



## Animal choreography of song and dance: a case study in the Montezuma oropendola, *Psarocolius montezuma*

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Many multimodal displays incorporate choreography, which occurs when animals modulate how body movements are timed across the display. Choreography typically involves pairing specific gestures with vocalizations. This allows the signaller to effectively produce a display that is more complex than either of its components in isolation. Moreover, some animals appear to use a special case of choreography that can augment vocal performance. Expanding the multimodal framework to incorporate choreography is therefore a necessary step towards understanding how combining two signals into one impacts a display's structure. We explore this in a case study of free-living Montezuma oropendolas, *Psarocolius montezuma*, a polygynous songbird that performs a dramatic song and dance. We found that two elements of this display (bow and wing spread), are each choreographed with the song's loudest note ( $\text{dB}_{\text{max}}$ ) and lowest peak frequency (LPF), respectively. This suggests that oropendolas electively time the swing and wing spread gesture with key song elements. Interestingly, there was a correlation between the depth of an individual's swing and LPF, which was not explained by body size or social context. However, social context did predict a difference in vocal performance in terms of frequency modulation. Meanwhile, there was no relationship between wing display performance and  $\text{dB}_{\text{max}}$ . This means that oropendolas choreograph their swing gesture to predict LPF, which might reflect an individual's motor skill or even directly influence vocal performance. Altogether, our data suggest that animals can incorporate phenotypically distinct forms of choreography into their display repertoire, where each instance of choreography serves as an opportunity to generate a novel signal when one did not exist before.

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Many animals communicate using complex multimodal displays, which incorporate two or more signalling elements across sensory modalities (Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013; Rowe, 1999). Each component of a multimodal display can independently influence receiver behaviour (Hebets & Uetz, 1999), but the very act of combining two signals into one can essentially generate a 'third signal' with its own unique structure and function (Taylor & Ryan, 2013; Uetz & Roberts, 2002). The temporal patterning of gestural displays (ritualized body movements) is called choreography, a phenomenon that typically involves performing certain gestures instead of others with a given acoustic signal (Dalziell et al., 2013; Ullrich, Norton, & Scharff, 2016; Williams, 2001). Considering the ongoing challenge presented by understanding how even single signals evolve and function, it is

unsurprising that we know relatively little about how choreography works. Nevertheless, expanding the current multimodal framework to consider the role played by choreography is vital to advancing our understanding of how animals communicate.

Some of the most common multimodal displays include both vocalizations (calls or songs) and visual signals in the form of dance, which is at its essence a high-complexity gestural display (Fuxjager et al., 2015; Miles & Fuxjager, 2017; Miles, Cheng, & Fuxjager, 2017; Soma & Garamszegi, 2015). Although both song and dance are phenotypically diverse across animal species, there also appears to be profound variation in the ways that two signals are combined into one integrated display. First, just as human dance is coordinated with music on multiple hierarchical levels (Krumhansl & Schenck, 1997), some species exhibit variation in the fine-scale timing of dance with song (Ullrich et al., 2016), whereas other species elect to perform specific gestures with some songs over others (Dalziell et al., 2013). Although there may be functional differences in choreography at these two scales, they share one important factor: individuals can behaviourally vary the timing or

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pattern with which they pair song and dance. In other words, choreography is elective: it is a behavioural trait that is sometimes produced and sometimes not (e.g. singing without dancing or vice versa). This is fundamentally distinct from other multimodal displays constructed from components that are impossible to produce separately, as in some frog species that must inflate their vocal sac (thus producing a visual signal) to call (Starnberger, Preininger, & Hödl, 2014). We therefore make a distinction between such mechanistic dependence and true choreography because the former case does not allow for the signals to be produced independently (i.e. vocalizing without the visual signal is impossible due to physiological constraint).

Choreography can function in more than one way as part of a multimodal display. For example, male lyrebirds, *Melanura novae-hollandiae*, have a large vocal and gestural repertoire but choreograph their dance and song with surprising stereotypy (Dalziell et al., 2013), which likely serves to showcase a male's ability to perform a cognitively and/or physically challenging task in this highly polygynous species. Similarly, group-living zebra finches, *Taeniopygia guttata*, preferentially choreograph tap-dancing displays with the introductory portion of their song, possibly leveraging a more complex display to divert female attention towards the signaller (Ullrich et al., 2016). In both of these cases, choreography enhances a display's aesthetic function in mate attraction by increasing its overall complexity, which is known to be important for female choice across a variety of species (Hebets et al., 2013; Miles et al., 2017; Miles & Fuxjager, 2018).

By contrast, gesturing while singing can also influence acoustic output on a physiological basis (Cooper & Goller, 2004). Here, choreography takes on an additional function as a novel mechanism to modulate a target signal, while still enhancing display complexity. If this special case of choreography exists, it should result in a correlation between individual performance of gesture and song. Uncovering such a correlation is insufficient to conclude that gesture is physiologically impacting song performance, however. Instead, both song and gesture performance may be better explained by an external third factor, such as an individual's motor skill, or the innate ability to perform a challenging manoeuvre (Byers, Hebets, & Podos, 2010). Despite the fact that we cannot conclusively determine the function of correlated performance, this special form of choreography stands distinct from its uncorrelated cousin and is thus worth evaluating independently. Therefore, a given song–dance combination should be able to independently manipulate the signal receiver's behaviour, regardless of whether dancing modifies the song.

Theoretically, one species can exhibit multiple forms of choreography within a single display by producing different components of song and dance together. If this is true, then every pair of signals within a species' display repertoire can be combined in a different way, be it across different hierarchical scales or introducing novel ways that song and dance can influence each other. The behavioural and evolutionary ramifications of this possibility are entirely unknown, but one potential outcome is a novel route to increased display complexity without needing the evolutionary 'innovation' of a new song type or gesture.

Here we explore this possibility by studying the acrobatic displays performed by male Montezuma oropendolas, *Psarocolius montezuma*. These tropical songbirds compete intensely for mates at their nesting colonies and rely on multimodal displays to mediate both courtship and competition (Webster, 1994a, 1997). The oropendola's complex song (Fig. 1) can last as long as 3 s, combining high-frequency sweeps and a rapid, arhythmic series of low-frequency pulses (Price & Lanyon, 2004). While singing, males also perform a gestural display, which starts by slowly leaning forward until the centre of gravity is level with the perch (Jaramillo

& Burke, 1999). At this point, the bird rapidly spreads its wings while swinging forward and dangling upside down for up to 1 s. The song itself has multiple vocal elements that should be important for courtship and thus potential targets of choreography. These include the lowest peak frequency (LPF), known to be important in male–male competition (Price & Lanyon, 2004), and a song's maximum amplitude ( $\text{dB}_{\text{max}}$ ), the point at which the display is most audible (Janicke, Hahn, Ritz, & Peter, 2008; Ryan, 1988). Either could be accentuated by the high-intensity swinging display. Finally, both the length and frequency modulation ( $\Delta\text{F0}$ ) of a song are important in attracting females and signalling aggressive intent (Caro, Sewall, Salvante, & Sockman, 2010; Nelson & Poesel, 2011). These metrics reflect vocal performance over the song's entirety, rather than an isolated time point, and therefore cannot specifically be a target for fine-scale choreography. However, they provide an excellent basis of comparison for guiding inference into the function of choreography.

Here we use video analysis to examine how Montezuma oropendolas choreograph their body and wing displays with different vocal elements (LPF and  $\text{dB}_{\text{max}}$ ). We then examine the degree to which gestural and vocal performance are correlated. To distinguish whether correlations between song and gesture are due to physiological interdependence (rather than both modulated due to the influence of some third unknown factor), we also examine the effects of social context and body size on song performance. This is because both factors are well-known modulators of acoustic output in oropendolas and other species (Price, Earnshaw, & Webster, 2006). Considering what is currently known about animal choreography, we operationally defined a gesture as being choreographed with a given song element if the two signals (1) are combined electively and (2) occur together more often than predicted by chance alone. For each gesture choreographed with a different song element, individual gesture and song performance may be correlated or unrelated. When a correlation is present between the two, this suggests that both gesture and song performance are governed by an external factor such as individual motor skill (Byers et al., 2010). Alternatively, the correlation could be due to an intrinsic morphological or physiological link between producing the gesture and song simultaneously (Cooper & Goller, 2004). Here we consider this to be a special case of choreography that is structurally (and perhaps functionally) distinct from the more standard case of choreography with uncorrelated performance. Of course, one animal's display can contain numerous gestural and vocal elements, which makes it possible for multiple choreographic structures to exist within a single display.

## METHODS

### *Ethical Note*

This study relied exclusively on the analysis of videos collected from citizens around the world, who posted footage of free-living Montezuma oropendolas display on the Internet. Accordingly, institutional approval for this project was not required.

### *Study Species and Data Source*

To complete this study we relied on audiovisual analysis of displaying birds, an approach that has previously been used to successfully measure both gestural and vocal components of avian displays (Manica, Macedo, Graves, & Podos, 2016; Westneat, Long, Hoese, & Nowicki, 1993). Specifically, we took advantage of publicly archived video recordings (Supplementary Table S1), which are a valuable resource for biologists studying animal behaviour (Corn,

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