



DO SOCIAL INTERACTIONS PREDICT SIMILARITIES IN AUDIO-VISUAL COURTSHIP SIGNALS IN SPOTTED BOWERBIRDS?

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ABSTRACT

Spotted bowerbirds perform a multi-modal courtship display on dedicated structures – bowers – that are built by one resident male. Bower owners tolerate the presence of specific subordinate males at their bowers, yet the role of these male-male associations remains unclear. One explanation is that these immature males are learning the skills required for successful sexual signalling. Courtship in this species consists of a sequence of harsh calls, body postures and movements. If social learning occurs, male-male associations may result in similarities in acoustic and visual signals within owner-subordinate pairs. In this study, we tested whether the magnitude of social interactions can predict similarities in audio-visual display patterns in a single population of spotted bowerbirds. We video-recorded their courtship behaviour to examine whether bowerbirds (i) exhibit micro-geographical similarities in their audio-visual displays and (ii) are more similar in their courtship to conspecifics with whom they interact more frequently at bowers. For both acoustic and visual courtship components, we found evidence for micro-geographical variation that was not explained by genetic distance. However, social proximity covaried with similarities in acoustic – but not visual – displays. Our findings raise relevant questions about the mechanisms of social learning in audio-visual sexual signalling.

Keywords: *learning, multi-modal, courtship, bowerbird.*

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1. INTRODUCTION

Many territorial and sexual signals used in animal communication exhibit local patterns of similarities consistent with social learning and cultural transmission [1, 2]. Some of the best-known examples include acoustic signals in birds [1] and some mammals [3]. Social learning occurs when young individuals acquire specific variants of a signal in their natal area, typically from their parents, or via exposure to local tutors in the cases where learning is completed after dispersal [4, 5]. In the latter case, the social dynamics that mediate learning of specific signal variants are complex and diverse, and in a number of species these are not investigated in sufficient detail, particularly in the wild [6].

Direct social interactions have been shown to play a crucial role in guiding signal learning. Experiments in controlled conditions showed that exposure to live tutors is a critical aspect of learning in many species, particularly for acoustic signals [7, 8]. Indeed, song learning in some oscine birds has been described as a social process, shaped by prolonged social interactions during song development [6]. For example, song sparrows (*Melospiza melodia*) acquire complex vocal repertoires via social interactions with multiple tutors after dispersal [9]. Juvenile individuals have been shown to increase their exposure to socially relevant stimuli by means of specific behavioural strategies, such as by interacting selectively with certain tutors [10, 11]. Furthermore, adult tutors appear to tolerate younger birds during the early phases of song development in some species [12], and these interactive same-sex relationships have been cited occasionally as examples of active teaching [10, 13]. However, while the role of such interactions in guiding social learning has been investigated

primarily in controlled laboratory conditions, relatively fewer studies have attempted to link same-sex social dynamics to patterns of similarities in courtship signals in the wild. Furthermore, evidence is restricted to birdsong and little is known about the impact of social interactions on multi-modal displays that involve both acoustic and motor components [14, 15].

The spotted bowerbird (*Chlamydera maculata*) is an excellent candidate for investigating the mechanisms by which same-sex interactions mediate social learning of multi-modal courtship signals. Male bowerbirds construct a structure of sticks – the bower – to attract mates during the breeding season [16]. These spatially dispersed arenas are used as display sites where males perform an elaborate and multi-component courtship display, which includes a sequence of conspicuous postural and motor components, accompanied by harsh vocalisations with chaotic acoustic structure (Fig. 1) that are co-opted from aggressive displays [17]. Bowers are built and defended by one resident bower owner, yet other non-territorial males, so-called ‘subordinates’, are commonly tolerated by bower owners, and males of both statuses (owners and subordinates) can be seen displaying at established bowers over multiple breeding seasons [18, 19]. These long-term social interactions between bower owners and subordinate males have been described by some scholars as a form of apprenticeship [18], and may therefore result in matching courtship displays within owner-subordinate pairs (apprenticeship hypothesis). Yet, it remains unclear whether subordinate males indeed acquire audio-visual patterns of courtship displays from their tutors while attending adults’ arenas.

Several lines of evidence suggest that courtship signals are learned and transmitted socially in a number of bowerbird species. First, previous work showed the existence of dialects in their vocalisations. For instance, different populations of Golden bowerbirds (*Prionodura newtonia*) have distinct dialects in their advertisement calls [20] (see also [21]). Second, bower structure and decoration style have been shown to exhibit patterns of geographic variation consistent with social learning. For example, spotted bowerbirds *C. maculata* exhibit local similarities in bower decorations at population scale, which cannot be explained by genetic relatedness or ecological differences in decoration availability [22] (see also [23]). However, the role that same-sex social interactions play in guiding learning of these local courtship variants is still unknown. Investigating whether social interactions can predict signal similarity is a crucial step for testing the apprenticeship hypothesis.

In this study, we investigated whether spotted bower-

birds exhibit patterns of variation in acoustic and visual courtship display components within a single population. We hypothesised that long-term male-male interactions on display arenas would give rise to patterns of similarities where male-male pairs with stronger social interactions have similar audio-visual courtship displays. We recorded acoustic and visual courtship components of resident and subordinate males that display at different bower sites within our study population. We calculated pairwise similarity values to test several predictions that follow from our hypothesis. First, we predicted that bowerbird courtship would exhibit geographic variation consistent with micro-dialects, such that, at a population scale, bowerbird would exhibit higher similarity in their audio-visual displays to their neighbours compared to individuals from more distant bower sites. Second, to determine whether social learning could contribute to the formation of micro-dialects, we predicted that the strength of social interactions would explain these patterns of local similarities in audio-visual courtship displays. Finally, we predicted that social proximity would be a better predictor of courtship similarities than geographic distance. We additionally controlled for genetic distance to investigate whether these similarities may instead be better explained by genetic inheritance.

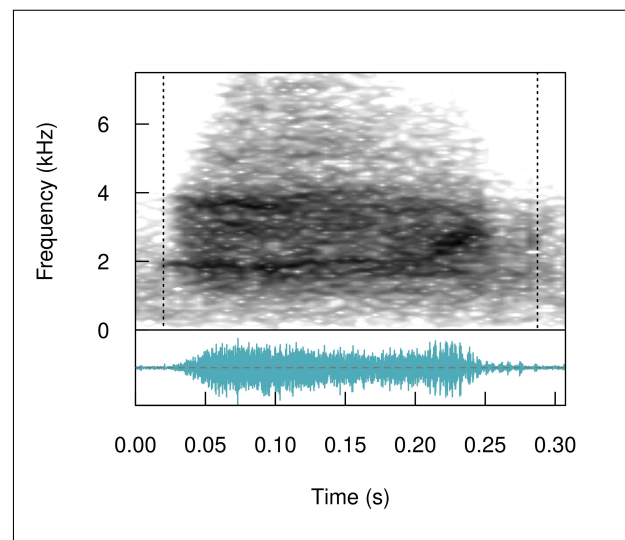


Figure 1. Spectrogram and oscillogram of a typical harsh vocalisation named “skrra” produced by a male spotted bowerbird during its courtship display.

2. MATERIALS AND METHODS

2.1 Study site and subjects

Data were collected from a population of wild spotted bowerbirds at Taunton National Park (Scientific), Queensland (23.54989 S; 149.24088 E) in two breeding seasons (July-December 2018, and August-December 2019). Birds were caught at bowers using mist-nets, then measured and marked with colour bands provided by the Australian Bird and Bat Banding Scheme (ABBBS). Blood samples (50-150 μ L) were collected upon capture using EDTA tubes and stored in 0.5 mL Queen's lysis buffer at 4 °C until DNA extraction.

2.2 Video recording and scoring of courtship displays

We monitored 13 active bowers in both breeding seasons using motion-activated camera traps (Browning Recon Force Advantage HD, 2018). Cameras were mounted on tripods and positioned in front of one of the bower entrances (distance from camera, mean \pm sd: 177 cm \pm 46.67 cm) for the entire duration of our fieldwork; video recordings were made at 30 frames per second. More details about camera specifications, video recording and processing are described in Spezie and Fusani [19].

We operationally defined as the start of a 'courtship bout' the first display element performed when a visitor entered the bower walls. Display elements are performed in quick succession, separated by intervals of variable length. The descriptive ethogram of all 19 display elements exhibited by *C. maculata* during courtship was described in detail elsewhere [16, 19]. Intervals longer than 10 seconds or departure of the courting male from the camera field of view were considered as the end of a courtship bout. We scored all display elements in 1600 courtship bouts of 22 males (12 subordinate males and 10 bower owners; range of display bouts per individual: 24 – 118), using the software Loopy (<http://loopbio.io>, Loopbio, GmbH, Austria). For each display bout, we annotated the element type, its duration, and the order of display elements in a sequence. Display elements that consist of a short and discrete movement were considered as 'events' with no duration.

2.3 Audio extraction

The audio tracks were extracted (as .wav files) from the videos (.mp4 files) where a single colour banded individual was producing courtship vocalisation. The function *autodetect* from the R package *warbleR* [24–27] was used to automatically detect the vocalisations within the audio

tracks. As background noises were rare and low and bowerbirds were vocalising close to the camera (up to 4 m), the automatic detection was based on sound amplitude. The detected fragments were then manually sorted by visual inspection of the spectrograms to keep only correctly detected "skrra" vocalisations without background noise. We operationally defined the "skrra" as any harsh call showing no recognisable harmonic structure in its spectrogram (Fig. 1). In total, we extracted 35304 vocalisations for 26 individuals (mean \pm sd = 1358 \pm 581.8).

2.4 Statistical analysis

To investigate whether distinctiveness in acoustic and visual display parameters co-varied with geographical, social or genetic distance, we compared four inter-individual dissimilarity matrices of the acoustic and visual courtship components to the three predictor matrices using Mantel test correlations in the R package *vegan* [28]. The significance of the Mantel test results were estimated using permutation testing, permuting the response matrix and recomputing the Spearman's rho (r) statistic 9,999 times. Values of Monte Carlo $p < 0.025$ or $p > 0.975$ indicate that the response matrix co-varies significantly with the predictor matrix.

2.5 Construction of response and predictor matrices

2.5.1 Construction of the vocal courtship proximity matrix

The function *spectro_analysis* of the R package *warbleR* [24–27] was used to measure the 27 acoustic variables describing intensity distribution of sound of time and over frequency (see *warbleR* [25] documentation for details about the variables). We then ran a linear discriminant analysis (LDA) with R package *ade4* [24, 29]) with bird IDs as a factor. This method allowed us to reduce the number of variables into 5 components maximising the inter-individual variances. Gaussian densities were fitted over the distribution of each individual on each of the 5 LDA components. For each pair of individuals, the proportion of overlap of the fitted densities was then computed with the overlap function of the R package *overlap* [24, 30] producing a pairwise matrix of proximity for each of the 5 LDA components. The values of these 5 matrices of proximity were then multiplied to obtain a single 5-dimensional value of overlap for each pair of individuals.

2.5.2 Construction of the visual courtship distance matrices

To measure dissimilarity in visual display components, we focused on three parameters: (i) sequences of display elements; (ii) duration and repetition of single display element categories (hereafter 'fine-scale parameters'); (iii) proportions of each display element. As all individuals displayed the full repertoire of visual display elements, its composition was not analysed. For display sequences, we focused on a specific and relatively stereotyped sub-sequence of display elements in which male bowerbirds pick up a decoration while performing a frontal *crest presentation*, then toss the decoration towards the bower entrance. We restricted our analysis to this sub-sequence as complete sequences of courtship elements in spotted bowerbirds are highly variable in duration and in the transition rates between display elements (unpublished data). Thus, we extracted and compared among individuals strings of 7 display elements ordered according to the order in which they were emitted in the *crest presentation* display ($n = 22$ birds; $n = 1652$ observations; mean \pm SD sequences per bird = 75.14 ± 30.72). For fine-scale parameters, we measured the duration of five display elements that were not scored as 'events' (*Body ripple* $n = 3234$ observations; *Crest presentation*, $n = 3910$; *Head circling* $n = 504$; *Rising* $n = 362$; *Mock attack* $n = 273$), and the repetition of two commonly repeated display elements (*Sneeze* $n = 3609$; *Nodding* $n = 2042$). For each of the three parameters (sequences, fine-scale, proportions), we calculated pairwise dissimilarity values using, respectively: (i) Jaro distance between display sequences using the *strindistmatrix* function in R; (ii) Euclidean distance between samples of fine-scale parameters, combined into one distance matrix after scaling all variables by z-transforming the available measures, using the *dist* function; (iii) Bray-Curtis dissimilarity index between the proportions of different display elements with the *vegdist* function. To build response matrices with individuals as the sampling unit, we used individual accumulated repertoire proportions, mean pairwise sequence dissimilarity for each individual, and individual average values for fine-scale parameters.

2.5.3 Construction of the predictor matrices (geographic distance, social proximity and genetic distance)

The geographic dissimilarity matrix was built based on the distance between the preferred bower of each individual in the breeding season of 2019. We considered as 'preferred' the bower where the bird was filmed most often. Haversine

distances were calculated given latitude and longitude of bower positions using the R package *geosphere* [24, 31].

As a measure of social proximity, namely strength of association among male pairs, we used the proportion of time a male was filmed attending the display of another male during the 2019 breeding season (corrected by the total time this male was attending the display and by the total time the bower was video recorded). Our rationale is that social learning should occur during male-male interactions where subordinate males are exposed to the courtship signals of another male. In the rare case where two males were both attending the display of each other (two pairs of males), the maximum value of this metric was selected to keep a single value for each pair of birds.

To generate the genetic distance matrix, we obtained relatedness scores among individuals using a next-generation sequencing method for DNA genotyping (MobiSeq; [32]) from blood samples collected in the field (see Spezie et al. in prep). We used the pairwise Queller and Goodnight estimator of relatedness (QGE) to calculate pairwise relatedness scores and generate the pairwise distance matrix (Spezie et al. in prep).

2.6 Comparison between geographic distance and social proximity matrices

In the cases where the dissimilarity in a courtship component could be explained by both geographic distance and social proximity, we used the following method to better understand what the best predictor was. We built two new matrices using the social proximity matrix as a filter to select parts of the geographic distance matrix. In the first, hereafter called 'interacting pairs', we kept the geographic distance of only the pairs of males that were socially related. In the second, hereafter called 'non-interacting pairs', we kept the geographic distance only of the pairs of males that were not socially related. If geographic distance is a better predictor, we expect both 'interacting pairs' and 'non-interacting pairs' matrices to show a significant correlation with the dissimilarity in courtship components. Conversely, if social proximity is a better predictor, we expect to observe this correlation only for the 'interacting pairs' matrix and not in the other one.

3. RESULTS

3.1 Acoustic components of the courtship displays

We found a significant correlation between overlap in 'skrra' vocalisations and both geographical distance among

bowers (Fig. 2; Mantel $r = -0.18$, nbirds = 26, $p = 0.986$) and social proximity (Mantel $r = 0.19$, nbirds = 26, $p = 0.001$). Moreover, when we compared the acoustic overlap with 'interacting pairs' geographic distance, the correlation was even stronger (Fig. 2, Mantel $r = -0.47$, nbirds = 26, $p = 0.986$) while when we compared it with the 'non-interacting pairs' geographic distance, the correlation was lost (Mantel $r = -0.07$, nbirds = 26, $p = 0.799$). These differences could not be explained by genetic distance (Mantel $r = -0.02$, nbirds = 16, $p = 0.618$).

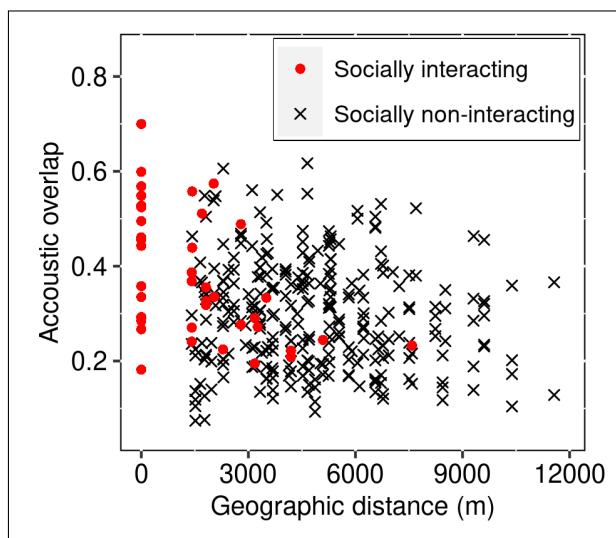


Figure 2. Relationship between the pairwise geographical distance between preferred bowers (in m) and the pairwise acoustic overlap of “skrra” vocalisations. The red points show the pairs that are interacting socially. The black crosses show the pairs that do not interact socially.

3.2 Visual components of the courtship display

We found a significant correlation between display sequence dissimilarity and geographical distance among bowers (Fig. 3; Mantel $r = 0.31$, nbirds = 21, $p = 0.003$), and these differences could not be explained by genetic distance (Mantel $r = -0.22$, nbirds = 12, $p = 0.950$). However, sequence dissimilarity did not covary with social proximity (Mantel $r = -0.02$, nbirds = 21, $p = 0.649$).

We found no correlation between combined fine scale parameters and geographic distance between bowers (Mantel $r = -0.15$, nbirds = 21, $p = 0.951$), social proximity

(Mantel $r = -0.02$, nbirds = 21, $p = 0.393$), or genetic distance (Mantel $r = 0.09$, nbirds = 12, $p = 0.246$).

Similarly, we found no correlation between display element proportions and social proximity (Mantel $r = 0.01$, nbirds = 21, $p = 0.555$), geographic distance (Mantel $r = 0.11$, nbirds = 21, $p = 0.106$), and genetic distance (Mantel $r = -0.06$, nbirds = 12, $p = 0.702$).

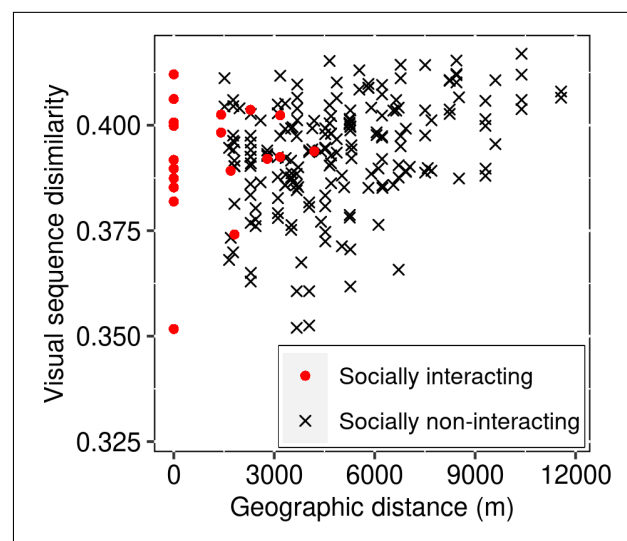


Figure 3. Relationship between the pairwise geographical distance between preferred bowers (in m) and the pairwise mean dissimilarity of visual display sequences. The red points show the pairs that are interacting socially. The black crosses show the pairs that do not interact socially.

4. DISCUSSION

This study presents novel data on the variation in audio-visual courtship components within a single population of spotted bowerbirds *C. maculata*. It was speculated in previous studies that subordinate males associate with experienced bower owners as part of an apprenticeship [18, 19]. Our results indicate that subordinate males and bower owners that engage in stronger social interactions exhibit more similar courtship signals than males that do not interact repeatedly on display arenas. These results support the apprenticeship hypothesis for male-male associations in this species, and therefore provide indirect evidence for social learning as an explanation for the patterns of local similarities in sexual signals. However, our predictions

were only supported for acoustic courtship components, and we found overall only partial support with regard to visual display components.

The fact that acoustic signal components may be learned socially in bowerbirds is supported by a large body of prior evidence. First, bowerbirds are proficient vocal mimics [16, 33], and many heterospecific sounds are incorporated into courtship routines in at least three bowerbird species [16], though spotted bowerbirds appear to mimic sounds primarily in distressful contexts [34]. Second, prior research identified vocal dialects in territorial and/or courtship calls in golden [20] and satin bowerbirds [35]. Yet, geographic variation *per se* is not sufficient to invoke social transmission, as genetic inheritance or ecological factors may also explain local similarities in signal patterns. In this study, we show that this variation was not explained by genetic relatedness in this species. Thus, repeated interactions with local tutors followed by social learning may give rise to patterns of local similarities in acoustic courtship signals – i.e. dialects – in *C. maculata*, and these similarities are detectable within a single population.

Although most of the dialects described span broad geographical scales, dialects have also been shown to occur at smaller geographic scales, and these are referred to as ‘microdialects’ [36, 37]. In most species, however, it remains challenging to identify the specific social dynamics that drive the emergence of small-scale variation in acoustic signals, particularly in the wild. Our study sheds more light on the social dynamics leading to local patterns of similarities at small geographic scale in spotted bowerbirds. The fact that subordinate males attend established bowers over multiple breeding seasons and watch resident males displaying may mediate imitative vocal learning of courtship calls after dispersal. Here, we show that calls with chaotic acoustic structure used in courtship may also be acquired from tutors via processes analogous to those responsible for learning of harmonic vocalisations of other songbirds. Very few studies have investigated dialects in courtship calls without harmonic structure typical of courtship calls [38]. Our results suggest that vocal learning may play an important role in other courtship vocalisations and that harsh calls may also encode information about individual quality on which mate choice can act.

In the second part of our analysis, we investigated whether patterns of local similarities also occur in visual courtship components. Despite the importance of postural components of courtship across taxa [15, 39], evidence for local traditions of visual displays is still scarce. For instance, to the best of our knowledge, only one study has

documented patterns of variation consistent with social transmission in the visual displays of long-billed hermits *P. longirostris* [14]. The results of our study seem to suggest that visual displays in spotted bowerbirds show little variation within a single population, at least for the parameters we considered for our analysis. We found evidence of geographical variation in the sequences of courtship display elements, and this variation was not explained by genetic relatedness. Yet, these patterns did not co-vary with social proximity between individuals. For visual signals, our data therefore did not support the apprenticeship hypothesis.

Three factors may explain the lack of support for our predictions. First, some scholars have deemed action copying – namely, learning of a novel action from a demonstrator – to be a challenging cognitive task [40]. Bowerbirds may thus be unable to learn a novel action by observing a conspecific. These scenarios seem however unlikely, as prior research showed that spotted bowerbirds in this population exhibit local similarities in bower decorations that are consistent with social learning; therefore, spotted bowerbirds seem to be capable of visual learning [22]. Second, we focused here on the occurrence and temporal features of specific postural displays, not on the variability of the postures themselves. Thus, the parameters we quantified may not measure courtship movements with sufficient detail. A third explanation is that variation in visual displays may be more pronounced at larger geographical scales. Future studies should investigate the variation in visual displays in *C. maculata* between more distant locations. A number of courtship display traits in bowerbirds exhibit geographical variation between populations. For example, Diamond [23] reported that the colour of preferred decorations and bower style in the Vogelkop bowerbird (*Amblyornis inornatus*) depend on geographical variation in male colour preference, which is independent of genetic differences [41].

Cross-fostering and rearing experiments are the ideal experimental paradigm to draw more direct evidence about the role of social learning in the development of courtship (e.g. [42]). Yet, these experiments may not be feasible in bowerbirds or other model systems with slow life histories and delayed sexual maturity [18, 43]. Thus, correlational studies are fundamental to inform hypotheses about learning (e.g., [14]). With this approach, we showed here that courtship calls and some of the visual display variables in our study population showed geographical variation consistent with micro-dialects, yet social proximity among male bowerbirds co-varied with signal similarity only for acoustic display components. Future studies should further

focus on fine-scale parameters of visual displays, for example by means of motion capture techniques [44], to explore whether patterns of local variation may occur in postural components of visual displays.

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