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

**ABSTRACT**

In polygynous lek mating systems, males perform elaborate 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 addressing another level—syntax complexity—which focuses on how organisms arrange the elements of their display. We analyze 353 displays of lek-mating Golden-winged Manakins, *Masius chrysopterus,* by coding their dances as strings of behavioral elements. In addition to the simple measure of repertoire complexity (number of unique elements in a display), we use methods from information science to calculate multiple measures of syntax complexity (entropy and compressibility). 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, n = 13) 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 between context (SOLO, AUDI, COP) than between individual. Females chose to copulate after simple displays building to a dramatic high-speed element (the audible log-approach dive). These results raise questions about the difference between song and dance displays, the role of audience participation, and a third level of complexity—element complexity—that reckons with the aesthetic content of 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). Milpe comprises 100 ha of west slope Chocó-Andean forest (1,100 m elevation) 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. We only included sequences that lasted >60 s and included two core behavioral elements, “Audible log-approach dive” and “Side-to-side bow” (Table 1; $PRUM\_JOHNSON, $TAYLOR).

*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 displays featuring multiple dancing males (n = 26) or a single, identified male audience (n = 3, all predefinitive Male #980, including one copulation). We retained 21 displays where an audience member was suspected as a predefinitive male based on plumage but performed no display behavior. A comparison of displays for female and suspected predefinitive male audiences is given in Supplementary Material.

We categorized the remaining 353 male displays into three categories: SOLO (n = 251), AUDI (n = 89), and COP (n = 13). SOLO displays were solo male performances, AUDI displays featured one or two audience members at some point during the display but did not end in successful copulation, and COP displays ended in a successful copulation. For our main analyses, we ended COP displays at the moment of copulation. A comparison of before- and after-copulation displays is given in Supplementary Material.

We coded display elements using Behavioral 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 (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 male behaviors not directly involved in display dances (e.g. “Vocalization,” “Gardening”). Finally, we combined paired elements into single behaviors (e.g., “Side-to-side bow Left” and “Side-to-side bow Right” become “Side-to-side bow”) and excluded “Attempted copulation” and “Copulation” elements. The 12 remaining, core display behaviors—including pauses (“Zero”)—are described in Table 1.

### *Repertoire complexity*

We calculated three simple metrics related to the repertoire of individual *Masius* displays: (A) Duration, in seconds; (B) Length, in number of total elements; and (C) Repertoire size, in umber of unique elements. Display duration was calculated from the raw data, and thus included the timing of some elements excluded from other behavioral analyses.

We compared repertoire complexity measures across context (SOLO, AUDI, COP) with ANOVA and Tukey’s HSD. To address our small sample size of COP displays (n = 13), we compared our COP metrics to a randomized distribution. Across each of 10,000 replicates, we randomly selected (without replacement) 13 displays from any context in our full dataset. We then compared the distribution of randomly-selected display metrics to the empirical COP values. All analyses were conducted with the *tidyverse* packages in Program R v4.2.2 ($TIDYVERSE, R).

*Syntax complexity*

We quantified syntax complexity of displays with two related measures: entropy and compressibility. We began by translating displays into strings of individual characters (Table 1). We computed the first-order entropy display strings with *entropy* function in R package *acss* ($CITE). The resulting values depend on the empirical frequency of each element in each individual display. We thus scaled each value by the maximum possible entropy for a display—given as log2(number of unique elements)—giving a final metric between 0 and 1 (Vanderbilt, Kelley, & DuVal 2015). We computed compressibility using a standard text compression algorithm (LZ77 and Huffman Coding) implemented with default parameters in the R package *brotli* ($CITE). The final compressibility metric was taken as the ratio of the length of the uncompressed string to the compressed string.

We compared syntax complexity measures across context (SOLO, AUDI, COP) with ANOVA and Tukey’s HSD. As with repertoire complexity, we used a randomization procedure to compare the small sample of 13 COP displays to a randomized distribution of both entropy and compressibility metrics (10,000 random sets of 13 displays from the full dataset, drawn with no replacement).

Entropy and compressibility are fundamentally intertwined metrics. In theory, high entropy systems produce outputs that lack well-defined, repeated motifs and are therefore difficult to compress ($CITE). We assessed the empirical correlation between entropy and compressibility in our data and investigated displays diverging from that correlation.

*Context vs. individual variation*

We asked whether displays varied more in terms of context (i.e., SOLO *vs.* AUDI *vs.* COP) or in terms of male individuality using Jaro string distances. 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 calculated Jaro distance among all display strings using R package *stringdist* ($CITE). Using only displays from identified males in each context, we compared four sets of distances: (A) same-male/same-context, (B) same-male/different-context, (C) different-male/same-context, and (D) different-male/different context.

## **RESULTS**

*Displays and behavioral elements*

Our final dataset includes 353 *Masius* displays across 15 display logs (1-102 displays per log). Of these displays, 341 were performed by one of 10 identified males (2-172 displays each, Table S2). All displays occurred between 24-Jun and 14-Jan, with the bulk of displays (278/353) between October and December (Fig. S1). The earliest AUDI display was 30-Jun and the earliest COP display was 26-Oct.

The dataset featured 36 AUDI displays with one of 11 identified females (1-7 attendances each) and 5 COP displays with one of 3 identified females (1-2 copulations each; Table S3). All 13 COP displays were performed by one of 3 identified males (1-9 copulation each; Table S4).

By definition, every display in our dataset featured at least one Audible log-approach dive and Side-to-side bow. Representation of the remaining behaviors differed in terms of display context (Table 1, see Table S5 for raw frequencies). Silent log-approach dives were frequent across SOLO displays but present in only 1 AUDI display and 0 COP displays. To-and-fro flights were common in AUDI displays (77/89 displays) but relatively rare in SOLO (63/251) and COP (2/13). Neck twists were common in AUDI (86/89) and COP (9/13), but rare in SOLO (21/251). Head-down bows were nearly universal in SOLO (248/251) and AUDI (88/89) displays, but absent from COP. However, there were Head-down bows and the rare Metronome element in 2 and 1 after-copulation displays, respectively (Supplementary Material). Pauses, Mixed, and Other behaviors were more common across SOLO displays than AUDI and COP displays (Table 1).

*Repertoire complexity*

In terms of raw display duration, AUDI displays (mean ± S.D.: 217 ± 130 s) were significantly longer than both SOLO displays (136 ± 65 s) and COP displays (126 ± 41 s; overall ANOVA *P* < 0.001; Fig. 1A). In terms of the total number of display elements, AUDI displays (101 ± 72 elements) were again significantly longer and more variable than SOLO display (62 ± 16 elements), which in turn were significantly longer than COP displays (24 ± 13 elements; overall ANOVA *P* < 0.001; Fig. 1B).

In contrast to these patterns in display length, COP displays had significantly smaller repertoires (3.2 ± 0.8 unique elements) than the similar SOLO displays (5.9 ± 1.1 unique elements) and AUDI displays (5.9 ± 1.0 unique elements; overall ANOVA *P* < 0.001; Fig. 1C). Across 10,000 replicates of 13 randomly-drawn displays from our dataset, mean repertoire size was never less than the empirical mean of the 13 COP displays (Fig. S2).

*Syntax complexity*

SOLO displays showed significantly higher scaled entropy values (0.87 ± 0.07) than AUDI displays (0.71 ± 0.12), which in turn had significantly higher scaled entropy than COP displays (0.26 ± 0.16; overall ANOVA *P* < 0.001; Fig. 2A). There was an identical pattern in compressibility, measured as the ratio of uncompressed to compressed display string length. SOLO display strings had significantly lower compression ratios (1.07 ± 0.30) than AUDI display strings (2.80 ± 1.15), which were significantly less compressible than COP display strings (3.65 ± 1.01; overall ANOVA *P* < 0.001; Fig. 2B). None of 10,000 random sets of 13 displays for each metric had a lower mean entropy or higher mean compression ratio than the empirical set of 13 COP displays (Fig. S2).

As expected, entropy and compressibility were significantly correlated across our dataset (linear regression, adjusted *R2 =* 0.53, *P* < 0.001;Fig. 2C). However, wide variation highlighted the differences between these metrics. For example, the most compressible display string (AUDI ID-1487, compression ratio = 7.45) had intermediate entropy (0.63) but was long, with 365 total elements, and primarily made up of long stretches of Side-to-side bows and Neck twists. A display with similar entropy but much lower compression ratio (AUDI ID-453, scaled entropy = 0.64, compression ratio = 2.53) was shorter, with 81 elements, and featured a tail of individual behaviors (coded “*IEDBA*”; Table 1) that made it difficult to compress. Indeed, our choice of compression algorithm (LZ77 and Huffman Coding) and our final compression ratio metric created an overall positive correlation between display length and compressibility (Fig. S3).

The lowest entropy display (COP ID-1533, scaled entropy = 0.11, compression ratio = 4.71) was simply 66 Side-to-side bows followed by an Audible log-approach dive. A closer look revealed a characteristic syntax for COP displays (Table S2). Ten of 13 COP displays, across all 3 copulating males, ended with long (34+) stretches of Side-to-side bows followed by an Audible log-approach dive. One display (ID-1455) was similar except for the insertion of a single Half-bow before the dive, while another (ID-1987) had a short sequence of two additional elements—To-and-fro flights and then a Neck twist—before the final bow and dive combination. The remaining display (ID-1824) was primarily stretches of Neck twists, yet still ended with a bow and dive combination (Table S2).

*Context vs. individual variation*

Displays in every context (SOLO, AUDI, COP) had average shorter Jaro distances to displays of the same context than to displays of other contexts, regardless of the individual male performing the display (Fig. 3). Across all contexts, the distances among displays from the male in the same context (mean ± SD, 0.37 ± 0.11) was only slightly lower than among displays in the same context by different males (0.39 ± 0.11). In contrast, displays in different contexts were more distant whether given by the same male (0.53 ± 0.10) or different males (0.54 ± 0.10). Mean Jaro distance (different male, same context) was shorter among COP displays (0.14 ± 0.10) than among either AUDI displays (0.36 ± 0.10) or SOLO displays (0.39 ± 0.11).

Average similarity comparisons were not absolute rules. Across the 13 COP displays, 6 were closest to another COP display by the same male and 3 to another COP display by a different male. However, 2 COP displays were most similar to an AUDI display by the same male and 2 to an AUDI display by a different male.

**LITERATURE CITED**

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