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Variation in the performance of cross-contextual displays suggests selection on dual-male phenotypes in a lekking bird

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Complex displays play an important role in female mate choice and male–male interactions for many species. Displays used in both inter- and intrasexual interactions offer an opportunity to examine how the ordering and structure of complex displays may vary with context. To understand how social context can influence the performance of complex displays, we investigated the predictability of display elements across displays in the presence and absence of females. The lance-tailed manakin, *Chiroxiphia lanceolata*, is a small lekking bird that performs complex, acrobatic displays. Pairs of alpha and beta males cooperatively display for females, but they also perform very similar displays in the absence of females. We quantified the performance of individual alpha and beta males within the dual-male display and the joint performance of the two males using Shannon's information entropy, and compared these values to understand how male display predictability varies with social context. Differences were assessed using generalized linear mixed models to account for repeated measures of male pairs. Predictability of individual performance within the dual-male interaction did not differ with female presence; however, entropy metrics describing the interaction of the alpha and beta male indicated that displays for females were more predictable and coordinated. This study provides a quantitative assessment of display element performance across different social contexts of female presence and absence, and suggests that the dual-male phenotype may be an important factor in female mate choice for cooperatively displaying species.

Many courtship displays across the animal kingdom are complex and incorporate a variety of different behavioural elements. For example, wolf spider (*Lycosa rabida*) courtship includes palpal rotations, leg waving and abdomen vibration (Rovner, 1968); fruit fly, *Drosophila melanogaster*, courtship includes wing vibrations, leg rubbing, wing waving, licking and circling (Spieth, 1974); and superb lyrebird, *Menura novaehollandiae*, courtship includes jumps, varying tail positions, wing flaps and multiple song types (Dalziell et al., 2013). The performance of different behavioural elements in a complex display may be an important factor in predicting the outcome of mate choice or status signalling (Byers, Hebets, & Podos, 2010). Because of the inherent complexity of these displays, the function of display element performance in mate choice and male–male competition remains poorly understood (Hebets & Papaj, 2005). Some animals perform complex displays in both inter- and intrasexual contexts, and this contextual variation makes it even more difficult to understand which selective forces shape display element performance (Hebets, 2011). However, by comparing inter- and intrasexual displays we can begin to disentangle which aspects of displays are important in different social contexts, and thus further understand their function in sexual selection (Berglund, Bisazza, & Pilastro, 1996).

Most studies on display behaviour have investigated performance in either male–male competition or female mate choice. For example, male chestnut-sided warblers, *Dendroica pensylvanica*, with more consistent song performance have higher rates of extrapair paternity (Byers, 2006). In the golden-collared manakin, *Manacus vitellinus*, females prefer males with faster displays that only differ in speed on the scale of tens of milliseconds (Barske, Schlinger, Wikelski, & Fusani, 2011). Additionally, red deer, *Cervus elaphus*, stags vocalize more often and with deeper calls in response to playbacks of stags with deeper calls, suggesting that vocal performance is important in male–male competition (Reby et al., 2005). One study of cross-contextual displays found that in male wolf spiders (*Schizocosa ocreata*), courtship rate and duration accurately predict mating success in male–female interactions, but

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only male size predicts the outcome of male–male interactions (Delaney, Roberts, & Uetz, 2007). Similar results have also been found in scaled quail, *Callipepla squamata*, where display rate and body size predict the outcome of male–male contests, whereas body size and dominance are important in female mate choice (Hagelin, 2002). By investigating displays across contexts, these authors were able to determine that different aspects of the display are important in different social contexts, suggesting that separate components of the display serve independent functions.

Species with complex multimale displays are particularly interesting to study because of their cooperative nature (Díaz-Muñoz, DuVal, Krakauer, & Lacey, 2014). Male wild turkeys, *Meleagris gallopavo*, sometimes form partnerships of two to four males and display for females by strutting together and helping to chase away other male competitors (Krakauer, 2005). Additionally, several species of manakins (Aves: Pipridae) perform complex cooperative multimale displays to attract females, including all members of the genus *Chiroxiphia*, three *Pipra* and one *Corapipo* (Jones, DuVal, & Boyle, 2014; Prum, 1990). In some of these species, males have also been reported to perform these displays in the absence of females. Several studies of multimale displays have demonstrated a link between social interactions and sexual selection. For instance, in long-tailed manakins, *Chiroxiphia linearis*, a young male's early interactions with other males predicts his later rank in the social hierarchy (McDonald, 2007). Similarly, the strength of adult male interactions predicts male fitness in wire-tailed manakins, *Pipra filicauda* (Ryder, Parker, Blake, & Loiselle, 2009). Thus, social interactions are likely an important component of complex multimale displays.

For cooperatively displaying species, the performance of the dual-male display as a comprehensive unit may be an important aspect of sexual selection. It is suggested that in species with dual-male displays, females may be choosing a mate based on the dual-male phenotype, and not simply the skill of an individual male (Trainer & McDonald, 1995). Male long-tailed manakins with longer partnerships have more consistent duet vocalizations, and it is hypothesized that these duet songs are used for female attraction (Trainer, McDonald, & Learn, 2002). However, variation in the dual-male phenotype with respect to female presence has to our knowledge never been examined, and could provide insight into the selective forces influencing cooperative male display performance.

Shannon Information Entropy (H) offers one method for analysing the performance of a complex display. This method quantifies the uncertainty in a signal to the receiver and is mathematically calculated as

$$\mathrm{H}(X) = -\sum_{x\varepsilon X} P(x)\log P(x) \tag{1}$$

where $H(X)$ is the entropy for signal (X) and $P(x)$ is the probability of an element (x) occurring within the signal (Shannon, 1948). A higher entropy value denotes a more unpredictable signal. While most often used in mathematical information theory, entropy can be applied to behavioural research to calculate the unpredictability of a complex display based on order and timing of display elements (Briefer, Osiejuk, Rybak, & Aubin, 2010; Dalziell et al., 2013; Kojima & Doupe, 2011). This technique has been used for studying the relationship between song and movements in the superb lyrebird, where male displays are coordinated between auditory and visual stimuli (Dalziell et al., 2013), and also to examine song performance trade-offs in the spectacled warbler, *Sylvia conspicillata* (Palmero, Espelosín, Laiolo, & Illera, 2014).

For dual-male displays, calculating joint display entropy and mutual information allows for a quantification of the display performance between two males. Joint entropy, *H(X,Y)*, describes the average uncertainty of a display between two individuals X and Y, taking into account their shared information and is calculated as

$$\mathrm{H}(X,Y) = -\sum_{x\varepsilon X}\sum_{y\varepsilon Y} P(x,y)\log P(x,y) \tag{2}$$

where $P(x,y)$ describes the probability of element x being performed simultaneously with element y for the signals of X and Y. In contrast, mutual information, $I(X;Y)$, describes what the behaviour of the one individual (X) can predict about the behaviour of the other individual (Y) and is calculated as

$$I(X;Y) = \sum_{x\varepsilon X}\sum_{y\varepsilon Y} P(x,y)\log\frac{P(x,y)}{P(x)P(y)} \tag{3}$$

Higher joint entropy denotes a more unpredictable display, whereas higher mutual information denotes a more coordinated display (Shannon, 1948). These entropy measures provide a useful method to investigate the dual-male complex display as a whole and also to quantify each individual's performance within the joint display for comparison.

In this study, we investigated variation of complex display performance in the contexts of courtship and male-only displays by quantifying display entropy in the lance-tailed manakin, *Chiroxiphia lanceolata* (Aves: Pipridae). In this species, alpha and beta males form long-term partnerships and display cooperatively for females (DuVal, 2007). Motor performance is an integral part of display behaviour, with displays involving up to 11 unique elements consisting of leaps and rapid flights. Males perform modified versions of courtship displays in the absence of females, allowing for behavioural comparisons between the different contexts of sexual selection. The usage of the same display elements across these two contexts leads us to the question of how males alter their displays in inter- and intrasexual contexts. If males perform more predictable displays during courtship and less predictable displays in strictly male–male contexts, then this could suggest that higher display predictability has been selected for through female mate choice. However, selection of display predictability (or unpredictability) could also result from male–male competition for alpha status or from a change in motivational state. In this study, we tested the hypotheses that in the presence of a female, (1) individual performance in a dual-male display will be more predictable (lower entropy), and dual-male interactions will be (2) more predictable (lower joint entropy) and (3) more coordinated (higher mutual information), in comparison to male–male displays in the absence of females. Additionally, we predicted that the (4) social context of female presence influences display element order and we assessed this prediction by calculating transition frequencies of display elements. These results provide insight into how social context can affect the performance of a complex display.

METHODS

Study Site and Data Collection

This research was conducted in a long-term study population of lance-tailed manakins on 46 ha of Isla Boca Brava, Chiriquí, Panamá (8°12′N, 82°12′W). Data collection took place during the peak of the breeding season, from February to April of 2013. All alpha–beta male pairs had been previously colour-banded for individual identification, and their statuses assigned based on observations of copulations or solo courtship displays, as these are behaviours only the alpha male performs (DuVal, 2007). The Florida State University Animal Care and Use Committee approved all methods (protocol