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.

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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 (Dalziel 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 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, & Learn, 2002). 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 et al., 2002). However, variation in the dual-male phenotype with respect to female presence has 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

$$H(X) = - \sum_{x \in X} P(x) \log P(x) \quad (1)$$

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

$$H(X, Y) = H(P(X, Y)) = -\sum_{x \in X} \sum_{y \in Y} P(x, y) \log P(x, y) \quad (2)$$

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

$$I(X; Y) = \sum_{x \in X} \sum_{y \in Y} P(x, y) \log \frac{P(x, y)}{P(x)P(y)}. \quad (3)$$

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 number 1101), and research permits were obtained from Autoridad Nacional del Ambiente (ANAM), Panamá.

To capture display sequences of alpha and beta interactions, we built permanent, camouflaged camera mounts approximately 5 m from the primary display perches of 12 independent alpha–beta male pairs spaced across the study site (Fig. 1). A display site can have more than one display perch (up to four); when this was the case, we filmed at the most active perch. Display perches are horizontal saplings or vines approximately 0.5 m high, and are typically used throughout a breeding season and occasionally across years. We used Canon Vixia HF-M500 high-definition cameras (recording at 29 frames/s), which provided the image quality necessary for identifying individual males by colour band combinations, even in the often low-light conditions of the forest. Cameras were connected to 12 V batteries using modified RCA-AH765R and Wagan EL-2190 universal power adapters that allowed for approximately 9.5 h of continuous recording per day (0730 to 1700 hours $\pm$ 1 h).

Behavioural Video Coding

We viewed and scored displays using Sony Vegas Movie Studio HD11 video-editing software. A subset of recordings from each display perch were analysed with a focus on the beginning of the breeding season (late-February to mid-March), although sites with fewer alpha–beta interactions sometimes had to be sampled at later time points to achieve appropriate sample sizes (filmed through 17 April 2013). Both male–male and male–female interactions are

expected to occur and affect fitness in this early portion of the breeding season, as this is when initial mating decisions are being made and males may most benefit from securing and maintaining alpha status.

We coded the timing of eight display elements performed on the display perch in lance-tailed manakin displays: up-and-down, quick-down, leapfrog, back-and-forth, wing-up back-and-forth, paired slow-flight, eek and que-rico (DuVal, 2007). Note that this approach separated variants of two earlier-defined display types (up-and-down versus quick-down, and back-and-forth versus wing-up back-and-forth). We excluded several possible display elements from this analysis (swoop, bounce, bow and solo slow-flight) as these are late-stage elements that are almost always performed after the dual-male portion of the display has ended. All elements analysed are used in the presence and absence of females, except the que-rico, which is only used in displays with no females present and so was not originally defined as a display element (DuVal, 2007). We coded the start and end times of all elements within a display for 32 displays with female absent and 30 displays with female present, performed by nine different alpha–beta male pairs. The same male pairs performed all displays analysed from a given display perch. We limited our analysis to displays that included dual-male portions of alpha and beta male displays, that lasted for at least 30 s and that included at least one behavioural element switch per male. For displays with female present, we only analysed displays where a single female was present on the display perch at some point in the display (i.e. displays were excluded if more than one female was present). In addition, displays with female absent had to be separated by at least 5 min from a display with female present to avoid the possibility that a female was in the area but not on the display perch, which could potentially affect male display behaviour in a display with no female. We excluded three of the 12 originally video monitored sites (Fig. 1) from the

analyses because they were either (1) not regularly attended by an alpha and beta male, (2) did not have both a display with female present and a display with female absent that fit the necessary qualifications outlined above, or (3) shared a beta male with another site, which could introduce additional pseudoreplication. Because some alphas displayed with multiple beta partners, we restricted the data to interactions between the alpha and the most frequent beta within the videos that were viewed.

The beginning of a display was designated as the time when the first male initiated a display element. All analysed movement elements of the display involved leaps from the display perch, and so the start of each element was defined as the time of the last video frame where at least one foot still grasped the display perch, and the end was the time of the first frame where both feet again grasped the display perch. The start for que-ricos and eeks (vocal display elements) was the time of the last frame before throat movement or sound was produced, and the end was the time of the last frame where a throat movement or vocalization could be observed. The start for slow-flights was the time of the first frame where any part of the male was visible performing laboured, stalled flights, as this display type does not involve landing on the display perch. We considered there to be a break between two instances of the same element type if there was a pause greater than 2 s between the execution of the individual display movements, which is an appropriate amount of time based on natural element transitions. For example, if the end time of an up-and-down leap was at 15 s and the start of a second leap was at 17.1 s, then these would be considered as separate up-and-down elements with a 2.1 s break in activity. In subjectively continuous bouts of leaping, interleap intervals averaged at 0.9 s making 2 s an appropriate amount of time to designate a departure from the normal display. We occasionally needed to approximate element start or end times when a foot or throat was obscured by

vegetation; in these situations, we estimated timing based on downward perch movement and/or vocalization sounds associated with the element type.

Entropy

We measured the entropy of dual-male lance-tailed manakin displays to determine whether there are differences in display predictability across the social contexts of female presence and absence. Because entropy can have a strong relationship with display duration, and displays with female present were, on average, longer than displays with female absent, we restricted our entropy analysis to only the first 30 s of all displays (Shannon, 1948). Eight of the displays with female absent were between 27.3 s and 29.9 s but were included in the final data set; we repeated analyses excluding these data to assess their influence. Although displays can last much longer than 30 s, we focused only on the beginning of displays, rather than on the display as a whole.

We divided display activity into 0.1 s time intervals across the first 30 s of each display for each individual, and we used the R package ‘entropy’ to calculate individual alpha and beta entropies, joint entropy and mutual information from the display sequences. We considered breaks between display elements as no activity, and coded these breaks as a unique display element in the display sequence, for a total of nine display elements possible. All analyses used R version 3.1.2 (R Core Team, 2014).

Statistical Analysis

To determine the effect of female presence on display entropy, we used generalized linear mixed models (GLMMs) with a random effect of pair identity to account for the multiple samples from the same alpha–beta pairs (R package ‘lme4’). Individual entropy is bounded by 0 and $\log_2 x$, where x is the maximum number of possible display elements (Shannon, 1948). With our maximum of nine display elements, individual entropies and mutual information were constrained by 0 and 3.17, and joint entropy was constrained by 0 and 6.34 (double the individual entropy maximum because it involves the displays of two individuals). The entropy results were transformed into proportions by dividing the entropy values by their maximum possible value. Using these proportions in the GLMMs resulted in extreme underdispersion (dispersion parameters: alpha entropy = 0.015; beta entropy = 0.015; joint entropy = 0.007; mutual information = 0.009). Underdispersion can be a significant issue for interpretation if the data do not fit the assigned distribution, if residual variance differs between group types of a fixed effect, or if there are outliers strongly affecting the data (Zuur, Ieno, Walker, Saveliev, & Smith, 2009, Chapter 9, page 225). Therefore, we logit-transformed the entropy proportions to better fit a Gaussian distribution (R package ‘car’). Underdispersion remained (dispersion parameters: alpha entropy = 0.29; beta entropy = 0.28; joint entropy = 0.15; mutual information = 0.67). To determine whether the underdispersion was influenced by the two social contexts (female present versus female absent), we ran a F test on each model and found that female presence influenced the residuals of the GLMMs for beta entropy ($F_{29, 31} = 2.46$, $P = 0.02$) and joint entropy ($F_{29, 31} = 2.40$, $P = 0.02$), but not for alpha entropy ($F_{29, 31} = 1.24$, $P = 0.55$) or mutual information ($F_{29, 31} = 0.78$, $P = 0.51$). This was largely due to heterogeneity of variances between the two social contexts for both individual beta entropy and joint entropy. Therefore, for each entropy metric we used a GLMM (using the gamm function in R package ‘mgcv’) with a

variance structure (varIdent) that allowed the variances of each social context to differ. We also ran a Cook's distance test on all GLMMs to determine whether any outliers were affecting our results and contributing to the underdispersion (R package 'influence.ME'). All Cook's distances for individual displays were less than 0.20, suggesting that no outliers strongly affected the dispersion of our models. Therefore, we concluded that underdispersion should not affect the interpretation of our results (Zuur et al., 2009). Additionally, we used a Spearman's rank correlation to assess relationships between entropy measures.

Transition Probabilities

For each starting behaviour (e.g. all transitions starting with a back-and-forth), we calculated percentage transitions out of all transitions made from that behaviour during the first 30 s of each display used in the entropy analyses ($N = 32$ displays with female absent and 30 displays with female present across nine display sites). We only used the alpha's display behaviour to avoid pseudoreplication since the alpha and beta perform similar displays together. Breaks in activity were not considered as an element type in this analysis, as we were simply interested in which elements followed each other. We then calculated means for each transition type for each display. We used binomial GLMs with complementary log-log link functions (accounting for zero inflation) for each transition type to test how transition usage differed between displays in a female's presence and absence. Male ID was not included as a random effect due to a lack of statistical power. We only report results of transition types with at least 10 instances across the two social contexts to exclude rarely performed transitions. We applied a

Bonferroni correction because of multiple tests so that $P < 0.0038$ was needed for statistical significance.

RESULTS

Entropy Models

Social context was unrelated to variation in individual entropy for alphas or betas performing paired displays. However, in the presence of a female, joint entropy was significantly lower (more predictable) and mutual information was significantly higher (more coordinated; Table 1, Fig. 2, Supplementary Fig. S1). Results were unchanged when we excluded the eight displays with female absent that were slightly shorter than 30 s from the analysis, except for mutual information (GLMM with data restricted to only 30 s displays: $t = -1.82$, $N = 54$, $P = 0.07$). We attribute this change in results for mutual information to a lack of power to statistically detect a marginal difference in a smaller sample size, but suggest caution regarding the interpretation of mutual information results. Mutual information and joint entropy were uncorrelated, indicating that these measures provide independent information ($r_S = 0.14$, $N = 62$, $P = 0.28$).

Transition Frequencies

Eleven of the 13 transition types analysed differed in their frequency of usage depending on female presence and absence (Table 2, Fig. 3). Six transitions were used more often with female presence, and five transitions were used more often in female absence.

DISCUSSION

Our results demonstrated no change in the predictability of an individual alpha or beta's performance in a dual-male display when a female was present. However, there was a difference in the predictability of the dual-male display with social context when analysing the joint properties of alpha and beta displays. Specifically, element performance in the dual-male display was more predictable when in the presence of a female, suggesting increased coordination of the same behaviours in the context of mate attraction compared with strictly male–male interactions. This change in display predictability across contexts suggests that the dual-male phenotype may be an important factor in sexual selection. For example, female choice may be focused on the dual-male interaction instead of an assessment of the individual performances of the alpha or beta. It is also possible for male social behaviour to have selected for more unpredictable displays during dominance contests when females are not present, resulting in the difference in performance between social contexts. In addition, motivational or performance state may change with social context, affecting the males' joint display predictability; male-only displays might act as practise for courtship, where males increase display predictability when motivated by female presence. Our results suggest that selection in either context focuses on the dual-male aspects of the performance.

One explanation for increased predictability in dual-male displays performed for females in the lance-tailed manakin is that repetitive signals may be important in mate choice (Mowles & Ord, 2012). Many courtship displays across the animal kingdom involve repetitive elements (examples: roaring in red deer: Clutton-Brock & Albon, 1979; leaping displays of blue-black grassquits, *Volatinia jacarina*: Carvalho, Carlos, Macedo, & Graves, 2006; claw waving in fiddler crabs, *Uca annulipes*: Backwell, Jennions, Passmore, & Christy, 1998). The ability of an individual to accurately perform repetitive, energetically costly elements may signal male quality to the female (Byers et al., 2010). Dual-male displays might also involve a high level of cognitive ability, as these displays not only involve the alpha male's individual ability to perform a complex display, but also to perform it in a coordinated fashion in response to the beta male's behaviour. Therefore, it is possible that the predictability of a coordinated display may act as a signal of cognitive ability, and thus evolve as an honest indicator of male quality used in female mate choice (Boogert, Fawcett, & Lefebvre, 2011). In two species of bearded manakins that perform single-male displays (*Manacus candei* and *Manacus vitellinus*), females actively engage in courtship by participating in a coordinated 'duo dance' with the male, where the female is the one who paces the jumps of the display. It is hypothesized that this coordinated display acts to challenge the male, and is another example of display coordination potentially acting as an honest signal of male cognitive and/or motor ability (Barske, Schlinger, & Fusani, 2015). As our study investigated only the first 30 s of each display to standardize sampling across contexts, we were unable to analyse whether the predictability of paired displays was related to reproductive success. Courtship displays generally last 5 min, making it unlikely that a female would make a choice based on this brief period; our analyses also did not capture the variation present later in these displays. However, since we found a significant difference between displays when females

were present versus absent, even during the first 30 s of the display, this suggests that there was an important difference in display performance based on social context.

Another explanation for the change in dual-male display predictability across contexts is that selection has acted to decrease predictability of male-only displays, rather than increase predictability with female presence. For example, alphas may be actively challenging betas when females are absent, so that it is harder for the males to coordinate behaviours. There could also be selection for different aspects of the display that were not investigated in this study, so that while joint-male display predictability may be under selection in displays for females, another variable such as leap height or display element rates may be more important in male-only displays. On the flip side, there may only be selection on cooperative displays with female presence and no selection with female absence. For example, zebra finches, *Taeniopygia guttata*, adjust song quality with social context; males sing directed song in the presence of females and undirected song in isolation. While these songs are superficially similar, the directed song is more stereotyped and less variable. This difference in song quality between contexts is likely due to a change in motivational and performance state instead of active selection for lower quality in the male-only context (Woolley & Doupe, 2008). However, the interpretation of our results are probably different from that of the directed and undirected song; male–male interactions in the lance-tailed manakin are thought to be an essential aspect of social hierarchy maintenance (DuVal, 2007), whereas zebra finch undirected song appears to be separate from intrasexual selection since it is performed in isolation. Therefore, it seems that selection functions on display predictability and/or other display variables in both inter- and intrasexual contexts.

Entropy calculations are time-based measurements, and reflect time spent performing particular elements in addition to the number and order of different elements performed.

Therefore, we also investigated the ordering of elements independent of their element duration. Displays with female present and displays with female absent used the same elements (with the exception of the que-rico); however, the displays differed in the degree of ordering and which elements were used most consistently, and as such these elements potentially have different purposes (Fig. 3). For example, some elements appear to be used to attract females to the male pair but are not used once the female lands on the display perch (up-and-down and quick-down). Yet, these same elements are also used in strictly male–male contexts but in a less structured manner. Once a female is on the display perch and the males are actively courting, the pair typically performs leapfrog behaviour interspersed with other display elements (slow-flight and back-and-forth). In contrast, in the female absent context, there is an evident cycling pattern between leapfrog, up-and-down and quick-down transitions, which is likely due to a difference in their respective functions between contexts. While it is possible for a female to have been present at a display area but not on the display perch during what we classified as a female absent context, we remain confident that this was generally not the case. Leapfrog behaviour has never been observed during a courtship display before the female is on or near the display perch (i.e. visible on the video), and the fact that leapfrog was often performed when females were not visible in the female absent context confirms that we accurately defined the social context. Therefore, despite the similarities in elements used between contexts, the displays are markedly different in their level of organization and the types of transitions used.

Our results suggest that social context is an important factor in display performance and that continued investigation into social context as a potential source of variation in display performance is warranted. Several studies have analysed male performance when females are absent and have used those measurements to describe a male's overall performance to correlate

with female visits or mating success (examples: Barske et al., 2011; Shorey, 2002). However, as we have shown, performance can differ markedly across contexts of female presence and absence, and thus measurements performed in the absence of a female may not be reliable when investigating mate choice. Future research should determine whether there is a female preference for the multimale phenotype in species with multimale displays, and continue considering display predictability as a potential source of sexual selection. We have demonstrated that coordinated displays are more predictable when used in the context of courtship, despite the similarities in display elements used across social contexts.

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Supplementary Material

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Table 1

Results of the GLMMs examining performance of alpha and beta lance-tailed manakin males during dual-male displays, with male pair ID as a random effect and variance structure specified for social context (female present vs absent)

Response variable	Estimate of social context	<i>t</i>	<i>P</i>
Individual entropy of alpha, $H(X)$	0.16±0.14	1.14	0.26
Individual entropy of beta, $H(Y)$	0.17±0.14	1.25	0.22
Joint entropy, $H(X,Y)$	0.32±0.10	3.21	0.002*
Mutual information, $I(X;Y)$	-0.45±0.20	-2.11	0.031*

Individual entropy measures of the alpha and the beta male were not related to social context of male displays, while mutual information was higher and joint entropy was lower with female presence.

* $P < 0.05$.

Table 2

Results of binomial GLMs of transition types used at least 10 times by lance-tailed manakin males during dual-male displays across both contexts (female present vs absent)

Transition	Estimate of social context	z	P
BF to LF	-0.94±0.17	-5.57	<0.001*
LF to QD	1.58±0.14	11.62	<0.001*
LF to SF	-1.33±0.14	-9.39	<0.001*
LF to UD	0.47±0.13	3.62	<0.001*
QD to LF	—	—	—*, ^a
QD to SF	-0.02±0.12	-0.20	0.84
QD to UD	1.56±0.12	13.09	<0.001*
SF to BF	-1.51±0.18	-8.56	<0.001*
SF to LF	-2.93±0.23	-12.67	<0.001*
SF to UD	-0.80±0.10	-8.37	<0.001*
UD to LF	0.27±0.12	2.19	0.03
UD to QD	1.06±0.09	11.37	<0.001*
UD to SF	-0.75±0.13	-5.90	<0.001*

SF: slow-flight; UD: up-and-down; QD: quick-down; LF: leapfrog; BF: back-and-forth. $N = 32$ displays with female absent with 171 total transitions and $N = 30$ displays with female present with 140 total transitions, across nine display sites. Negative z values indicate that the transition was used more frequently with female presence; positive z values indicate that the transition was used more frequently with female absence.

* $P < 0.0038$ from a Bonferroni correction.

^a The QD to LF transition was never performed in the presence of a female, and the statistical test used could not analyse data with only zeros in a category. Because this transition was used more than 10 times in the absence of a female, we concluded that QD to LF was performed more frequently in female absence.

Figure 1. Locations of active alpha–beta pair display sites of lance-tailed manakins on Isla Boca Brava in 2013. The 12 black circles indicate display sites that were video monitored; white circles indicate active display sites that were not video monitored; the three black circles with asterisks are display sites where no displays were analysed (see Methods for more details).

Figure 2. Relationship between entropy and social context of dual-male displays of lance-tailed manakins using backtransformed fitted values from the final GLMMs (a–d). Error bars show standard errors. $N = 32$ displays with female absent and 30 displays with female present across nine display sites. $*P < 0.05$.

Figure 3. Transition probabilities of display elements of male lance-tailed manakin displays for the first 30 s of displays with female absent (grey arrows; $N = 32$ displays and 171 total transitions, across nine display sites) and displays with female present (black arrows; 30 displays and 140 total transitions, across nine display sites). Display elements presented are quick-down (QD), up-and-down (UD), slow-flight (SF), back-and-forth (BF) and leapfrog (LF). Solid lines denote statistical significance between contexts ($P < 0.0038$), whereas dashed lines denote no statistical significance of differences in transition frequencies between contexts.