Biogeography predicts macro-evolutionary patterning of gestural display complexity in a passerine family

Meredith C. Miles,[1] Samantha Cheng,[2] and Matthew J. Fuxjager[1,3]

[1]*Department of Biology, Wake Forest University, Winston-Salem, North Carolina 27109*

[2]*National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, California 93106*

[3]*E-mail: mfoxhunter@gmail.com*

Gestural displays are incorporated into the signaling repertoire of numerous animal species. These displays range from complex signals that involve impressive and challenging maneuvers, to simpler displays or no gesture at all. The factors that drive this evolution remain largely unclear, and we therefore investigate this issue in New World blackbirds by testing how factors related to a species' geographical distribution and social mating system predict macro-evolutionary patterns of display elaboration. We report that species inhabiting temperate regions produce more complex displays than species living in tropical regions, and we attribute this to (i) ecological factors that increase the competitiveness of the social environment in temperate regions, and (ii) different evolutionary and geological contexts under which species in temperate and tropical regions evolved. Meanwhile, we find no evidence that social mating system predicts species differences in display complexity, which is consistent with the idea that gestural displays evolve independently of social mating system. Together, these results offer some of the first insight into the role played by geographic factors and evolutionary context in the evolution of the remarkable physical displays of birds and other vertebrates.

Sexual selection is responsible for the relatively fast evolution of a wide range of animal structures and behaviors (Andersson 1994). Sexual signals produced by male animals to secure a mate can manifest across any type of sensory cue—visual, auditory, olfactory, tactile, etc.—so long as the signal is detectable to the receiver. Signal evolution theory predicts that sexual selection favors the production of displays that are detected over ambient signaling "noise" (Guilford and Dawkins 1991). In this way, increasing signal complexity by adding additional display components or modes increases the probability that the signal will convey appropriate information to the receiver (Girard et al. 2015; Uetz et al. 2009). Despite the well-established significance of alternative signal modes to behavioral evolution, little is known about the macro-evolutionary drivers of complexity in multimodal signals.

Among the many signaling modes are gestural displays: visual (or sometimes acoustic) signals produced through movement of the body and appendages to aid in both competition with rivals and courtship of potential mates (Byers et al. 2010; Fuxjager and Schlinger 2015). They run the gamut of complexity, from elaborate displays of motor skill that integrate multiple body regions (Vliet 1989; Fusani et al. 2007) to rudimentary displays that incorporate only basic limb movements (Walls and Semlitsch 1991). Species in nearly every major animal group employ gestural displays for signaling, including arthropods (Girard et al. 2011), teleosts (Masonjones and Lewis 1996), crocodilians (Vliet 1989), amphibians (Grafe et al. 2012; Walls and Semlitsch 1991), squamates (Ord et al. 2001), mammals (Voigt et al. 2001), and birds (Vehrencamp et al. 1989). However, despite the near ubiquity of gestural displays in animals, ultimate factors contributing to their evolution remain elusive.

The evolutionary context set by biogeography is one factor that can shape variable patterns of selection in the evolution

of complex displays. Different biogeographic zones exhibit different macro-evolutionary patterns: while species richness is remarkably high in the tropics, rates of phenotypic evolution are greater at temperate latitudes (Chek et al. 2003; Weir and Schluter 2007). Among the potential mechanisms for this pattern are climate-derived ecological variables. For example, seasonal and climatic differences between tropical and temperate zones are connected with latitudinal differences in nest predation (Skutch 1985) and concurrent life-history changes such as longer life span, reduced rate of biparental care, and smaller clutch size (Martin 2000). Meanwhile, species inhabiting temperate zones will undergo more intense sexual selection based on a shorter breeding season (Stutchbury and Morton 2008), a condition that favors elaboration of displays (West-Eberhard 1983).

Hemispheric differences in signal complexity can also be predicted by factors beyond ecological changes associated with species richness and breeding season length. For example, color complexity increases with latitude in bird plumage, a trend that is attributed to historic instances of fast and repeated allopatry and secondary contact (Martin et al. 2010). Geological events such as orogeny, fluvial action, and glaciation can serve as mechanisms for geographic isolation of animal populations (e.g., Boubli et al. 2015; Gascon et al. 2000; Toussaint et al. 2014). Of these, Martin et al. (2010) implicate glacial advance and retreat driven by Milankovitch climate oscillations (Imbrie et al. 1993) as the primary driver of tropical-temperate differences in plumage. These 100,000-year cycles affect temperate species more strongly than tropical ones (Dynesius and Jansson 2000) and can facilitate faster evolution of complex displays at high latitudes by repeatedly forcing secondary contact between partially differentiated populations, resulting in greater signal divergence (Martin et al. 2010). During the cooling portion of the Milankovitch cycle, glacial advance acts as the isolating agent that allows both male traits and female preferences to differentially evolve between populations enough to be preserved and exaggerated upon secondary contact following warming and glacial retreat (Servedio 2007, 2016). Meanwhile, trait divergence will be comparatively depressed in tropical sympatric populations undergoing milder effects of Milankovitch oscillations, as the effects of Fisherian sexual selection alone in sympatric populations suppress trait divergence (Arnegard and Kondrashov 2004; Servedio and Burger 2014). However, plumage coloration is a static signal and not a behavioral display, and thus it is unknown if this evolutionary pattern is similar in regard to behavioral traits, like gestural display. We do know that the evolution of complex gestural displays reflects modern range overlap in lizard sister species (Ord et al. 2004), but no existing studies test the evolution of gestural display complexity on a large biogeographic scale.

Beyond biogeography, social factors such as mating system may also drive the evolution of male signal complexity. The effect of social mating system (monogamy, polygyny, etc.) is most obvious in lekking species, where an extreme polygynous mating system has driven remarkable elaboration of multimodal signals that include gesture (Vehrencamp et al. 1989; Prum 1994). However, the tendency for polygynous animals to evolve complex signals outside the context of a lek is also observable (Ord et al. 2001; Price and Whalen 2009). In many species, competition between males will be for access to females or a desirable territory, and this effect is considered to be a major driver of male-biased sexual size dimorphism resulting in the evolution of diverse gestural signals (Ord and Martins 2006). Yet, the connection between mating system and display complexity has yet to be investigated in any animal group.

To understand the macro-evolutionary drivers of display complexity, we must also consider the nature of signal complexity itself (i.e., the difficulty of producing a given signal). Sexual selection by female choice for complex displays is certainly a major driver for signal evolution in diverse animal groups (e.g., Catchpole 1980; Thresher and Moyer 1983), but complexity can manifest differently across species and signal modes. This is because sexual signals are shaped by sexual selection and constrained by natural selection (Endler 1980), which results in a wide range of possible signals for any given purpose. For example, intrasexual selection drives the evolution of display complexity in lizards, but larger species exhibit reduced signal repertoires as constrained by diet and physiology (Ord and Blumstein 2002). Signal complexity can also be inherently difficult to characterize, as the performative difficulty of a display can be increased in several ways, including: (i) adding additional behaviors or modes to the display repertoire (Ord and Blumstein 2002), (ii) exaggerating preexisting behaviors to enhance their visibility or distinctiveness (Galván 2008), (iii) altering the temporal/spatial patterning of display production (Ord and Martin 2006), (iv) changing the degree of coordination between display modes (Cooper and Goller 2004), and (v) performance of more physically challenging displays to demonstrate motor skill (Byers et al. 2010). Of these five indices of signal complexity, counting the distinct displays that comprise a species' repertoire is both a robust and realistic method for assessing evolutionary trends in display complexity across a large phylogeny (Ord and Blumstein 2002; Ord and Martin 2006).

The New World blackbirds (Family: Icteridae) are an excellent example of an animal group that has evolved a broad spectrum of gestural display complexity, typically combined with other signal modes (Jaramillo and Burke 1999). Examples of individual gestures in this group, including complex flight (Mather and Robertson 1992) and postural displays (Howell and Bartholomew 1952) that incorporate different combinations of head, tail, and wing movement, as well as selective feather ruffing (Price 2004). However, there are also some species in this group that perform much simpler displays, or that dispense with gesture altogether.

As in other birds, a male blackbird's display will combine varying degrees of plumage ornamentation, vocalizations, and gestures to serve in either male–male competition over resources or eligible females, and courtship of females (Berglund 1996).

Furthermore, since their origin in North America some 11 million years ago (Barker et al. 2012), blackbirds have spread as far north as Alaska and deep into South America (Jaramillo and Burke 1999). Along with their extensive range, Icterid social structures, and mating systems are diverse, encompassing both polygynous and monogamous mating systems as well as more variable social structures (Price 2009). The family also exhibits great geographic diversity in social behaviors; in the tropics, for example, there are species in which females perform song facultatively or as part of a duet with a social mate (Odom et al. 2015), and yet others that form impressive woven-nest colonies with intricate social hierarchies (Robinson 1985). Together, the high variation of display in blackbirds, combined with variable ecological factors including mating systems, intensity of sexual selection, and home range, make it an excellent group for studying the factors that drive evolution of gestural displays.

In this study, we tested the degree to which geographic and social factors drive the evolution of gesture in the Icteridae. Based on the frameworks described in the paragraphs above, we predict that (i) temperate species will produce more complex displays than their tropical counterparts, and (ii) species with a polygynous mating system will have higher display complexity than monogamous species. To address these questions, we computed gestural display complexity on not only a body-wide scale, but also in specific body regions or appendages. We then examined how this variation is patterned across a broad biogeographic scale and between social mating systems.

Methods

DISPLAY COMPLEXITY SCORES

We assessed gestural display in blackbird species largely based on descriptions by Jaramillo and Burke (1999), but included updated information on a variety of taxa (Fraga 2005; Rodriguez-Ferraro 2006; Grilli et al. 2012). In this study, we considered gestural displays used for courtship, reproductive competition, or both, and we focused exclusively on male displays. While some female blackbird species do in fact perform adaptive signals (Price et al. 2009), the extent to which female gestural displays occur in the family remains unknown (Jaramillo and Burke 1999).

To characterize displays, we quantified the total complexity of a species' physical display repertoire using a numerical scoring system outlined previously (Fuxjager et al. 2015; Lindsay et al. 2015), where display complexity is defined as the number of discrete physical outputs incorporated into the species' gestural display repertoire. Using this system, scores on a display complexity index enable comparison of the behavior among species, because they quantified the number of discrete physical maneuvers produced within a species' given display repertoire.

Note, however, that this approach does not allow for a qualitative comparison of displays (i.e., comparing the physical descriptions of different display movements). Not all discrete gestures are equally challenging to perform, and thus there is variation in complexity between each gesture. However, there is insufficient information detailing this aspect of display across our phylogeny, and because of this, we do not employ a qualitative analysis of display behavior in this study. Instead, we focus on an index of complexity that emphasizes the significance of employing multiple distinct gestures that comprise a single display.

We computed display complexity scores by assigning each species a single point for each discrete and unique physical maneuver they incorporated into their physical display routine. Thus, 1 point was awarded if the gesture was present, and no point was awarded if not. If there was insufficient information about a species' physical display repertoire available in the literature (Fraga 2005; Grilli et al. 2012; Jaramillo and Burke 1999; Rodriguez-Ferraro 2005), we removed that species from the analysis; in this way, we only included species in which the physical display repertoire is recorded in detail and published ($n = 83$ species included out of 111 total).

As we generated a list of display characters and combined information from multiple sources (Table 1S), we carefully avoided double-counting maneuvers in which the same behavior had been assigned different names by different researchers. The criterion for determining whether two gestures were discrete was whether they reflected a unique kinematic output. For example, tail flicks produced when an animal is stationary represent a different maneuver than tail flicks produced while flying, because the kinematic operation and aesthetic production of this behavior are unrelated. We also considered movements such as cocking the tail and fanning the tail's feathers to be discrete, as they can be produced independently of each other. In the supplemental materials, we include a complete list of the discrete behaviors used in the display complexity framework (Table 1S), as well as each species score within this framework (Table 2S) (further definitions and descriptions of the various gestural maneuvers are provided by Jaramillo and Burke (1999).

Based on this framework, we assigned each species a score on five separate indices encompassing total complexity and complexity of specific body regions (Table 3S). To compute scores, we summed all the points relative to a specific index; higher scores always reflect greater levels of complexity, whereas lower scores always reflect lower levels of complexity (Fig. 1, Table 2S). Notably, some species have total display complexity scores that are greater than the summed scores of the four included body region indices: wing movement, head movement, tail movement,
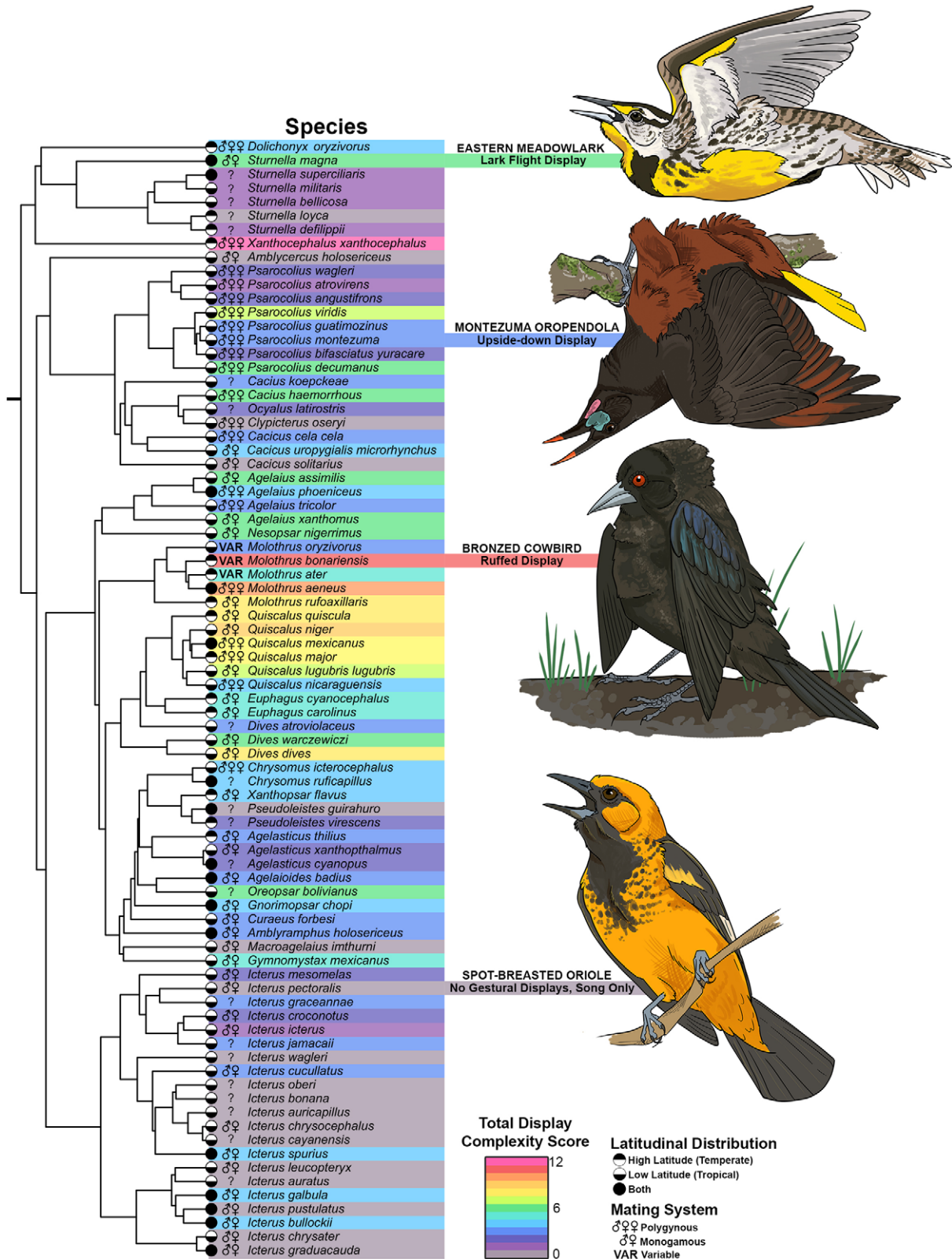
Figure 1. Phylogeny of the New World blackbird family highlighting species included in the analyses, from Powell et al. (2004). At each species' node in the phylogeny is its hemispheric designation, mating system, and name; display complexity score is denoted by the colored bar behind this information. Highlighted are examples of family members that represent a broad range of display complexity scores, as well as geographic distributions and mating systems.

and body movement. This is because other display maneuvers—particularly those that require leg movement—were incorporated into the total display complexity index, but were not assigned to their own index due to insufficient presence across species.

An individual blind to the hypotheses examined herein computed all display complexity scores. A second individual, similarly blind to the study, computed index scores in a subset of the species to verify that the method is repeatable across researchers; the scores obtained by these two individuals were highly correlated ($r^2 = 0.99$, $t = 14.4$, $P < 0.001$).

DATA COLLECTION

We determined latitudinal distribution and social mating system of each New World blackbird species (Fig. 1) based on data obtained from previously published literature (Jaramillo and Burke 1999; Price 2009). For latitudinal distribution, we employed a scheme that has been used previously with great success to delineate species inhabiting temperate and tropical climates (Goymann et al. 2004; Macedo et al. 2008; Reif and Štěpánková 2016). Namely, we examined each species' geographic range described in Jaramillo and Burke (1999), and we then assigned it to one of the three following categories: (i) high latitude (temperate) inhabitant, (ii) low latitude (tropical) inhabitant, or (iii) both high and low latitude (temperate and tropical) inhabitant. Temperate inhabitants were considered species with a range exclusively above the Tropic of Cancer (23.5°N), whereas low latitude (tropical) inhabitants were considered species whose range was exclusively in-between these latitudes. Species labeled as being both temperate and tropical had a range spanning across either of these latitudinal boundaries, or that had ranges spanning from the tropical regions into the austral temperate zone (i.e., south of Tropic of Capricorn (23.5°S). Notably, there are no blackbird species that are exclusive inhabitants of the austral temperate region, and thus this was not a factor considered in our study.

Next, we followed the scoring scheme of Price (2009) to characterize each species' social mating system as either monogamous or polygynous. We considered socially monogamous species to be those in which only one male and one female engage in a mating relationship that persists across the breeding season, whereas we considered socially polygynous species to be those in which males actively mate with more than one female concurrently during the breeding season. While there are some species with fluid mating systems that depend on local habitat or adult sex ratio, the number of species in this category with a sufficiently described gestural display repertoire was too small to merit inclusion in our analysis ($n = 3$). After Price (2009), we did not consider extra-pair mating in these scores, because this information is not available in most blackbird species.

STATISTICAL ANALYSES

In comparative analyses, nonindependence of data due to common ancestry among taxa can confound results (Felsenstein 1985). To avoid this pitfall, we used one-way phylogenetic ANOVA (Garland et al. 1993) to examine whether display complexity scores differed according to species variation in latitudinal distribution or social mating system. This approach was most suitable to our data set because it allowed us to compare a continuous-dependent variable (scores on a display complexity index) between unordered, categorical independent variables (geographic region and mating system). Accordingly, for each of these independent variables, we ran a total of five separate ANOVAs that each used a different display complexity score as the dependent variable. Models with the same independent variable were considered to be in the same family, and thus inflation of alpha within each family was controlled using false discovery rate (FDR) procedures (Benjamini and Hochberg 1995; Pike 2001); as such, we report FDR-adjusted p-values for each test. All significant ANOVA models were followed by phylogenetic posthoc comparisons, in which Holm-Bonferroni methodology was used to control for multiple contrasts. Statistics were calculated in R Studio (version 0.98) using the phytools package (Revell et al. 2012 in Geiger (Harmon et al. 2008) and ape (Paradis et al. 2004).

All statistical analyses were based on a phylogenetic tree published elsewhere (Fig. 1) (Powell et al. 2014). This represents the most recent and comprehensive estimation of relatedness among New World blackbirds. If information regarding a species' distribution or social mating system was equivocal or unknown, we dropped the species from any analyses that incorporated the independent variable in question. As such, our results are based only on species for which there is accurate data regarding distribution and reproductive behavior.

Results

Complexity scores vary substantially among many New World blackbirds (Fig. 1, Table S2). Some species, such as the bronzed cowbird (*Molothrus aeneus*) produce complex displays that incorporate movements across multiple body regions. By contrast, other species perform no gestures at all, including many species of *Icterus* orioles (Fig. 1).

Display complexity scores significantly differed among species based on their latitudinal distribution. This effect was present with respect to measures of total complexity (Fig 2A; $F_{2,79} = 5.87$, $P = 0.016$), wing movement complexity (Fig. 2B; $F_{2,79} = 6.14$, $P = 0.016$) and head movement complexity (Fig. 2C; $F_{2,79} = 4.72$, $P = 0.016$), with a marginally nonsignificant effect in tail movement complexity (Fig. 2D; $F_{2,79} = 3.28$, $P = 0.078$). In all three of these models, species living in high-latitude (temperate) regions produce displays that are more complex than those
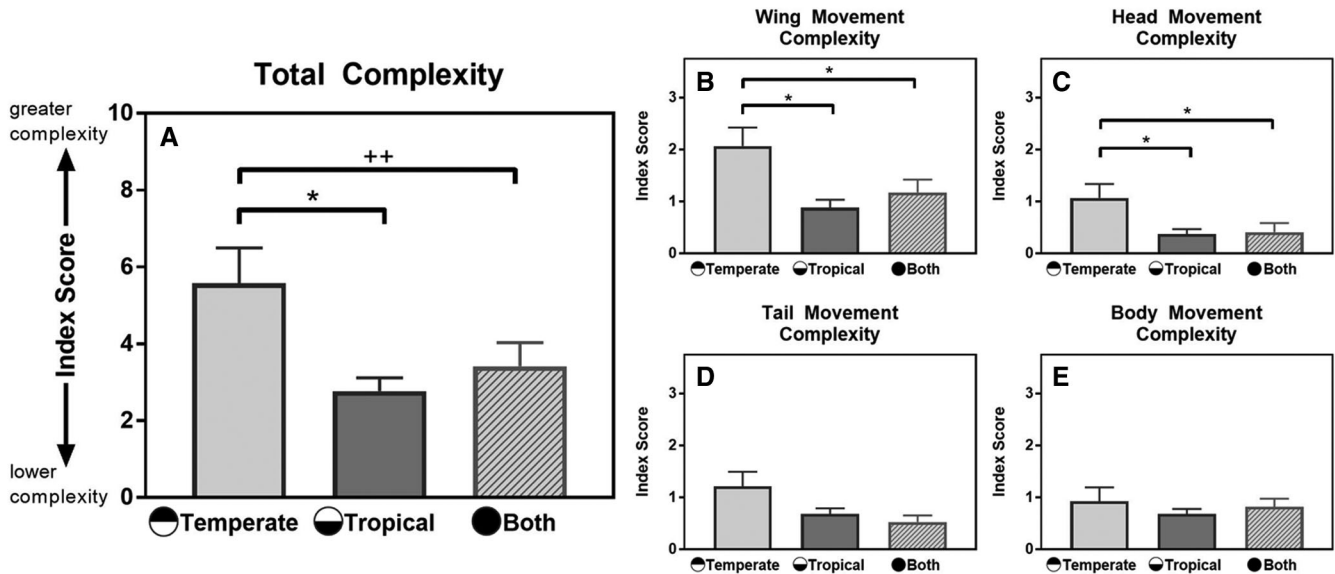
Figure 2. Differences in gestural display complexity as a function of latitudinal distribution (temperate vs tropical range). On all indices, higher scores reflect more complex gestural displays. Data are presented as the mean index score, and error bars represent 1 SEM. Asterisks (*) indicate significant differences indicated by posthoc tests (*P* < 0.05). Double plus signs (++) indicate marginally nonsignificant differences (total complexity: *P* = 0.068).

species living in low-latitude (tropical) regions, as demonstrated by posthoc analyses (total complexity: $P = 0.009$; wing movement complexity: $P = 0.015$; head movement complexity: $P = 0.024$). Wing movement complexity and head movement complexity also differed between exclusively temperate species and species with ranges spanning both high and low latitudes (wing movement, $P = 0.040$; head movement, $P = 0.032$), while there were only marginally significant differences in post hoc effects between these two groups in models for total complexity ($P = 0.068$). Finally, we found no effect of latitudinal distribution on the complexity of either tail movements (Fig. 2D; $F_{2,79} = 3.29$, $P = 0.078$) or body movements (Fig. 2E; $F_{2,79} = 0.72$, $P = 0.55$).

We found no evidence that social mating system predicted display complexity (Fig. 3). This occurred for all measures: total display complexity (Fig. 3A; $F_{2,55} = 1.34$, $P = 0.31$), wing movement complexity (Fig. 3B; $F_{2,55} = 2.05$, $P = 0.18$), head movement complexity (Fig. 3C; $F_{2,55} = 0.59$, $P = 0.47$), tail movement complexity (Fig. 3D; $F_{2,55} = 0.0099$, $P = 0.92$), and body movement complexity (Fig. 3E; $F_{2,55} = 1.71$, $P = 0.23$). These nonsignificant relationships are not solely due to a lack of statistical power resulting from being restricted to the subset of species for which there exists clear social mating system data. We determined this by rerunning our latitudinal distribution model, but only on this subset of species. Among the taxa for which we do have positive identification of the mating system, we still found that latitudinal distribution predicted display complexity in the same way as our original model that was based on all the

species within our phylogeny ($F_{2,55} = 4.19$, $P = 0.034$). Because of this we can conclude that there is enough statistical power in our models to assess effects of social mating system on display complexity measures, even though these models are restricted to a subset of species included in the entire phylogeny.

Discussion

We found that latitudinal distribution is a predictor of gestural display complexity in New World blackbirds: species that live at temperate latitudes produce displays that are significantly more complex, compared to their tropical counterparts. This geographic difference in male sexual display likely stems from a range of ecological and evolutionary variables, which differentially affect populations living in these two dissimilar biogeographic regions. Interestingly, we detected this latitudinal effect not only in overall complexity, but also in complexity of two isolated body regions: wing and head. By contrast, we did not detect any association between display complexity and social mating system, which implies that complex gestural routines are equally likely to evolve in socially monogamous and polygynous species. Taken together, these findings suggest that a strong evolutionary driver for display complexity is present in North American temperate regions, but is weaker or missing in the Neotropics. This work therefore collectively establishes a novel framework for discussing the evolutionary contexts in which complex physical gestures will—or will not—emerge or change over time.
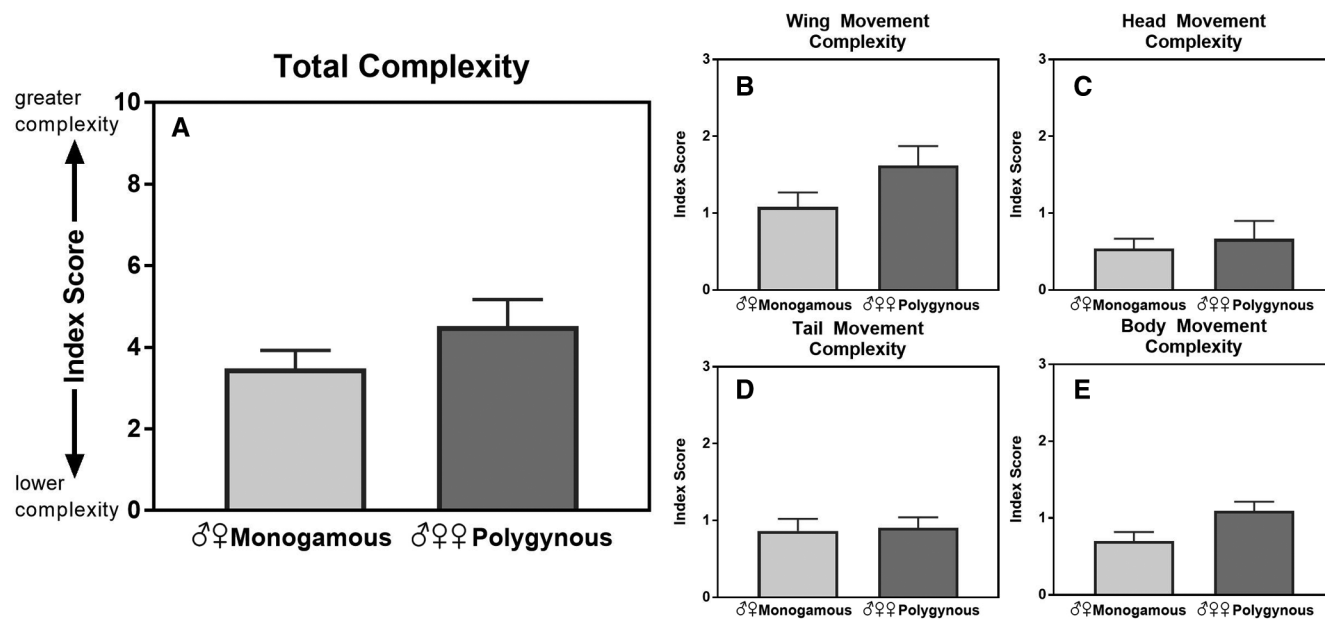
Figure 3. Differences in gestural display complexity as a function of social mating system (monogamous or polygynous). Species with variable mating systems were removed from the analysis due to low sample size ($n = 3$). On all indices, higher scores reflect more complex gestural displays. Data are presented as the mean index score, and error bars represent 1 SEM.

GEOGRAPHIC FACTORS DRIVING SEXUAL SELECTION PRESSURE AT HIGH LATITUDES

For temperate species, breeding is restricted to the high-productivity summer, when there is sufficient food and warmth to successfully raise offspring, and this temporal resource clumping favors the evolution of more complex displays due to higher sexual selection pressure (Emlen and Oring 1977). Indeed, species inhabiting high latitudes produced gestural displays that were more complex than those living in the tropics, a phenomenon that we primarily attribute to variation in breeding context across temperate and tropical habitats. The relatively brief boreal summer offers a short but high-productivity breeding period that animals must exploit efficiently to successfully rear offspring (Robinson et al. 2010). In accordance with sexual selection theory, limited breeding season resources will increase the intensity of intrasexual competition, which is a major factor implicated in driving species to evolve complex signals used to navigate aggressive interactions between males (Ord and Blumstein 2001). This is because a more complex signal that integrates multiple movements allows for a reduction in decision errors on the part of the signal receiver (Guilford and Dawkins 1991); thus, the short breeding season may necessitate efficient mate selection by female receivers, and increasing display complexity by adding more gestures may be one way to accomplish this (Ord and Blumstein 2001; Ord and Martins 2006).

The tropical-temperate divide in breeding seasonality affects complex phenotypes beyond behavior, such as life history and physiology. In addition to a shorter breeding season, temperate species display a larger average clutch size (Skutch 1985), higher basal metabolic rate (Londoño et al. 2014), and higher circulating steroid hormone levels (Goymann et al. 2004). By contrast, tropical species exhibit a "slow pace of life" (Wiersma et al. 2007) that has been connected to seasonality, resource availability, and increased rate of predation on eggs and chicks. Taken together, this wide range of life-history traits all connected with breeding season length and intensity lend credence to our idea that latitude drives gestural display complexity among species. These conditions set up a competitive environment not only favoring great display complexity, as shown here, but also an increased degree of sexual size dimorphism (Payne 1984) and the rise of polygynous social mating strategies (Emlen and Oring 1977).

GEOLOGIC CONTEXT OF EVOLUTION IN DIFFERENT HEMISPHERES

Our observed increase in gestural display complexity in high latitude species may also be driven by geological factors that repeatedly forced populations through predictable phases of allopatry and secondary contact. This idea was proposed by Martin et al. (2010) to explain an increase in plumage color complexity with increasing latitude, which was otherwise not observed after controlling for sympatry. Because gestural displays can serve to accentuate plumage (Galván 2008), it is possible that color and gesture are subject to similar patterns of selection.

In the absence of periodic geographic isolation, sexual selection alone is typically insufficient to generate necessary trait divergence in male signals to result in the high complexity of displays

we observe in temperate blackbird species today (Fitzpatrick et al. 2009; Servedio 2016). Therefore, a difference in the degree of temporary geographic isolation of blackbird populations at temperate and tropical latitudes may have facilitated the evolution of novel gestures, thereby increasing overall gestural complexity. One mechanism for this is 100,000-year Milankovitch climate cycles that differentially affect high and low latitudes; the cold extremes affect temperate zones more than the tropics (Dynesius and Jansson 2000). Periods of glacial advance, for example, may separate populations long enough to produce sufficient trait divergence for speciation, so that upon secondary contact, the effects of assortative mating and trait preference are sufficient to preserve behavioral differences between populations (Servedio 2016). These differences may have been exaggerated due to postzygotic complications associated with hybridization (Mendelson and Shaw 2012), although the true significance of hybridization to promoting or diminishing divergence between populations remains a subject of debate (Abbott et al. 2013; Servedio et al. 2013).

Although there has been both historic and modern glacial activity in the tropics, this is restricted to only the highest elevations in the Andes (Vuille et al. 2008) and would be unlikely to cause the same pattern of repeated secondary contact thought to have occurred at higher latitudes. Moreover, the Andean orogeny itself is responsible for novel patterns of avian diversity (e.g., Chaves et al. 2011), but this likely did not affect our analysis—most Icterids inhabit broad and low elevational ranges, with very few species at exclusively montane elevations (three species of 102 in our analysis).

SOCIAL MATING SYSTEM AND THE EVOLUTION OF GESTURAL DISPLAY

Our data support the idea that mating system is not a driver of gestural display complexity in New World blackbirds, either in overall complexity or when divided into individual body regions. Because they have evolved a wide array of mating systems, the New World blackbirds provide the testable variation in mating system necessary to determine what role, if any, mating system plays in the evolution of complex gestural displays. Our data, however, are consistent with the idea that pressures other than mating system drive the evolution of gestural displays.

In some groups, the evolution of polygyny (or the loss of monogamy) possibly preceded the evolution of gestural display; this is especially visible in manakins (Pipridae), an exclusively Neotropical passerine family in which males perform elaborate dances on display grounds (Prum 1994). However, it is impossible to test for the effect of mating system on display complexity in manakins, as the family is almost completely polygynous and thus does not offer testable variation in mating system. It is possible that in New World blackbirds, polygynous mating systems do drive display elaboration, but in modes separate from gesture.

Polygynous oropendolas, for example, have evolved contrasting plumage patches more quickly than the closely related monogamous caciques (Price and Whalen 2009). For this reason, it is important to investigate factors shaping all aspects of multimodal display both combined and separately.

GESTURE AS ONE FACET OF MULTIMODAL DISPLAY

Here we present a novel approach for characterizing and assessing gestural displays in birds. In any study of animal signaling, it is important to consider the entire signaling scope of a species. In birds, sexual and aggressive signaling is largely multimodal: most species will combine some mix of song, gesture, and ornamentation. Some species like bowerbirds even incorporate environmental modification into their display (Borgia 1995). More recently, it has become apparent that some bird species even use olfaction—once thought to be entirely unimportant to birds—as a signaling mode, as in the crested auklet (*Aethia cristatella*), which expresses a citrus odor in its crest during the breeding season (Hagelin 2007).

As discussed above, our results demonstrating increased diversity of gestural displays among temperate species are echoed in plumage color as well (Martin et al. 2010). Although sexually selected male color complexity evolves faster at high latitudes, tropical birds of both sexes are more colorful on average than temperate birds (Dale et al. 2015). This apparent discrepancy is easily explained by considering that while both plumage color and gestural display (at least for the most part) serve as visual signals, the fixed nature of body coloration is strongly constrained by natural selection as well as elaborated by sexual selection (Endler 1980). While the precise reason allowing tropical birds to be more colorful remains unclear, the effect can be partially attributed to reduced evolutionary constraint placed on color due to inhabiting a visually cluttered environment (Dale et al. 2015).

Visual cues are not the only sexually selected signals to be preferentially elaborated between biogeographic zones. In oscine passerines, a group that includes the New World blackbirds, the rate of song evolution (estimated by syllable diversity) in temperate species is over 20 times greater than in tropical species (Weir and Wheatcroft 2010). The parallelism of these results suggests that both signal modes are subject to the same selection pressures. However, that is not to say that they necessarily coevolve; one study in Estrildid finches, for example, suggests that song, dance, and plumage ornamentation evolved independently, with each communicating different information about the individual (Soma and Garamszegi 2015).

Adding a novel signaling mode to the display repertoire can also be a potent method of reinforcing conspecific mate preference mechanisms, either by adding redundancies to increase the efficacy of a single message or by encoding different information altogether (Girard et al. 2015). For some species, multimodal

signaling is necessary to ensure appropriate mate choice: in experimentally mixed populations of otherwise-allopatric swordtail fish, females express a directional preference for large males, which results in females from both species consistently choosing to mate with males of the larger species (Ryan and Wagner 1987). However, females also respond to olfactory cues produced by males, and in the presence of olfactory cues alone, they prefer conspecifics (de Caprona and Ryan 1990).

Using different signal modes in mating display can also serve to hone signal efficacy at different distances from the signal receiver. For example, the Bornean rock frog (*Staurois parvus*) and torrent frog (*Micrixalus saxicola*) are both species that breed in an acoustically cluttered environment, surrounded by noisy, fast-moving streams (Preininger et al. 2013). Like other frogs, they use calls as a long-range acoustic signal, but the call is less audible next to the stream. Once a female is visible, the males will produce a foot-flagging gesture as a short-range signal instead (Grafe et al. 2012). Similarly, Icterids and other birds that combine gesture with song could potentially be using gesture as a close-range signal to reinforce or convey more information about individual fitness that is not encoded in song. For example, it is possible that certain gestures are physically challenging to produce either alone or in combination with other display modes, and that female blackbirds evaluate a male's ability to combine acoustic and visual signaling in such a way that gestural signals either facilitate or hinder vocal output (Cooper and Goller 2004).

In New World blackbirds alone, there are grounds on which to expand this work to encompass both song and plumage ornamentation in addition to gestural displays as they relate to phylogeny, biogeography, and social factors. Most blackbirds combine gesture with song (Jaramillo and Burke 1999), and recent research shows that some species synchronize gestural and vocal output so tightly that it is unlikely that the two modes evolved independently (Cooper and Goller 2004). Methods for assessing plumage coloration in birds can be combined with existing knowledge of song, gestural displays, and life-history characteristics to obtain a more complete understanding of the evolutionary pressures that shape and diversify multimodal signals.

Conclusions

In a family that spans across a wide range of New World latitudes, we find that biogeography helps drive the evolution of complex gestural displays used in both courtship and aggression. Species inhabiting the high latitude temperate zone produce more complex displays than low latitude tropical species, a phenomenon potentially driven by multiple mechanisms. One is the greater intensity of intrasexual selection present at high latitudes derived from a short breeding season, an evolutionary context that favors signal elaboration to reduce decision errors made by signal receivers.

Another possibility is repeated cycles of allopatry and secondary contact, which allows ample time for divergence of both male gestural displays and female preference for those displays. Furthermore, we present these results in a heretofore-overlooked mode of sexual and aggressive signaling in animals. This is the first time that the evolution of gestural displays in a bird family has been assessed both geographically and phylogenetically, and provides a methodological framework for future analyses of gestural displays. Understanding what factors drive the evolution of gesture, as well as other components of multimodal displays, will be necessary to develop a cohesive model for the evolution of display behavior in animals, and further study in the system will accelerate our knowledge of the mechanisms by which sexual selection can act to shape biodiversity.

LITERATURE CITED
Abbott, R., D. Albach, S. Ansell, J. W. Arntzen, S. J. Baird, N. Bierne, J. Boughman, A. Brelsford, C. A. Buerkle, R. Buggs, and R. K. Butlin. 2013. Hybridization and speciation. J. Evol. Biol. 26:229–246.

Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton.

Arnegard, M. E., and A. S. Kondrashov. 2004. Sympatric speciation by sexual selection alone is unlikely. Evolution 58:222–237.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. Roy. Stat. Soc. Ser. B. Stat. Method 57:289–300.

Berglund, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biol. J. Linnean Soc. 58:385–399.

Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette. 2012. Going to extremes: contrasting rates of diversification in a recent radiation of New World passerine birds. Syst. Biol. 62:298–320.

Borgia, G. 1995. Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations. Anim. Behav. 49:1291–1301.

Boubli, J. P., C. Ribas, J. W. Lynch Alfaro, M. E. Alfaro, M. N. F. da Silva, G. M. Pinho, and I. P. Farias. 2015. Spatial and temporal patterns of diversification on the Amazon: a test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. Mol. Phylogenet. Evol. 82:400–412.

Byers, J., E. Hebets, and J. Podos. 2010. Female mate choice based upon male motor performance. Anim. Behav. 79:771–778.

Crapon de Caprona, M.D.C. and M. J. Ryan. 1990. Conspecific mate recognition in swordtails, *Xiphophorus nigrensis* and *X. pygmaeus* (Poeciliidae): olfactory and visual cues. Anim. Behav. 39:290–296.

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74:149–165.

Chaves, J.A., J. T. Weir, and T. B. Smith. 2011. Diversification in *Adelomyia* hummingbirds follows Andean uplift. Mol. Ecol. 20:4564–4576.

Cooper, B. G., and F. Goller. 2004. Multimodal signals: enhancement and constraint of song motor patterns by visual display. Science 303:544–546.

Dale, J., C. J. Dey, , K. Delhey, B. Kempenaers, and M. Valcu. 2015. The effects of life history and sexual selection on male and female plumage colouration. Nature 527:367–370.

Emlen, S., and L. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. Evolution 34:76–91.

Felsenstein, J. 1985. Phylogenies and the comparative methods. Am. Nat. 125:1–15.

Fitzpatrick, B. M., J. A. Fordyce, and S. Gravrilets. 2009. Pattern, process and geographic modes of speciation. J. Evol. Biol. 22:2342–2347.

Fusani, L., M. Giordano, L. B. Day, and B. A. Schlinger. 2007. High-speed video analysis reveals individual variability in the courtship displays of male golden-collared manakins. Ethology 113:964–972.

Fuxjager, M. J., J. Eaton, W. R. Lindsay, L. H. Salwiczek, M. A. Rensel, J. Barske, L. Sorenson, L. B. Day, and B. A. Schlinger. 2015. Evolutionary patterns of adaptive acrobatics and physical performance predict expression profiles of androgen receptor—but not oestrogen receptor—in the forelimb musculature. Funct. Ecol. 29:1197–1208.

Fuxjager, M. J., and B. A. Schlinger. 2015. Perspectives on the evolution of animal dancing: a case study of manakins. Curr. Opin. Behav. Sci. 6:7–12.

Galván, I. 2008. The importance of white on black: unmelanized plumage proportion predicts display complexity in birds. Behav. Ecol. Sociobiol. 63:303–311.

Garland, T., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. 42:265–292.

Gascon, C., J. R. Malcolm, J. L. Patton, M. N. F. da Silva, J. P. Bogart, S. C. Lougheed, C. A. M. Peres, S. Neckel, and P. T. Boag. 2000. Riverine barriers and the geographic distribution of Amazonian species. PNAS 97:13672–13677.

Girard, M. B., D. O. Elias, and M. M. Kasumovic. 2015. Female preference for multi-modal courtship: multiple signals are important for male mating success in peacock spiders. Proc. R Soc. B 282:2015222.

Girard, M. B., M. M. Kasumovic, and D. O. Elias. 2011. Multi-modal courtship in the peacock spider, *Maratus volans* (O.P.-Cambridge, 1874). PloS One 6:e25390.

Goymann, W., I. T. Moore, A. Scheuerlein, K. Hirschenhauser, A. Grafen, and J. C. Wingfield. 2004. Testosterone in tropical birds: effects of environmental and social factors. Am. Nat. 164:327–334.

Grafe, T. U., D. Preininger, M. Sztatecsny, R. Kasah, J. M. Dehling, S. Proksch, and W. Hödl. 2012. Multimodal communication in a noisy environment: a case study of the Bornean rock frog *Staurois parvus*. PLoS One 7:e37965.

Grilli, P., G. Soave, and R. M. Fraga. 2012. Natural history and distribution of selva caciques (*Cacicus koepckeae*) in the Peruvian Amazon. Ornitol. Neotrop. 23:374–382.

Hagelin, J. C. 2007. The citrus-like scent of crested auklets: reviewing the evidence for an avian olfactory ornament. J. Ornithol. 148:195–201.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129.

Howell, T. R., and G. A. Bartholomew. 1952. Experiments on the mating behavior of the brewer blackbird. The Condor 54:140–151.

Imbrie, J., A. Berger, E. A. Boyle, S. C. Clemens, A. Duffy, W. R. Howard, G. Kukla, J. Kutzbach, D. G. Martinson, A. McIntyre, et al. 1993. On the structure and origin of major glaciation cycles 2. The 100,000-year cycle. Paleoceanography 8:699–735.

Jaramillo, A., and P. Burke. 1999. New World blackbirds: The icterids.Princeton Univ. Press, Princeton.

Lindsay, W. R., J. T. Houck, C. E. Giuliano, and L. B. Day. 2015. Acrobatic courtship display coevolves with brain size in manakins (Pipridae). Brain Behav. Evol. 85:29–36.

Londoño, G. A., M. A. Chappell, M. del Rosario Castañeda, J. E. Jankowski, and S. K. Robinson. 2014. Basal metabolism in tropical birds: latitude, altitude, and the "pace of life." Funct. Ecol. 29:338–346.

Macedo, R. H., J. Karubian, and M. S. Webster. 2008. Extrapair paternity and sexual selection in socially monogamous birds: are tropical birds different? The Auk 125:769–777.

Martin, P. R., R. Montgomerie, and S. C. Lougheed. 2010. Rapid sympatry explaining greater color pattern divergence in high latitude birds. Evolution 64:336–347.

Martin, T. E. 2000. Parental care and clutch sizes in North and South American birds. Science 287:1482–1485.

Mather, M. H., and R. J. Robertson. 1992. Honest advertisement in flight displays of bobolinks (*Dolichonyx oryzivorus*). The Auk 109:869–873.

Masonjones H. D. and S. M. Lewis. 1996. Courtship behavior in the dwarf seahorse, *HIppocampus zosterae*. Copeia 1996:634–640.

Odom, K. J., K. E. Omland, and J. J. Price. 2015. Differentiating the evolution of female song and male–female duets in the New World blackbirds: Can tropical natural history traits explain duet evolution? Evolution 69:839–847.

Ord, T. J., and D. T. Blumstein. 2002. Size constraints and the evolution of display complexity: why do large lizards have simple displays? Biol. J. Linnean Soc. 76:145–161.

Ord, T. J., D. T. Blumstein, and C. S. Evans. 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. Proc. Roy. Soc. B 268:737–744.

Ord, T. J., and E. P. Martins. 2006. Tracing the origins of signal diversity in anole lizards: phylogenetic approaches to inferring the evolution of complex behaviour. Anim. Behav. 71:1411–1429.

Paradis, E., J. Claude, and K. Strimmer. 2004. ape: analysis of phylogenetics and evolution in R language. Bioinformatics 20:278–290.

Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. Ornithol. Monogr. 33:1–52.

Pike, N. 2001. Using false discovery rates for multiple comparisons in ecology and evolution. Methods Ecol. Evol. 2:278.

Powell, A. F. L. A., F. K. Barker, S. M. Lanyon, K. J. Burns, J. Klicka, and I. J Lovette. 2014. A comprehensive species-level molecular phylogeny of the New World blackbirds (Icteridae). Mol. Phylogenet. Evol. 71:94–112.

Preininger, D., M. Boeckle, A. Freudmann, I. Starnberger, M. Sztatecsny, and W. Hödl. 2013. Multimodal signaling in the small torrent frog (*Micrixalus saxicola*) in a complex acoustic environment. Behav. Ecol. Sociobiol. 67:1449–1456.

Price, J. J. 2004. Patterns of song evolution and sexual selection in the oropendolas and caciques. Behav. Ecol. 15:485–497.

———. 2009. Evolution and life-history correlates of female song in the New World blackbirds. Behav. Ecol. 20:967–977.

Price, J. J., S. M. Lanyon, and K. E. Omland. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. Proc. Roy. Soc. B 276:1971–1980.

Price, J. J., and L. M. Whalen. 2009. Plumage evolution in the oropendolas and caciques: different divergence rates in polygynous and monogamous taxa. Evolution 63:2985–2998.

———. 1994. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). Evolution 48:1657–1675.

Fraga, R. M. 2005. Ecology, behavior and social organization of saffron-cowled blackbirds (*Xanthopsar flavus*). Ornitol. Neotrop. 16:15–29.

Reif, J., and K. Štěpánková. 2016. Global analysis of threat status reveals higher extinction risk in tropical than in temperate bird sister species. Eur. J. Ecol. 2:13–20.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3:217–223.

Robinson, S. K. 1985. Coloniality in the yellow-rumped cacique as a defense against nest predators. The Auk 102:506–519.

Robinson, W. D., M. Hau, K. C. Klasing, M. Wikelski, J. D. Brawn, S. H. Austin, C. Tarwater, and R. E. Ricklefs. 2010. Diversification of life histories in New World birds. The Auk 127:253–262.

Rodriguez-Ferraro, A. 2006. Notes on the behavior of the olive oropendola (*Psarocolius yuracares*) during the breeding season. Ornitol. Neotrop. 17:57–62.

Ryan, M. J., and W. E. Wagner Jr. 1987. Asymmetries in mating preferences between species: female swordtails prefer heterospecific males. Science 236:595–597.

Servedio, M. R. 2007. Male versus female mate choice: sexual selection and the evolution of species recognition via reinforcement. Evolution 61:2772–2789.

———. 2016. Geography, assortative mating, and the effects of sexual selection on speciation with gene flow. Evol. Appl. 9:91–102.

Servedio, M. R., and R. Bürger. 2014. The counterintuitive role of sexual selection in species maintenance and speciation. PNAS 11:8113–8118.

Servedio, M. R., J. Hermisson, and G. S. Doorn. 2013. Hybridization may rarely promote speciation. J. Evol. Biol. 26:282–285.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol. Monogr. 36:575.

Soma, M., and L. Z. Garamszegi. 2015. Evolution of courtship display in Estrildid finches: dance in relation to female song and plumage ornamentation. Front. Ecol. Evol. 3:4.

Stutchbury, B. J. M., and E. S. Morton. 2008. Recent advances in the behavioral ecology of tropical birds. Wilson J. Ornithol. 120:26–37.

Thresher, R. E., and J. T. Moyer. 1983. Male success, courtship complexity, and patterns of sexual selection in three congeneric species of sexually monochromatic and dichromatic damselfishes (Pisces: Pomancentridae). Anim. Behav. 31:113–127.

Toussaint, E. F. A., R. Hall, M. T. Monaghan, K. Sagata, S. Ibalim, H. V. Shaverdo, A. P. Vogler, J. M. Pons, and M. Balke. 2014. The towering orogeny of New Guinea as a trigger for arthropod megadiversity. Nat. Commun. 5:4001.

Uetz, G. W., J. A. Roberts, and P. W. Taylor. 2009. Multimodal communication and mate choice in wolf spiders: female response to multimodal versusunimodal signals. Anim. Behav. 78:299–395.

Vehrencamp, S. L., J. W. Bradbury, and R. M. Gibson. 1989. The energetic cost of display in male sage grouse. Anim. Behav. 38:885–896.

Vliet, K. A. 1989. Social displays of the American alligator (*Alligator missis-sippiensis*). Am. Zool. 29:1019–1031.

Voigt, C. C., O. von Helversen, R. Michener, and T. H. Kunz. 2001. The economics of harem maintenance in the sac-winged bat, *Saccopteryx bilineata* (Emballonuridae). Behav. Ecol. Sociobiol. 50:31–36.

Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G., Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers: past, present and future. Earth Sci. Rev. 89:79–96.

Walls, S. C., and R. D. Semlitsch. 1991. Visual and movement displays function as agonistic behavior in larval salamanders. Copeia 1991:936–942.

Weir, J. T., and D. Wheatcroft. 2010. A latitudinal gradient in rates of evolution of avian syllable diversity and song length. Proc. Roy. Soc. B 278:1713–1720.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. Quart. Rev. Biol. 58:155–183.

Wiersma, P., A. Munoz-Garcia, A. Walker, and J. B. Williams. 2007. Tropical birds have a slow pace of life. PNAS 104:9340–9345.

Associate Editor: G. Rosenthal
Handling Editor: M. Noor

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Detailed description of characters in the display complexity scoring system. One point is given to each species that incorporates each character into its display routine, with one exception outlined below.
Table S2. Display complexity scores assigned to each species (listed alphabetically) within the New World blackbird family.
Table S3. Display complexity indices.