybridization. Although many traits could potentially influence hybridization, we predict that the traits that are most likely to influence hybridization are those associated with the breeding system and sociality. Specifically, we predict that species that maintain long-term social bonds will tend to have lower likelihoods of hybridizing due to the opportunity to assess a mate repeatedly. We also predict that species associated with leks will have

lower rates of hybridization as conspecifics will be rejected from leks by competitors on the lek.

2. Methods

(a) Dataset

To investigate macroevolutionary drivers of hybridization, we targeted several avian families that vary in hybridization, sociality, and breeding system. We used the *Handbook of Avian Hybrids of the World* [23] to quantify the extent of hybridization (i.e. the number of species with which a focal species is known to hybridize with) and relied on numerous sources for social and breeding system data [24,25]. Additionally, we acquired information on social bond length and territoriality from Tobias *et al.* [26], and acquired data from the *The Handbook of Birds of the World* [25] to assign each species to a class of breeding system. If males and females in a species differed in external morphology or plumage in any way, we assigned them to 'dimorphic', and if they showed no observable difference, then they were classified as 'monomorphic'. We combed species accounts to determine if a species engaged in leks. Finally, if species were migratory or partially migratory then we designated them as 'migratory'. For both lek behaviour and migration behaviour, we relied on the *The Handbook of the Birds of the World* (now *Birds of the World*). Although specific migratory locations in the handbook may not be perfectly exact, they are likely to be sufficient for a binary classification of migration.

We took a liberal approach and included any reported hybridization where an individual was identified by sight as a putative hybrid. For instance, a phenotypically intermediate individual would be counted as an example of a hybrid. Although genetics are the only definitive method to identify hybridization, there is a lack of genetic information for most putative hybrids. We also were not specifically concerned with the fertility of hybrids because our focal questions centre on the likelihood of two parental species pairing to produce offspring (fertile or not). We recognize that the fertility of hybrids is a critical component that would dictate the dynamics of selection against hybridization. More detailed work is required to determine if any potential species-specific traits prevent F1 hybrids from reproducing.

Though we employed several analyses to examine drivers of hybridization (see below), we were concerned about the autocorrelation in our data above what is already present due to phylogeny. Specifically, the existence of hybridization in one species necessarily implies the existence of hybridization in another species. We therefore employed certain analyses on a 'comprehensive' dataset (containing all species) and repeated certain analyses on a 'conservative' dataset (containing species sets trimmed to eliminate autocorrelation). We wrote a custom script that conservatively thinned the dataset by identifying each hybridization event involving species A, and subsequently removing any following species that also hybridize with species A (e.g. species B that hybridizes with species A). Importantly, this means that even though species B may hybridize with species C, all of species B's hybridization data was removed due to its hybridization with species A. Because this script deals with species sequentially, we shuffled the data 100 times, and analysed each of these conservative datasets. Overall, we have a comprehensive dataset for all observations, a comprehensive dataset for only those species with hybridization, and a conservative dataset for all observations.

Finally, we were concerned that research effort may explain the prevalence of observations for hybridization in some species rather than others, especially since our dataset contains species from both the tropics and temperate areas. We therefore randomly sampled a subset of species and used the Web of

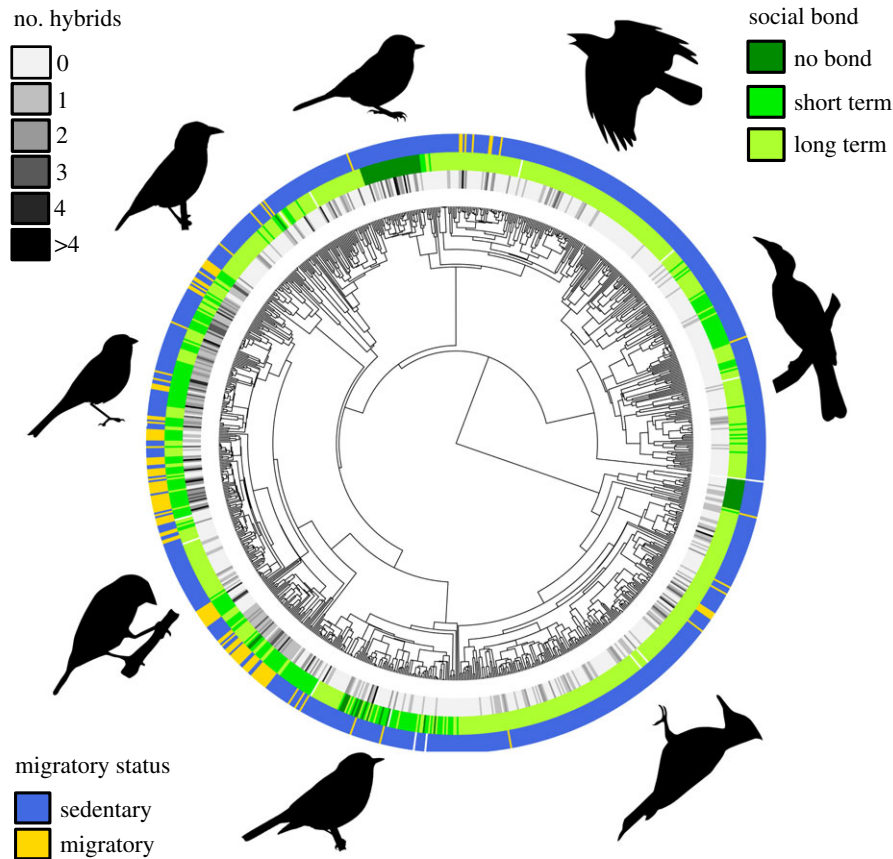


Figure 1. Phylogenetic distribution of hybridization (grey, inner circle), social bond length (green, middle circle), and migratory status (blue/yellow, outer circle). Silhouettes acquired from phylopic.org (see electronic supplementary material for details). Placement of species' silhouettes is not exact but approximates the correct position on phylogeny. (Online version in colour.)

Science database to assess the effect of research effort on the presence and extent of hybridization.

(b) Phylogenies

We identified and used several bird families that have species that vary in life history, sociality and breeding system. To analyse these species, we retrieved 100 separate phylogenies from bird-tree.org (constructed by Jetz *et al.* [27]) and performed all analyses on a subset of 50 phylogenies (following [28]) from the larger set of trees. The phylogenetic mixed models produce a single summary, modal values for each tree in the analyses. Specifically, the model summaries yield single *p*-values, posterior means and other variables. We take the final summary value for each tree and report the median value and range of values across all trees (following Leighton [24]).

(c) Analyses

We employed several types of comparative models to investigate both variables that might lead to the origin of hybridization, and variables that might lead to the expansion of hybridization. Specifically, we used Bayesian phylogenetic logistic regression to compare the species with and without hybridization. We repeated the Bayesian phylogenetic logistic regression on the conservative dataset. For the presence and absence of hybridization, we computed the D-statistic [29] to determine the phylogenetic signal of the binary trait. For the binary trait, we employed Mk models [30,31] to determine the rate of transitions between the state of hybridizing and the state of not hybridizing. In the Mk model, we allowed all rates to vary and compared that to models where rates were constrained to be the same.

After analysing hybridization as a presence or absence trait, we removed species without reported hybrids and employed phylogenetic Poisson regression to determine factors associated with

the extent of hybridization. The extent of hybridization is the number of other species with which a focal species has been observed to produce hybrids. In addition to full analyses on the presence of hybridization and the extent of hybridization, we also performed two sub-analyses on the full dataset. First, we removed all species that had unknown data for predictive variables. Second, we incorporated the research effort as a predictive variable. To estimate research effort, we searched all of the Web of Science database from 1864 to 2020 by searching the species scientific name in either the title or the abstract for a random subset of 250 species. We include the number of publications that meet the search terms in sub-analyses. All phylogenetic analyses used MCMCgmm as implemented in R package MCMCgmm [32]. For all analyses, we employed uninformative inverse-Gamma priors (shape and scale are equal to 0.002). We ran MCMC chains for 3 000 000 iterations for each chain per tree, thinned by 5000 and employed a burn-in of 50 000. We employed four chains for every tree, yielding a total of 12 000 000 iterations per tree; we used the function 'autocorr' and found negligible autocorrelation in sampling. We assessed chain mixing visually and we assessed chain mixing quantitatively by employing the Gelman-Rubin criterion [33]. We employed the deviance information criterion (DIC) to select final models. We computed the median phylogenetic signal of the extent of hybridization in Bayesian phylogenetic analysis following Garamszegi [34]. To assess the robustness of results, we also performed a phylogenetic generalized least-squares analysis (PGLS). All analyses were carried out in R v. 3.5.1 [35].

3. Results

Our comprehensive dataset contained 1011 species from 202 genera within 16 families (figure 1). In this dataset, there

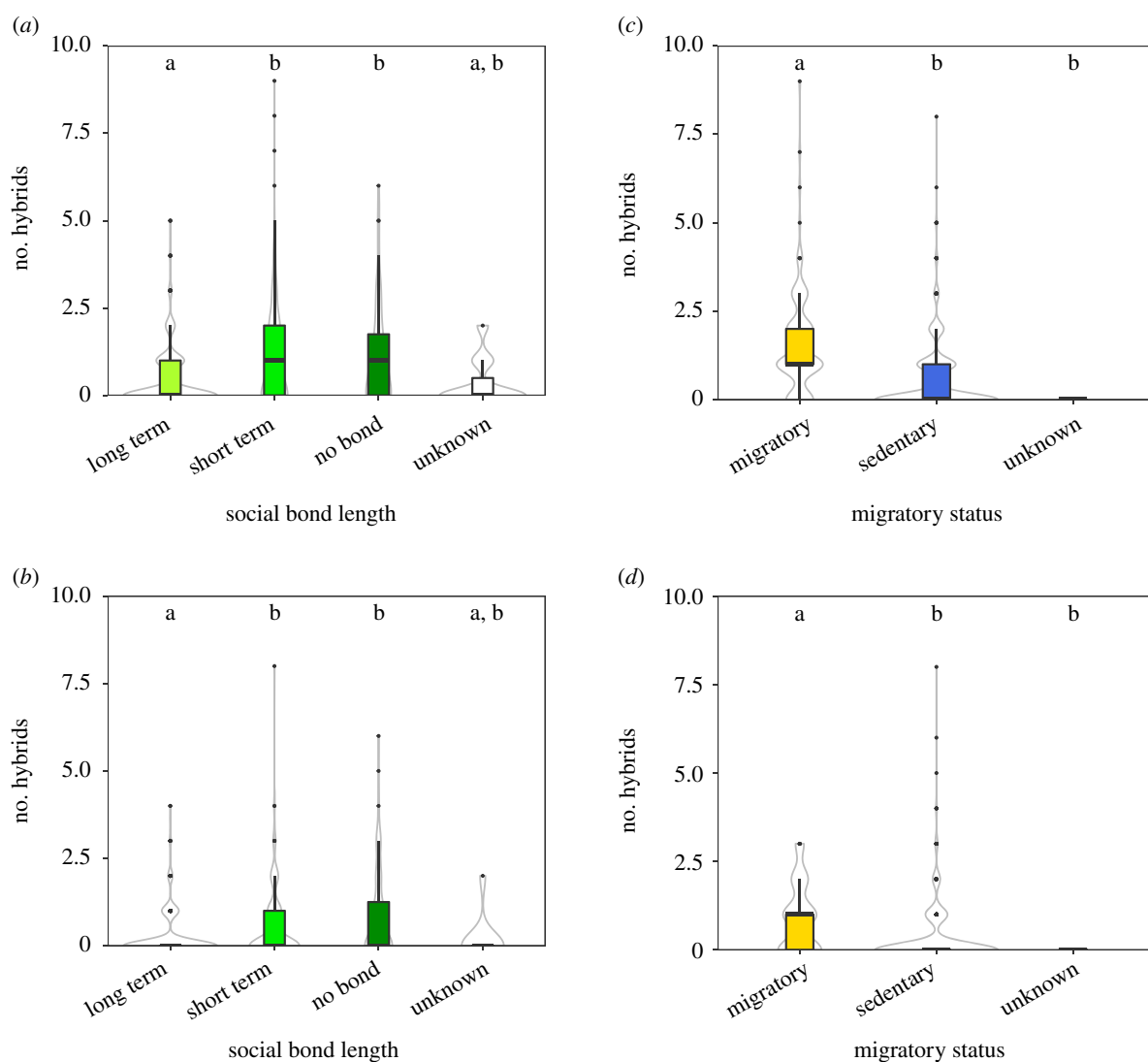


Figure 2. Hybridization is lower in species with long-term social bonds (*a,b*) and those with sedentary life histories (*c,d*). Boxplots, overlaying grey violin plots and coloured to match phylogenetic information in figure 1, indicate patterns of hybridization for the comprehensive (*a,c*) and an example conservative (*b,d*) dataset. Lower case letters in each plot represent significant differences among groups. (Online version in colour.)

were 392 total species that were classified as producing hybrids. In the full, comprehensive dataset, the mean number of hybrids per species was 0.66 species and the median number of hybrids per species was 0 (though unequally spread across families; electronic supplementary material, figure S1). The median phylogenetic signal (D) for the presence of hybridization was 0.47. Additionally, the median phylogenetic signal for the extent of hybridization was 0.45, indicating an intermediate phylogenetic signal of hybridization in our dataset. Our conservative datasets contained between 820 and 843 species (median = 831 species) from 16 families. The DIC preferred final models that we report values for in electronic supplementary material, tables S1 and S2. For all models, the acceptance ratio during analysis was between 0.4 and 0.99. For all models, our median Gelman–Rubin criterion values were near 1.000 (electronic supplementary material, table S3 and figure S2).

In the comprehensive dataset, we found that the length of social bonds was significantly associated with the presence of hybridization across species (all p -values < 0.05; figure 2*a*). Species with long-term social bonds are less likely to hybridize than either species with short-term social bonds (median p -value = 0.039) or species with no social bonds (median p -value = 0.003, electronic supplementary material, table S3).

In addition to social bonds, we found that sedentary species are less likely to hybridize than species that are migratory (median p -value = 0.002; electronic supplementary material, table S3). Two other variables had significant effects but only because of species for which these variables were ambiguous or not present. Species with unclear migration patterns (median p -value = 0.002) and unclear habitat (median p -value = 0.005) significantly affected the presence of hybridization, though we suspect these effects are due to a small sample size and biased estimates. After removing the species with unknown values for independent variables, we found similar qualitative results. Specifically, migratory species are more likely to hybridize and species with long-term social bonds are less likely to hybridize (electronic supplementary material, table S4).

In the sub-analysis on the presence of hybridization that includes research effort, we retained the significant predictors and found that in addition to social bonds and migratory status, research effort is also a significant predictor of hybridization (median p -value = 0.003, range = 0.001–0.01). Species that have been subject to more studies also are more likely to be observed to hybridize (electronic supplementary material, table S5).

Our analysis of the conservative dataset found qualitatively similar results as the full analysis and sub-analyses on

the presence of hybridization (electronic supplementary material, table S6). In the analysis across shuffled, conservative datasets sedentary species had a reduced likelihood of hybridization (median p -value = 0.002); species with short-term social bonds (median p -value = 0.03) or no social bonds (median p -value = 0.017) had a higher likelihood of hybridization compared to species with long-term social bonds. Across all models on the presence of hybridization, no other variables consistently predicted the presence or absence of hybridization.

In terms of transitioning between the presence and absence of hybridization, we found that the transition rate from absence to presence (Q_{12}) was 0.053, and the transition rate from presence to absence (Q_{21}) was 0.101 (electronic supplementary material, figure S3). Models with different rates were preferred by AICc comparisons. Δ AICc (ARD – ER) was between –47.1 and –9.2, with a median of –24.6. Hybridization is therefore lost more readily than it is gained.

In our analysis of the comprehensive dataset that focused on the extent of hybridization, only social bond length influenced the number of species a focal species hybridized with (figure 2c; electronic supplementary material, table S7). Species with long-term bonds had significantly fewer hybrids than species with no bonds (median p -value = 0.04). Species with long-term bonds had fewer hybrids but not significantly less than species with short-term bonds (median p -value = 0.06). No other variables, including research effort in the sub-analysis, predicted the extent of hybridization (all p -values > 0.05).

To test the pseudo-null-hypothesis that the number of hybrids a species produces is simply a by-product of the number of closely related species, we examined if the number of species in the focal species' genus predicts the number of hybrids produced by the focal species. We found no evidence of such an association (larger dataset values: median p -value = 0.84, range of p -values = 0.59–0.99; electronic supplementary material, figure S4), suggesting that hybridization is not consistently driven by congeneric species richness.

4. Discussion

Species with long-term social bonds and that are sedentary are less likely to hybridize than species that are migratory or those with shorter social bonds; species with no social bonds are more likely to hybridize with more species. What drives the associations between hybridization and these traits? In the case of social bonds, many species with long-term social bonds are species where individuals pair for multiple breeding seasons (or for life). Individuals in these species may suffer especially high fitness costs if they pair with a heterospecific. For example, individuals that pair with a heterospecific in a long-term bond may have to invest extra energy and behaviour in forming another pair bond if one of the two individuals abandons the pair. As a result, increased selection for conspecific recognition in species with long-term social bonds is likely.

In the case of migration, reduced hybridization in sedentary species may be explained by differences among species in mate assessment and temporal constraints. Sedentary species may have extended periods of mate searching and pair formation. Longer periods of pair formation may allow

individuals to more accurately assess potential partners, and consequently reduce the likelihood of hybridization. Indeed, a recent genomic study [36] dovetails with the results presented here; specifically, among eight trans-Beringian lineages, species with low levels of migration showed especially low admixture. Consequently, our results suggest the results of McLaughlin *et al.* [36] may be relevant across the avian phylogeny.

In addition to social bonds and migration, research effort also results in a higher likelihood of observing hybridization in a species. While the main effects remain significant predictors of the presence of hybridization, our results suggest that comparative studies on birds, and potentially other taxa, should often include research effort when performing large-scale macroevolutionary analysis. Including analyses or sub-analyses with research effort will help instill confidence that findings are true biological effects. To facilitate including research effort as a predictor variable in future comparative analyses, developing research methods that automate the search of scientific databases would be highly valuable.

There are several challenges about viewing hybridization as a phenotypic trait that can be reconstructed in a phylogenetic comparative framework. First, multiple assumptions contribute to viewing hybridization as a trait that can be estimated on a phylogeny. One notable assumption we make is that the number of species with which a given focal species forms hybrids is a reasonable indicator of the overall likelihood of hybridization. However, other studies have also used simple species counts to infer the extent of biological phenomena. For instance, simple species counts of predators have been associated with avian longevity across a large set of bird species [37]. We are also concerned with confidence in the species that are labelled as having no hybrids reported. The lack of hybrids could be due to a real effect of low hybridization, or alternatively could be due to a relative lack of study effort compared to other species in the database. However, many of the main effects emerge as trends through all large bird families (electronic supplementary material, figures S5 and S6), including families that have received more study (e.g. Corvidae and Picidae). Assessing changes in the presence of hybridization is conceptually challenging as traits associated with species recognition will dictate the presence of hybridization. However, assessing the presence or absence of hybridization as an indirect trait still provides useful insight. Finally, hybridization as a trait is a consequence of other interacting traits. Sensory systems and choosiness are going to contribute to individual decisions about mating. Consequently, hybridization behaviour is a result of other traits and is therefore an indirect view of the evolutionary history of other traits.

Macroevolution of hybridization in birds is associated with species-specific traits; specifically, longer social bonds are associated with reduced extent and presence of hybridization whereas migration is associated with the increased presence of hybridization. The results suggest that conspecific recognition systems may undergo selection as a consequence of the specific ecology or life history of a species. We suggest that the study of these traits and their effects on hybridization warrants further study to better determine the mechanisms that link these traits over evolutionary time. Our results also bear on recent biological literature that uses hybrid zones to understand speciation and adaptation. If certain species show a higher extent of hybridization due to life history and ecology, and these species are used to understand evolution, it is possible

that evolutionary inferences from hybridizing species are incomplete. Consequently, research on speciation and adaptation focusing on species that are sedentary, or with longer social bonds, or both, will yield important comparative insight to better understand the generality of insights from previous studies on speciation and adaptation.

Ethics. No research was performed on live animals.

Data accessibility. Data and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.905qfthz> [38].

Authors' contributions. G.M.L. and R.A.L. conceived the study. All authors collected data. G.M.L. performed analyses. All authors contributed to manuscript preparation.

Competing interests. The authors declare no competing interests.

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