**Multiple meanings of complexity in the courtship displays of a lek-mating birds**

**ABSTRACT**

In polygynous lek mating systems, males perform complex courtship displays for females. Studies of courtship displays, especially vocal displays in birds, have linked reproductive success to behavioral complexity. These studies often address a simple level of complexity—repertoire complexity—which focuses on e.g., the number of unique display elements in a display. More recent work has begun to address another level—syntax complexity—which focuses on how organisms arrange the elements of their display. We analyze 312 displays of lek-mating Golden-winged Manakins, *Masius chrysopterus,* by coding their dances as strings of behavioral elements. We calculate simple measures of repertoire complexity along with multiple measures of syntax complexity using methods from computer and information science (Shannon entropy, string compressibility, and Kolmogorov algorithmic complexity). We find that solo male displays (SOLO) were the most complex, whereas unsuccessful displays performed for a female audience (AUDI) were of intermediate complexity, and successful displays ending in copulation (COP) were the simplest in terms of both repertoire and syntax. Using Jaro string distance, a method from record-linkage theory, we find that COP displays were the most uniform and that displays varied more across context (SOLO, AUDI, COP) than across individual. Females chose to copulate after simple displays building to a dramatic high-speed element (audible log-approach dive). Our results raise questions about fundamental differences between song and dance displays and highlight the need for a third level of complexity—element complexity—that reckons with the aesthetic content of display behaviors themselves.

**KEYWORDS**

complexity, repertoire, syntax, courtship, display element, lossless compression, entropy, Jaro string distance, lek, manakin

## **INTRODUCTION**

## **METHODS**

### *Study Site*

We collected data in 2015-2016 (January, June-August) and 2017 (September-December) at the Milpe Bird Sanctuary of the Mindo Cloudforest Foundation, in northwestern Ecuador (~0°1’48”N, 78°57’12” W). At an of 1,100 m, Milpe comprises 100 hectares of west slope Chocó-Andean forest with a network of maintained trails.

*Study Species*

Male *Masius* tend small sections of fallen mossy logs (~20–60 cm2 surface) on which they perform elaborate gymnastic displays. Display logs are often in aural, but rarely in visual, contact with one another as part of a broader, dispersed lek (Bradbury, 1981). As in many other manakin species, female *Masius* have an overall green plumage while males undergo a process of plumage maturation from predefinitive (green) to definitive (black, golden-yellow, and/or orange-red) plumages over multiple years (Taylor et al. 2020, Schaedler et al. 2021). Some older predefinitive-plumaged males can be identified by waxy nape feathers, a golden horn-like crest, or golden forehead feathers. Females are only known to copulate with definitive-plumage males (*pers. obs.*).

### *Field Methods*

We used mist-nets (6 or 12 m length, 30mm mesh) to capture and mark individual birds. All *Masius* were banded with a numbered aluminum band and a unique combination of plastic color bands. Other species were released immediately. All field methods were approved by the University of Wyoming Institutional Animal Use and Care Committee (Protocol#20160602DM00242-02).

After regular observations to identify *Masius* display logs, we monitored logs with video cameras. We prioritized video surveillance at logs with high manakin activity or female visitation, or at snewly discovered logs. Individual cameras (Sony Handycam HDR-CX405 or Sony Handycam HDR-CX240, Sony Corp., Tokyo, Japan) were housed in weatherproof container and powered with an external batter (12v motorcycle battery or 10,000 mAh GETIHU power bank, Shenzhen Top Star Industry Co. Ltd., China). Recording ended when the memory card reached capacity, the batteries died, or weather necessitated camera retrieval. We ran 4 to 6 cameras daily, one per log, with each camera recording approximately 7 hrs of video. Footage was filtered with a liberal motion detection program ($GITHUB) using the OpenCV library ($CITE) in Python v. ($CITE). After being flagged by the motion detection program, motion clips were manually verified and bookmarked for subsequent coding.

*Displays and behavioral elements*

We defined a display as a sequence of distinct behavioral elements during which time males were never absent for >60 s. *Masius* displays can involve multiple males and females both as performers and audience members ($PRUM\_JOHNSON, Taylor et al. 2018). For this study, we excluded all 27 displays featuring multiple dancing males or a banded, known-male audience member. None of these displays ended in copulation, although one involved attempted copulation. We retained 23 displays where the audience member was suspected as a predefinitive male based on plumage but performed no display behaviors.

We categorized the remaining 459 male displays into three categories: SOLO (n=334), AUDI (n=111), and COP (n=14). SOLO displays were solo male performances, AUDI displays featured one or more audience members but did not end in successful copulation, and COP displays ended in a successful copulation.

We coded display elements using Behavioural Observation Research Interactive Software (BORIS), an open-source event logging tool (Friard & Gamba, 2016). A total of 41 elements occurred in the raw BORIS data files (see Table S1). We excluded tracking elements (e.g., “Start”), movement-based elements (e.g., “Male1 On Log”, “Female Movement”), female responses (e.g., “Female Tracking Male”), and some male behaviors not directly involved in display dances (e.g. “Vocalization,” “Gardening”). We also combined some paired elements into single behaviors (e.g., “Half-bow Left” and “Half-bow Right” become “Half-Bow”). The result was 14 key behavioral elements, including pauses (“Zero”), attempted copulation, and successful copulation (Table 1). Voucher videos of behaviors are archived at the Macaulay Library of Natural Sounds at Cornell University.

### *Repertoire complexity*

assess their sensitivity to the large discrepancy in sample size between COP bouts (*n* =14) and Mal (198) and female audience (AUDI, *n* =100) bouts. Across each of 10,000 replicates, we randomly selected (without replacement) 14 strings from the SOLO, MULT and AUDI bouts, and calculated the mean of the ensuing 14 entropy, compression or Jaro metrics. We then compared the distribution of the random replicate metrics to the values calculated using the full sample. All analyses were conducted in Program R (4.0.2) (R Core Team 2020).

*Syntax complexity*

We quantified syntax complexity of displays with three related measures: entropy, Kolmorgorov complexity, and compressibility.

$ENTROPY

$COMPLEXITY

$COMPRESSION

We compared syntax complexity measures across context (SOLO, AUDI, COP) with ANOVA and Tukey’s HSD. As with repertoire complexity, used a randomization procedure (10,000 random sets of 14 displays, drawn with no replacement) to confront our small sample of 14 COP displays.

$INDIVIDUAL DEVIATIONS

*Context vs. individual variation*

### *Entropy*

Here, we use entropy to explore variation across display contexts. For each bout type (Mal, Fem, Cop) we calculated the overall frequencies of the elements, *p*i. The maximum, zero-order entropy for bouts (14 possible elements) is given by log2(14) = 3.81 bits. The first-order entropy, in bits, is then given by

(1)

### Because the maximum possible entropy is dependent on the number of elements (here distinct behavioural elements) and because that number varied from 4 to 12 across bouts, we used the adjusted entropies, given by the raw entropy, divided by the maximum possible entropy determined by the number of elements (Vanderbilt, Kelley, & DuVal 2015). [THIS EXPLAINS our 0-1 ENTROPY SCORES] Thus, the entropy scores ranged from 0 to 1.

### *Compression Ratio*

Lossless compression of information is an important feature of many digital applications. As with entropy, many compression algorithms use a bit-based approach to compressing sequences of elements, which can then be applied to text, signal waves, pixels or sequences of *Masius* display elements. We term the extent to which a sequence of elements can be compressed its *compression ratio*. We computed compression ratio as the original length of a display string (using the same single-letter alphabetic abbreviations as for entropy), divided by the length of the string after compression by Huffman encoding (Huffman, 1952) and the LZ77 algorithm (Ziv & Lempel, 1977), using the *R* package *brotli* (Ooms & Google Inc., 2018). Huffman encoding (Huffman, 1952) creates optimal prefixes for subsequent compression of strings of elements (here, our *d*i), assigning the smallest bit length to the most common element. LZ77 (Ziv & Lempel, 1977) uses a sliding window, distance-length algorithm to detect and compress recurring motifs in the data stream. An increase in compression ratio, like a decrease in entropy, indicates more repetition of elements and motifs, and thus a decrease in complexity. One potential advantage of compression ratio over entropy is that the latter is computed just from the frequencies of display elements, whereas LZ77 compression also assesses the order of the display elements. Further, LZ77 compression counts repeated motifs, as well as single elements, via its sliding window, distance-length feature, providing an additional layer of pattern detection and compression. We compared the *compression ratio* values across the three categories (Mal, Fem, Cop) with ANOVA and Tukey's HSD.

### *Jaro String Distance*

Matching similar records has long been a goal of computer-assisted methodologies in a field known as record linkage (Fellegi & Sunter, 1969). Jaro (1989) developed a simple but elegant method for matching census records from disparate sources. The algorithm analyses the number of transpositions and mismatches between two strings, and assigns a distance between 0 (no matches) and 1 (complete match). We used Jaro distances to assess similarity of display sequences within and across contexts and within and between males, via the *R* package *stringdist* (van der Loo, 2014). If context-dependence is the major factor explaining behavioural variation, then we expect behaviours in a given context to resemble one another, regardless of male identity. That is Mal Jaro distances **within** a male's bouts should be similar to Mal Jaro distances **between** different males. If, however, individual differences are most important, Within-male Jaro distances, for both Mal and Cop, should be low and Between-male distances should be high, for both Mal and Cop bouts. We created a matrix of Jaro distances between a given string and all other strings to which we were comparing it (e.g., a 198 X 198 matrix between all the Mal strings). We then used the mean of the distance between a string (display sequence) and all others of its context, to assess similarity (low Jaro distances denote high similarity of the compared strings of display elements). Jaro string distances, unlike some alternative algorithms, are little affected by differences in string length (Pearson correlation coefficient for Jaro-distance matrix vs. string-length matrix for the 198X198 Mal display matrix = -0.038). The Expected values, under the hypothesis of individual differences as the driving force in generating variation in displays, were generated by simply labelling the Observed Jaro distance values, such that high Jaro distances were labelled Between and low values were labelled Within. Note that these Expected values are simply a vehicle for visualizing the differences between the predictions of the individual-difference and context-dependence hypotheses, not for any quantitative comparison of Observed vs. Expected. [DOES THIS NEED FURTHER CLARIFICATION?]

## **RESULTS**

All display bouts occurred in Julian weeks 25 through 3 (24-Jun to 14-Jan), with a pronounced peak from October to December (234 of the 312 display bouts), and a pronounced dip in June, July and August. Male-only displays (SOLO and MULT) were first observed on 24-Jun, female audience bouts (AUDI) were first observed on 15-Jul, and the first copulation was observed on 26-Oct. Males do a low-amplitude "*nurrt*" advertising call from various perches in the vicinity of the display log. (Prum & Johnson, 1989). For Jun-Aug 2014 (low courtship activity), 2,895 mins of observation yielded 2,182 nurrts (0.75 nurrts/min). For Nov-Dec 2017 (peak activity), 1,518 mins of observation yielded 3,311 nurrts (2.2 nurrts/min). Using broken-stick analysis (Sibly, Nott & Fletcher 1990), we defined bouts as sets of nurrts with no gaps > 46 sec. For the 2017 data, 48 nurrts were singletons. Of the 236 bouts with ≥ 2 nurrts, 106 comprised > 10 nurrts. For these 106 longer bouts, the nurrt rate averaged 4.23 nurrts/min (sd = 0.8) within calling bouts, with a median of 4.17 nurrts/min.

Table 2 describes and quantifies 11 major behavioural elements performed by male *Masius* during courtship displays at their logs for our three contexts (Mal, Fem, Cop). The full list of display elements and their abbreviations is in Table S1. When coding videos, we recorded whether the female was above or below the male on the log. Although virtually all displays logs were on slopes, "above," on level terrain would mean further along the log than the incoming trajectory of the swoop down during an ALAD. Overwhelmingly (Pearson's *Χ*2 with Yates' continuity correction = 4140.5, df = 1, p < 0.0001), the female was below the male for Bows (4,540/4,602), whereas she was above the male for Neck twists (553/607). However, most Neck twists (3,159/3,807 = 83%) were performed when the female was not on the log (females not on the log were not counted in the above-below comparison). Thus, males often performed a long series of Neck twists after females left the log following copulations, and, less frequently, when the female was close to, but not on, the log.

Table 2. A list of the common Masius courtship display behaviours, their abbreviations, descriptions and how many times they were performed in the 312 coded display bouts.

Table 3 presents rates (per min) for Bows, Neck twists, and ALADs in the three contexts (Mal, Fem, Cop). The rate for Bows (Mal 3.4 ± 3.1, Cop 16.6 ± 4.1) was far lower in Male-only display bouts than in Copulation bouts and lower, though not as dramatically, for Neck twists (Mal 6.4 ± 8.2; Cop 8.7 ± 6.4). Interestingly, males actually performed ALADs at a higher rate during Mal bouts (1.22 ± 0.5) than during Cop bouts (0.5 ± 0.2), likely because, during copulation bouts, ALADs almost always preceded a copulation or attempted copulation, and were therefore less likely to be repeated (X of Y Cop bouts had > 1 copulation). During copulation bouts, males performed many more Bows before the first copulation (54 ± 16.9) compared to before the second copulation (5.1 ± 13.3). The converse was true for Neck twists, with 21.6 ± 39.6 before the first copulation and 35.4 ± 28.3 thereafter. All but two of the 14 bouts leading to a copulation followed a consistent pattern of 1 to 17 behaviours (5.1 ± 4.9) followed by a long string of Bows (range 25 to 76), then an ALAD and the copulation. The two unusual bouts differed in that the female left the log one or more times, after 20 or more male display elements, before settling on the log for the copulation. The two males with multiple copulations (ID980 n = 3 range 51 to 67; ID296 n = 10, range = 25 to 76) did not differ in the number of Bows they performed prior to the first copulation (Welch's two-sample t-test: df = 8.16 effect size = 0.37 P = 0.44).

Table 3. Rates of Bow, Neck and ALAD display for Masius. During Cop bouts, mean Bow and Neck rates were higher, but had lower maxima, than during Mal and Fem bouts.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Bows/minute | | | | Neck twists/minute | | | | ALADs/minute | | | |
|  | Mean | s.d. | Min | Max | Mean | s.d. | Min | Max | Mean | s.d. | Min | Max |
| Mal | 3.35 | 3.08 | 0.2 | 22.72 | 6.43 | 8.23 | 0.18 | 30.65 | 1.22 | 0.46 | 0.39 | 2.8 |
| Fem | 10.96 | 6.21 | 0.39 | 26.71 | 8.69 | 6.09 | 0.16 | 32.22 | 0.53 | 0.2 | 0.18 | 1.15 |
| Cop | 16.57 | 4.05 | 7.97 | 22.36 | 8.71 | 6.35 | 1.33 | 27.05 | 0.49 | 0.16 | 0.22 | 0.80 |

Table 4 shows the first and last record (capture or sighting) for each of the 12 colour-banded males in the study, and the number of Mal, Fem and Cop bouts in which each participated. We observed 12 individually colour-banded females copulate with the three colour-banded copulator males. Some of those females had histories of visitation at multiple display logs. In addition, three other colour-banded females were observed watching displays, but never copulated during our video monitoring.

Table 4. Identities of males performing courtship displays. Note that 10 of the 12 banded males displayed for at least one female (i.e., participated in ≥ 1 Fem bout). Only three banded males copulated. In the MaleID column, Unb denotes bouts performed by an unbanded male. Span is the number of days over which they were observed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| MaleID | Total bouts | Mal | Fem | Cop | Date banded | Date last seen | Span (days) |
| 112 | 20 | 8 | 12 | 0 | 23-Sep-17 | 20-Dec-17 | 89 |
| 113 | 5 | 4 | 1 | 0 | 17-Sep-17 | 20-Nov-17 | 65 |
| 291 | 1 | 1 | 0 | 0 | 26-Jul-15 | 8-Aug-16 | 380 |
| 296 | 153 | 99 | 44 | 10 | 10-Jul-15 | 20-Dec-17 | 895 |
| 299 | 9 | 6 | 3 | 0 | 4-Jul-15 | 30-Nov-17 | 881 |
| 940 | 7 | 2 | 4 | 1 | 26-May-13 | 16-Jan-15 | 601 |
| 948 | 2 | 1 | 1 | 0 | 10-Jun-13 | 13-Sep-17 | 1557 |
| 965 | 20 | 15 | 5 | 0 | 3-Jul-14 | 3-Oct-17 | 1189 |
| 976 | 2 | 1 | 1 | 0 | 22-Jul-15 | 11-Jan-17 | 905 |
| 978 | 3 | 1 | 2 | 0 | 23-Jul-14 | 21-Aug-15 | 395 |
| 980 | 78 | 53 | 22 | 3 | 24-Jul-14 | 20-Dec-17 | 1246 |
| 982 | 1 | 1 | 0 | 0 | 24-Jul-14 | 17-Jan-16 | 543 |
| Unbanded | 11 | 6 | 5 | 0 | NA | NA | NA |

Time to first copulation in the 14 Cop bouts was 129.1 ± 41.3 secs, with a range from 70.4 to 212.7. The mean number of copulations in a Cop bout was 1.7 ± 0.8 (range, 1 to 4). Total bout length in Cop bouts averaged 270.0 secs (± 140; range, 134.7 to 690.3). The number of times that females left the display log (abbreviated *Fff* as a network node) was higher and more variable in Fem bouts (2.6 ± 2.8; range, 1 to 23; c.o.v. 1.08) than in Cop bouts (2.1 ± 1.1; range, 1 to 5; c.o.v. 0.53).

Ethogram networks for each of the three contexts (Mal, Fem, Cop) are shown in Figure 1 (with nodes representing the behavioural elements listed in Table 1). A clear progression is apparent, from dense, with high effective degree for the Mal network to sparse (low density), with low effective degree for the Cop network. None of the 10,000 randomly subsampled male-only networks had an effective degree as low as that of the copulation network (mean = 24.5 ± 0.83 for the Mal random replicates vs. 2.8 for the Cop network).

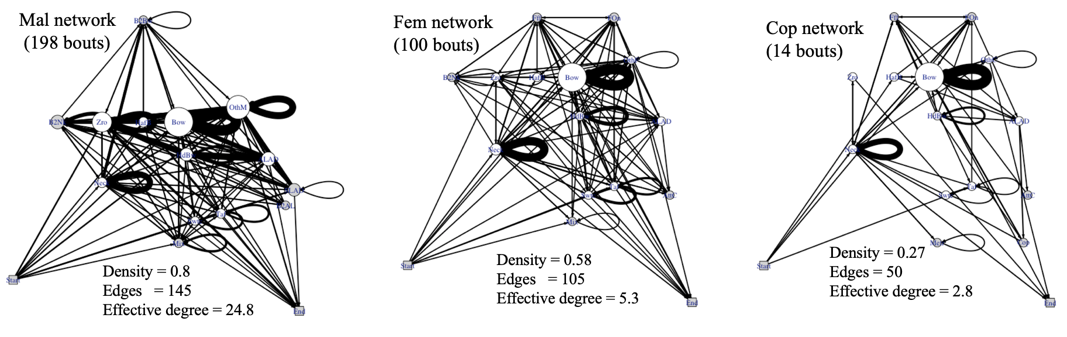


Figure 1. Masius display ethograms visualized as networks in three contexts (Mal, Fem, Cop). The nodes represent distinct behavioural elements (e.g., ALADs and Bows). The directed edges represent transitions between elements, with weights representing how often those transitions occurred. For example, Bows were often repeated in a long string, creating a self-loop (edge emanating from, and returning to, a node) with heavy weight. Size of node is proportional to eigenvector centrality. Start and End (lower left and lower right) are dummy nodes, to indicate the general direction of flow through the ethogram/network. The major difference across contexts is increasing simplicity – from dense, with high effective degreein male-only displays (Mal) to sparse (low density), with low effective degree,in displays leading to copulations (Cop). Effective degree is based on variance in edge weights. If all edges from a node have equal weight, effective degree equals the binary degree (number of distinct edges). As variance in edge weight increases, effective degree declines relative to binary degree. For the Cop network (effective degree 2.8), self-loops on Bow and Neck twist are, effectively, the only ones that really matter. In contrast, edge weight is much more evenly distributed in the Mal network (24.8 effective edges).

To assess the relative complexity of the Mal and Cop networks, we enumerated the number of simple paths through the Cop network. For the Mal network, because the enumeration was computationally intractable for the full network, we computed the number of simple paths for 200 subsampled Mal networks with a tractable number of edges (102), as described in Methods. The Cop network had 1,530 simple paths. The 200 resampled Mal networks, each with 102 of the 154 possible edges, had more than two orders of magnitude more simple paths (mean = 649,610; sd = 751,673; range 88,850 to 4,702,072).

Figure 2 summarizes the information entropy analysis. The 198 Mal bouts had high adjusted entropy (diversity, randomness or surprise), often approaching the maximum possible value of 1.0. In contrast, the 14 Cop bouts had low entropy. The adjusted entropies differed among the three contexts (Mal, Fem, Cop) under ANOVA followed by Tukey's HSD (P < 0.001). Higher-order entropies (Fig. S1) continue to decline beyond second-order for Mal bouts more than they do for Fem or Cop bouts. Those differences across higher-order entropies suggest that, in Fem and Cop bouts, the current element depends only on the preceding element. In contrast, Mal bouts elements depend, in complex ways, on earlier elements.

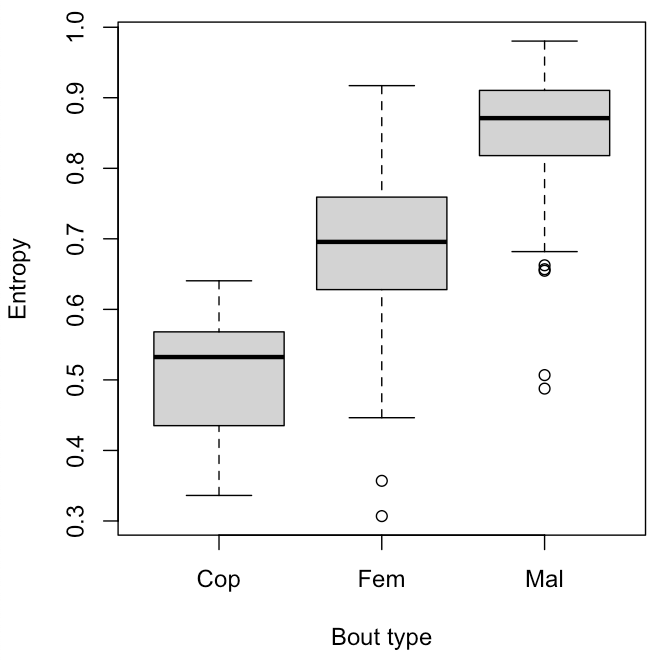


Figure 2. Entropy (relative to the maximum possible) for 14 Cop bouts, 100 Fem bouts and 198 Mal bouts. In contrast to the avian song repertoire literature, more successful (Cop) displays were simpler (had lower entropy) than were less successful (Mal and Fem) display sequences. We coded each display bout as a string of characters (*a* to *n*) representing the sequence of 14 discrete behavioural elements in Table 1, and then computed its information entropy (in bits). Mal strings had high entropy (diversity, surprise or randomness; mean 0.86; range, 0.49 to 0.98), often approaching the theoretical maximum of 1.0. In contrast, Cop strings had low entropy (mean 0.51; range, 0.34 to 0.64), indicating considerable redundancy (repetition of elements such as Bow. See self-loops in Fig. 1). Fem bouts (mean 0.68, range 0.31 to 0.92) had variable entropy, overlapping with both Mal and Cop bouts.

Figure 3 depicts compression ratio of the display sequences across the three contexts (Mal, Fem, Cop). Cop bouts had far higher compression ratios than did Mal bouts. The compression ratios differed among the three contexts (Mal, Fem, Cop) under ANOVA followed by Tukey's HSD (P < 0.001). Figure 4 shows the compression ratio of all bouts performed by our most prolific male (M296; Table 4), by sample day. M296 performed many Mal, Fem and Cop displays, but always had Mal bouts with low compression ratio, even after multiple copulation bouts.

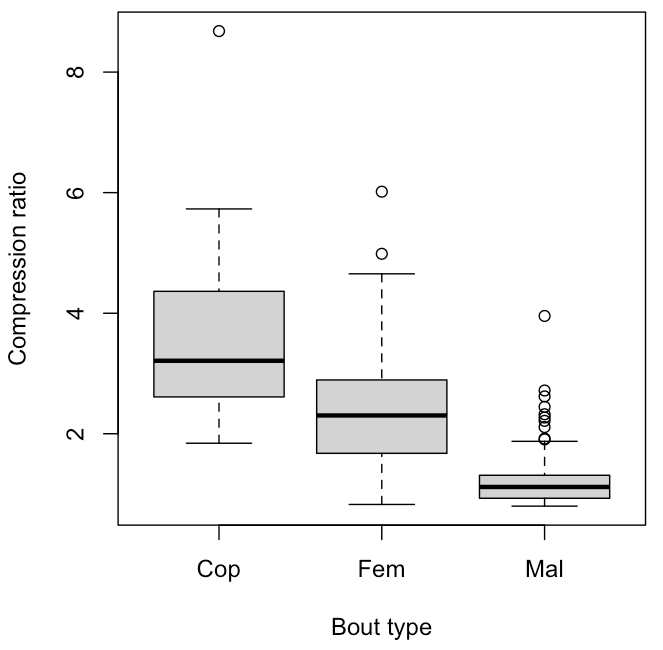


Figure 3. Compression ratio of *Masius* displays (strings of behavioural elements) for Cop, Fem and Mal bouts. Lossless compression was conducted with Huffman encoding and the LZ77 algorithm. Compression ratio is the ratio of the length of the uncompressed string to the compressed string. For example, the maximum compression ratio (8.68) was for a Cop sequence (upper left). Mal sequences had significantly lower compression ratios (range 0.8 to 3.96; mean 1.2) than did Cop sequences (range 1.8 to 8.68; mean 3.7). Mal sequences were often a complex jumble of disparate behavioural elements. Cop sequences, in contrast, generally had had oft-repeated elements, especially Bows, as well as repeated motifs of varying length. Fem sequences (mean 2.4) were intermediate. The repeated motifs detected (and compressed) by the length-distance, sliding window feature of the LZ77 compression algorithm are one major difference from the entropy analyses (Fig. 2), which depend only on relative frequencies of elements.

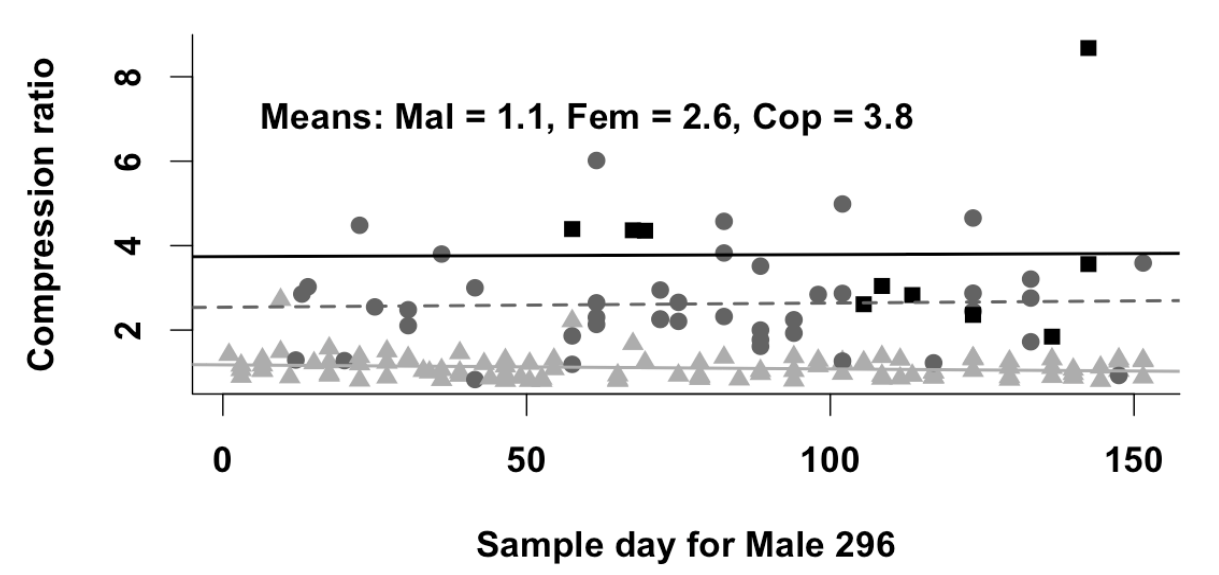


Figure 4. Compression ratio of the Mal (light gray triangles), Fem (dark gray circles) and Cop (black squares) bouts by Male 296, across his 152-day span of appearing in video clips. Note that, despite Cop bouts beginning as early as sample day 57, his later Mal bouts continued to have low (~1.1) compression ratios. The slope of compression ratio as a function of sample day was flat (- 0.001). That pattern runs counter to the hypothesis that males might perform more organized Mal displays after performing one or more successful, organized (high compression ratio) Cop displays, which would produce a positive slope. Instead, male display organization depends largely on the context (Mal vs. Fem vs. Cop) –always simple and with high compression ratio in displays containing copulations, always complex (diverse) and with low compression ratios in Mal displays.

Figure 5 shows expected Jaro string distances (left four bars) under the hypothesis that individual differences between different males ("personalities") drive variation in display sequences. Low Jaro distances mean the displays compared are similar. The four gray and black bars on the right show the observed Jaro distances, which support the hypothesis that display sequences according to context (Mal, Fem, Cop), and do not support the individual-difference hypothesis depicted by the four leftmost expected bars. The pooled Within- and Between Mal Jaro distances differed significantly from the pooled Within- and Between Cop Jaro distances (*t-test*: *t* = 17.24, *df* = 91.2 P < 0.0001). To examine the effect of the small sample size (43) of Cop Jaro distance pairs between males, we randomly selected sets of 43 distance pairs and computed their mean Jaro distances from one another for 10,000 replicates. The absolute differences between the means of the resampled distributions and the observed means were < 0.0002, and within 0.1% of each other. None of the 10,000 random Mal-Within replicates (mean = 0.39; 95% CI = 0.36 to 0.43) overlapped the random Cop-Within replicates (mean = 0.25, 95% CI = 0.22 to 0.28). Likewise, no Mal-Between values (mean = 0.42; 95% CI = 0.39 to 0.45) overlapped with the Cop-Between values (mean = 0.23; 95% CI = 0.21 to 0.26). Differences between the Jaro distances across the three contexts (Mal, Fem, Cop) are shown in Fig. S2.

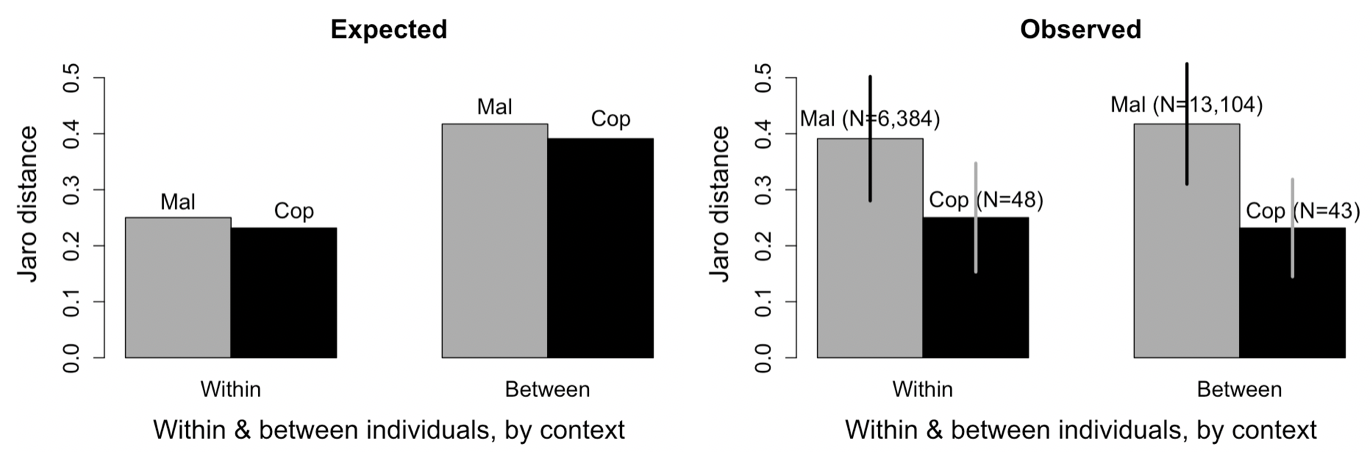


Figure 5. Expected (left four bars) Jaro string distance outcomes under the hypothesis that individual differences ("personalities") drive variation in display behaviour more than do contexts (Mal, Fem, Cop). If "personalities" mattered most, we would expect a male's own displays to be similar to each other (short Within Jaro distances; Mal-Within Cop-Within), regardless of context (Mal, Cop). We would expect a male's displays to be dissimilar to those of other males (high Mal-Between and Cop-Between). Instead (Observed, right four bars), a male's own Mal displays were almost as different from each other (Mal-Within = 0.39) as from those of other males (Mal-Between = 0.42). Cop displays were always very similar (short Jaro distances) whether Within or Between. In fact, males' Cop displays were slightly more similar (Cop-Between = 0.23) to those of other males, than to their own (Cop-Within = 0.25). Thus, variation in display is largely a matter of context; Mal Within resembles Mal Between and both differ greatly from Cop Between and Cop Within, which closely resemble each other, regardless of male or female identity. Vertical lines on rightmost four bars are ± 1 sd. None of the values in the Observed Mal-Within resampled distribution overlapped with any in the Observed Cop-Within resampled distribution. Likewise none of the values in the Observed Mal-Between resampled distribution overlapped with any of those in the Observed Cop-Between resampled distribution (see Methods and text for more details), meaning that the small sample size of Cop Jaro distances did not affect the conclusions.

## **DISCUSSION**

## Our major result is that context dependence and simplicity, not individual differences ("personalities") or complexity characterize variation in the courtship displays of male *Masius*. The pattern holds, across our three contexts (Mal, Fem, Cop), whether assessed in terms of weighted networks (Fig. 1), entropy (Fig. 2), compression ratio (Figs. 3 and 4) or Jaro string distance (Fig. 5). The emergent feature is a progression, from diverse (more random) display sequences that were dissimilar (from one bout to the next) when no female was present (Mal bouts), to redundant (predictable, organized) and similar to one another (within or between males) in displays leading to copulations (Cop bouts). In contrast, variation between males was relatively minor, especially in displays that included a copulation. Each of our analyses (networks, entropy, compression ratio, Jaro distances) contributes to a fuller understanding of how simplicity and context-dependence characterize the organization of *Masius* courtship displays.

## We assessed the comparative simplicity of the displays by analyzing them as networks (Fig. 1). Network density (proportion of all possible edges actually occurring) decreased from Mal to Fem to Cop, meaning that Mal bouts (density = 0.8) had many different kinds of transitions between display elements, while Cop bouts, especially (density = 0.27), had relatively few types of transitions. Low effective degree corresponds to high variance in edge weight, with one or a few edges dominating the transitions. With no variance in edge weights, effective degree equals simple binary degree (i.e., a simple count of the edges, disregarding weights). Cop bouts had low effective degree (2.8), meaning that most of the edge weight was concentrated on a few edges, particularly the repetition (heavy self-loops in Fig. 1) of Bows (before audible log-approach displays, ALADs) and Neck twists (after ALADs). In contrast, the Mal network had much higher effective degree (24.8), meaning a more even distribution of edge weights, and lower rates of repetition for any particular display element. All-simple-paths analysis showed a dramatic difference in the number of possible paths among nodes when comparing the Cop network (1,530 simple paths) to the Mal network (mean of 649,610 paths). That difference certainly underestimates the true difference by a wide margin, because we used a set of reduced-edge Mal networks to make the analysis computationally feasible.

## Commonly, increased song complexity, often assessed by entropy (Da Silva, Piqueria, & Vielliard, 2000; Palmero, Espelosín, Laiolo, & Illera, 2014) has been considered a positive attribute, associated with increased mating success. Here, we find that, to the contrary, Cop (successful courtship) bouts had significantly lower entropy (Fig. 2, mean = 1.57) than did Fem bouts (mean = 2.21) or Mal bouts (mean = 2.61). Thus, display bouts that include a copulation tended to be more predictable, with greater repetition of display elements, particularly Bows and Neck twists than do either Fem or Mal bouts. Concordant with our results, Vanderbilt, Kelley and DuVal (2015) found that in the dual-male courtship displays of Lance-tailed Manakins, *Chiroxiphia lanceolata*, displays for females had lower entropy than did displays in the absence of females.

## Compression ratio (Fig. 3) increased dramatically from Mal bouts to Fem bouts and thence to Cop bouts. Compression ratio was highest in Cop bouts, which featured long strings of repeated behaviours—particularly Bows and Neck twists—and the repeated motifs of elements detected by the LZ77 algorithm.

## Overall, Jaro string analysis (Fig. 5) indicated that Mal display bouts were variable within and between males, and that Cop bouts were similar, whether within or between males. Cop bouts (mean Jaro distance = 0.24) were more similar to each other than Fem bouts were to each other (mean Jaro distance = 0.38) or Mal bouts were to each other (mean Jaro distance = 0.41; the bars in Fig. S2). Thus, structural differences in the organization of courtship displays were due largely to the context—female present or not, and progressing toward copulation or not— and not to consistent differences between males in how they organized their displays. Although they measured similarity differently, Botero et al. (2009) stressed the importance of consistent song repertoires in Tropical Mockingbirds (*Mimus gilvus*), both as an ontogenetic trajectory and to explain reproductive success. Similarly, Janisch, Perinot & Fusani (2020) found that male *Manacus vitellinus* developed consistent courtship display sequences, in terms of movements around their courts.

## Why are Mal bouts (no female present) more random and disorganized than either Fem or Cop bouts? Displays with no female present (Mal bouts) could represent practicing, identifying the best trajectory for log-approach displays (ALADs and, particularly, SLADs), or maintaining control of a display log, to name but a few possibilities. None of these behaviours requires strict adherence to a fixed routine, possibly increasing the complexity and diversity of male-only displays (Mal) when compared to Fem or Cop bouts. The simple presence of a female appeared to suffice in galvanizing males to perform simpler and more organized display sequences.

## A feature that still puzzles us is how females choose which display logs to visit. In many lek-mating species, females can use fairly long-distance visual or acoustic cues to locate the courts of displaying males. In *Masius*, the "nurrt" advertising call is of surprisingly low-amplitude and is performed at a low rate overall, even at the height of display activity in Nov and Dec (2.2 nurrts/min at the two most active display logs) and within-bout vocalizations averaged only 4.2/min, reasonably similar to the calling rates documented by Prum & Johnson (1989). The call rate for *Masius* contrasts sharply with the far-carrying dual-male *toledos* of male Long-tailed Manakins, *Chiroxiphia linearis,* which occurred at overall rates > 5.4 toledos/min (McDonald, 1989) over the course of entire days (McDonald 2010, Fig. 1), with within-bout rates averaging 15.6/min (Trainer and McDonald, 1993). We conclude, provisionally, that males rely mostly on regular traffic of females to promote female visitation, as might be predicted under a hotspot model of lek placement (Bradbury, 1981; Beehler & Foster 1988). Further, our proportion of banded females and revisitation rates by banded females were far higher than in Long-tailed Manakins (pers. obs.), suggesting that female *Masius* may have much smaller home ranges that largely overlap the display logs of the males they sample.

## Our results do provide some insights into the bases and patterns of female mate choice, once they have chosen to visit a display log. The similarity of Cop displays across three distinct males, despite their being performed for at least 14 different females, suggests that a simple, rather invariant display worked well when females were ready to copulate, as indicated by females' steady presence on the display log during Cop bouts as compared to Fem bouts. A simple sequence of many Bows, followed by an ALAD, immediately followed by a copulation and then a series of Neck twists, was the consistent pattern for Cop bouts. One might suppose, that once having succeeded in copulating, males would modify their Mal and Fem displays to more closely resemble the simple rhythm of Cop displays. Our data do not support that hypothesis. Fig. 4 shows that M296's Mal displays did not become more organized and less complex as the breeding season progressed. Even immediately after Cop bouts with high compression ratios, M296's Fem and Mal bouts had low compression ratios was similar to those of bouts long before the first copulation.

## Once females chose to visit, an obvious feature of Fem and Cop displays was that male behaviour depended on the relative position of the female. When she was below him on the log, he would perform Bows until she moved or he left the log to perform an audible log-approach display (ALAD). When she was above him, or off the display log, he would perform Neck twists. If a female was not in the immediate vicinity of the display log, the male might still perform those same behaviours, but would tend not to repeat them for as long, and would perform them in broken series, in a less predictable order. Further, the male would intersperse other display elements that he did not perform while the female was on the log, such as Metronome displays. The result was long strings of disjointed behaviours and frequent male flights to and from the display log. Although it was not the primary focus of this paper, we found that female as well as male behaviour varied across contexts. Females moved on and off the display log more during Fem bouts, perhaps because it was their first visit to a particular display log that season, or because they lacked experience in evaluating males. The results suggest that when females were prepared to copulate, they moved much less on the log, providing some feedback to the male on the female's interest level, and causing males to settle into the simple and predictable rhythm of the peri-copulatory displays.

## The most dramatic behavioural element in the courtship display of *Masius* is the audible log-approach display (ALAD); it occurred just prior to all 24 observed copulations, and is perceived as a blur by the human eye (see slow-motion video at http://www.uwyo.edu/dbmcd/masiusvideo.html). Why should females respond to such an odd and rapid maneuver? One intriguing possibility is that it requires extreme agility that could be useful in a foraging context, for females as well as their offspring. Howe (1979) argued that small frugivores might be particularly vulnerable to predation at fruit trees, which are reliable sites for prey detection. Consistent with Howe's hypothesis, Uriarte et al. (2011) found that four species of manakins spent a mean of only 13 ± 4.3 secs at their fruit trees. Many of the visits had zero perch time, because birds often gulped (Levey, 1987) the fruits and departed, without ever perching. For larger frugivores, perch times can be considerably longer (median visit length 225 secs, Wheelwright, 1991). Ultra-rapid maneuvers while taking fruit might significantly reduce predation risk at these predictable locations. High-speed video of *Masius* at fruit trees, particularly in the event of a predation attempt, would be an interesting test of this hypothesis.

## Although we found that greater simplicity and uniformity characterized successful courtship displays, we are not arguing that simplicity or uniformity, per se, increases reproductive success in *Masius*. Instead, we conclude that context (presence or absence of a female), and behavioural feedback from female visitors, as demonstrated in the elegant experiment by Patricelli, Coleman & Borgia (2006; see also Rodríguez et al., 2012), together create a progression from diverse (unpatterned, with low repetition of elements), to orderly (highly patterned with repeated elements and motifs) in displays leading to copulations. Displays leading to successful copulations are simple and uniform from one iteration to the next, whether within the Cop displays of an individual male or between the Cop displays of different males. What remains an intriguing question is how and why females transition from fidgety (many landings and departures from the log in Fem bouts) to focused (steadily remaining on the log during Cop bouts). Gibson (1996) found that the inter-pop interval was positively correlated with the number of females visiting a sage grouse (*Centrocercus urophasianus*) male, but that eventual copulation was related to display rate. Similarly, McDonald (1989) found that female visitation correlated with the output of dual-male unison *toledo* song in Long-tailed Manakins. Copulatory success, however, correlated with the duration of the dual-male butterfly flights, which occur between bouts of dual-male backwards leapfrog displays. Those studies suggest that female preferences are based, not on a single male trait, but instead vary with a female's sampling context, experience and, very likely, her reproductive state. Thus, understanding prior female experience (both within and across years) may be critical to understanding how female response to courtship drives context-dependent variation in displays. The ball is back in the court of the difficult problem of assessing female sampling histories, often stretching back several years, and of ascertaining female motivational states.

*Conclusions*

## We conclude that *Masius* courtship displays progress from disorderly jumbles to tightly organized sequences characterized by repetition of major display elements (particularly Bows) as the context moves from male-only displays to those leading to copulations. We have provided a worked example of the utility of network, lossless compression and Jaro string-distance metrics that could be applied to many other sorts of sequences of behaviours. For example, the methods used here could be applied to the frame of reference, in terms of motor activity (sensu Miller, 1988), variation in song repertoires, other sorts of courtship display, animal movement trajectories and even sequences of environmental variables such as time series of temperature data. These metrics were powerful enough to differentiate between Fem bouts (female present) and Cop bouts (including one or more copulations) and to demonstrate that those differences arose due to differences in context, and not to individual differences between males. Despite the lack of individual variation in Cop displays, we do not conclude that behavioural syndromes are absent in *Masius*. They are just not a driving force behind the organization of and variation in courtship displays. Likewise, the simplicity of successful courtship displays (Cop bouts) does not mean that complexity and non-linearity (Bradbury & Vehrencamp, 2014; Patricelli & Hebets, 2016) are not important to many other aspects of the behaviour of *Masius* or other manakins. Nevertheless, for *Masius* displays, as found by Cardoso and Hu (2011) for wood warbler song, we conclude that "simple does it."

**DATA AVAILABILITY**

All R scripts used for the analyses are available, on request, from the corresponding author. [OR AS SUPPLEMENTARY MATERIAL?]

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**ACKNOWLEDGMENTS**

The Mindo Cloudforest Foundation (MCF) allowed us to use their Milpe Sanctuary for our study. Brian Krohnke and Maria José Guerrero of MCF were extremely helpful in providing logistical support. Support from the Fulbright Foundation, and the University of Wyoming's Flittie sabbatical fund helped enhance the field efforts. We are grateful to Grady Harris, Will McDonald, and many field assistants for hard work in the field that provided the scaffold on which we built our research. The University of Wyoming Education Abroad Program provided some of the travel funds for the authors. Gracias tambien a la vida silvestre, al pueblo y al gobierno del Ecuador.

**Compliance with Ethical Standards**

*Conflict of Interest*

The authors declare that they have no conflict of interest.

*Ethical Approval*

All applicable international, national, and institutional guidelines for the care and use of animals were followed. Capture by mist nets, handling and banding were approved by the University of Wyoming's Institutional Animal Use Committee (IACUC protocol #20160602DM00242-01) for each of the years of fieldwork.

**Supplementary Materials**

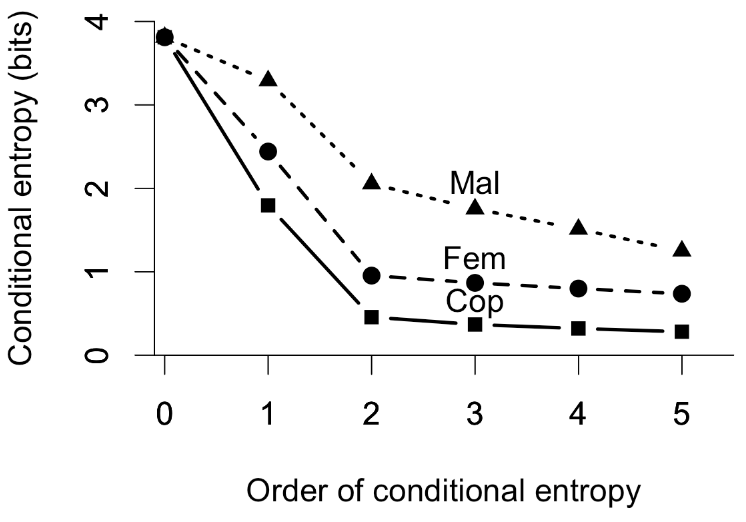


Fig. S1. Higher order (conditional) entropies for Mal, Fem, and Cop bouts. Order 1 is the first-order entropy of Fig. 2. Note that Mal continues to drop for higher-order entropies beyond Order 2. That difference suggests that in Fem and Cop bouts, the current element depends largely on the preceding element, whereas in Mal bouts, elements depend, in complex ways, on earlier elements. Nevertheless, the sharpest drop for all three is from Order 1 to Order 2, suggesting that the sequences are a reasonable fit to a first-order Markov chain process.

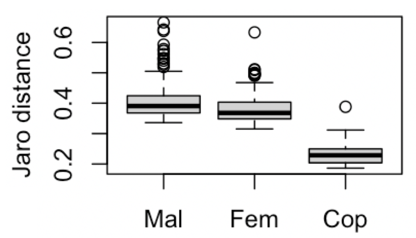


Fig. S2. Boxplots for Jaro distances in 198 Mal bouts, 100 Fem bouts and 14 Cop bouts. Cop bouts are considerably more similar to each other (low Jaro distances), than are either Mal or Fem bouts.

Table S1. List of 41 unmodified BORIS behavioural elements that were abbreviated, omitted or combined (indented in italics) to create the 21 numbered variables (ethogram elements) listed in Table 1.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Behaviour value in BORIS | Frequency | Abbreviation for analyses |
| 1 | Attempted Copulation | 11 | 1. AttCop |
| 2 | Bird2 ALAD | 55 | 2. B2AL |
| 3 | Bird2 BowLeft | 695 | 3. B2Bw |
| 4 | Bird2 BowRight | 677 | B2Bw |
| 5 | Bird2 Half-bow Left | 26 |  |
| 6 | Bird2 Half-bow Right | 21 |  |
| 7 | Bird2 HeadDownBowing | 56 |  |
| 8 | Bird2 Mixed Element | 13 |  |
| 9 | Bird2 NeckTwist | 1693 | 4. B2Nk |
| 10 | Bird2 On-log NO display | 79 |  |
| 11 | Bird2 SLAD | 1 |  |
| 12 | Bird2 TafLF\_Off | 28 |  |
| 13 | Bird2 TafLF\_On | 26 |  |
| 14 | Copulation | 24 | 5. Cop |
| 15 | End | 486 | 6. End |
| 16 | Female Looking Away | 1736 |  |
| 17 | Female Movement | 978 |  |
| 18 | Female Off Log | 320 | 7. Fff |
| 19 | Female On Log | 320 | 8. FOn |
| 20 | Female ResponseToALAD | 188 |  |
| 21 | Female Tracking Male | 1924 |  |
| 22 | FemaleSwitch | 406 |  |
| 23 | Male1 ALAD | 1104 | 9. ALAD |
| 24 | Male1 BowLeft | 8088 | 10. Bow |
| 25 | Male1 BowRight | 7950 | Bow |
| 26 | Male1 Half-bow Left | 296 | 11. HafB |
| 27 | Male1 Half-bow Right | 258 | HafB |
| 28 | Male1 HeadDownBowing | 2361 | 12. HdBw |
| 29 | Male1 Metronome\_Left | 11 | 13. Metr |
| 30 | Male1 Metronome\_Right | 25 | Metr |
| 31 | Male1 Mixed Element | 361 | 14. Mix |
| 32 | Male1 NeckTwist | 5618 | 15. Neck |
| 33 | Male1 Off Log | 41 |  |
| 34 | Male1 On Log | 39 |  |
| 35 | Male1 On Log No Display | 2225 | 16. Zero |
| 36 | Male1 Other Behaviour | 2142 | 17. OthX |
| 37 | Male1 SLAD | 655 | 18. SLAD |
| 38 | Male1 Switch | 1145 | 19. Swtc |
| 39 | Male1 TafLF\_Off | 1193 | 20. Taf |
| 40 | Male1 TafLF\_On | 1223 | Taf |
| 41 | Start | 486 | 21. Start |

Notes for 2022-2023 revision.

Fig. 1. Four measures of the gradient of complexity from complex male-only courtship display bouts (Mal) to courtship displays with one or more females present but no copulation (Fem) to least complex in courtship displays ending in a copulation (Cop)  
a. Elem count/BoutLength ratio (output of 10-Oct-22). Ratio of (distinct element count)/(string length) here.   
  
 Chart, box and whisker chart

Description automatically generated

b. Entropy is as much a measure of surprise as of complexity. Entropy goes from low (few surprises) in display bouts ending in a copulation (Cop) to high in display bouts involving only males (Mal), with intermediate entropy for display bouts attended by one or more females that did not end in a copulation (Fem).   
  
 Chart, box and whisker chart

Description automatically generated

c. Compression string length (raw or ratio?). Ratio here. A courtship bout whose string of display elements can be greatly compressed (high compression ratio on the ordinate), such as the Cop display bouts, can be viewed as less complex than ones that are not very compressible, such as the Mal display bouts.   
  
 Chart, box and whisker chart

Description automatically generated  
  
 d. Algorithmic complexity, as an approximation of Kolmogorov complexity. Again, the   
 complexity gradient goes from low complexity for display bouts ending in a copulation   
 (Cop), to high complexity in display bouts involving only males (Mal).

Chart, box and whisker chart

Description automatically generated

From Liam's email of 6-Oct-22

"Focusing on the compressibility score as the central value and explicitly comparing it to simple measures like "repertoire size" might make for a very simple+impactful presentation of the data.

A central figure might be as simple as a four subplot bar plot:

(A) Repertoire sizes. Mal vs. Fem (exclude cop) vs. Cop.

(B) Entropy. Mal vs. Fem (exclude cop) vs. Cop

(C) Length of compression string. Mal vs. Fem (exclude cop) vs. Cop

(D) If any different than (C), Algorithmic complexity from acss. M vs. F vs. C

Then another figure (or worked into the above) parsing within vs. between individuals.

Plot (A) gives us the background value that most investigators might have looked for.

Plot (B) tells us something about predictability -- from the view of the female, how "surprised" she might possibly be, given the available male display elements.

Plot (C) tells us something about an approximation of complexity -- from the view of the male, how simple is the display to produce (aesthetic structure, repetition, etc.).

Plot (D) bolsters plot (C) with a slightly different estimator of complexity."

Questions/comments for Liam (22-Oct-22)

Should we call the 11 elements "events" rather than "elements"? Some (Cop, AttC, FOn, Fff, Mix, Othr, Zro) are not display elements per se (especially in the Schaedler comparative scheme).

Are the (almost impercepible, except in slomo) neck bobs and tail wags after an ALAD worth attomizing?

Vault (male vaults over female when both are on the log): does it occur in context other than ALAD?

Gradient from Neck twist (*Neck*) to Head-down Bow (*HdBw*)

Nick's lower canopy flybys?

"Kichup" sound in ALAD is a vocalization. See "1519\_Taf&kichup ALAD voc.mp4" & "1519\_CreekLog\_11\_18\_17\_02,mp4"

I need to check on "Gaping", Nick's fly-bys and wing-flicks. Check email of 22-Oct-22 and new voucher videos in Dropbox.

Hasenjager, Matthew J., Victoria R. Franks, and Ellouise Leadbeater. “From Dyads to Collectives: A Review of Honeybee Signalling.” Behavioral Ecology and Sociobiology 76, no. 9 (September 2022): 124. <https://doi.org/10.1007/s00265-022-03218-1> Zotero.

Bosshard, Alexandra B., Maël Leroux, Nicholas A. Lester, Balthasar Bickel, Sabine Stoll, and Simon W. Townsend. “From Collocations to Call-Ocations: Using Linguistic Methods to Quantify Animal Call Combinations.” Behavioral Ecology and Sociobiology 76, no. 9 (September 2022): 122. <https://doi.org/10.1007/s00265-022-03224-3>. Zotero