



Multimodal duetting in magpie-larks: how do vocal and visual components contribute to a cooperative signal's function?



Paweł Rę́k^{a, b, *}, Robert D. Magrath^a

^a Research School of Biology, The Australian National University, Canberra, Australia

^b Department of Behavioural Ecology, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland

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Many animals communicate using multimodal signals, which simultaneously address different senses. Components may prompt similar or different responses when used alone, whereas the composite signal may have a similar meaning to one or both components, or a novel meaning. We used robot models to dissect the roles of visual and vocal components in the multimodal duets of Australian magpie-larks, *Grallina cyanoleuca*. Mated pairs produce antiphonal vocal duets, and coordinate them with visual duets, which usually entail alternating wing movements. Previous playback experiments show that purely vocal duets have a territorial function, but the role of visual displays is unknown. We measured territorial responses by pairs to each component independently, as well as to the multimodal signal, and analysed the choice of song and visual display used by partners during duets. Acoustic and multimodal playbacks prompted the same, strong territorial response, entailing both flight and vocal duetting by the resident pair. By contrast, purely visual playbacks did not prompt a strong territorial response. Furthermore, pairs used the same visual display within multimodal displays, independent of song type, implying that birds watch their partners when choosing the visual display, and suggesting that it could be a within-pair signal. We conclude that the vocal component of duets is a territorial signal to other pairs, whereas the visual component might either coordinate vocal duets within pairs, analogous to a conductor's baton, or have a restricted role in communication between rival pairs, perhaps especially at long range.

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Animals produce signals using single or multiple components, and perceive signals through all available sensory channels (Candolin, 2003; Hebets & Papaj, 2005; Partan & Marler, 2005; Rowe, 1999). Multimodal communication contains components that target different senses, and is widespread across taxa. Such signals can target all known senses, and include bimodal, trimodal or even more complex signals (Stevens, 2013). Signalling in multiple channels is linked with some specific benefits and costs to both the signaller and receiver (Partan & Marler, 2005), and we cannot understand multicomponent signals fully by studying their components independently (Rowe, 1999). Nevertheless, most studies on animal communication focus on one modality at a time.

The components of multimodal signals can communicate redundant or nonredundant messages (Johnstone, 1997; Møller & Pomianowski, 1993; Stevens, 2013). Multiple redundant

components can increase the efficiency of communication by providing insurance in case one component is not recognized, or by increasing the intensity of the composite signal compared with intensities of independent components (Preininger et al., 2013; Rypstra, Schlosser, Sutton, & Persons, 2009). In the fowl, *Gallus gallus*, for example, food-associated calls are typically accompanied by a distinctive visual display, with each modality acting as a backup to enhance signal efficiency. Hens need more time to begin food search when the display is silent, but the overall probability of response is similar among the multimodal, visual-only or acoustic only components (Smith & Evans, 2008). Multiple nonredundant components can convey increased information by having different roles or by targeting different recipients (Krakauer & Johnstone, 1995; Ratcliffe & Nydam, 2008). In the field cricket, *Gryllus integer*, for example, males produce long-distance calls and close-range chemical compounds. Although females demonstrate positive phono and chemotaxis, the responses to long-distance and close-range components are uncorrelated within females, suggesting that each modality has a different message (Leonard & Hedrick, 2010).

* Correspondence: P. Rę́k, Research School of Biology, The Australian National University, Canberra 2614, Australia.

E-mail address: pawel.rek@anu.edu.au (P. Rę́k).

The function of multimodal displays can be tested empirically by the analysis of responses by receivers to signal components and to full displays (Partan & Marler, 2005). Perceivers should respond with similar behaviours to signal components presented independently if components communicate redundant messages, but with different behaviours if components transmit different messages. When presented together, redundant components may lead to the same or equivalent effects, or may enhance the receiver's responses additively or even multiplicatively (Partan, 2013). Nonredundant components within complex displays may continue to elicit independent messages, produce novel responses, or modify each other (Partan & Marler, 2005).

Individuals can produce multimodal signals alone or together with others, and yet there has been no study of the role and integration of different components of multimodal signals when produced cooperatively with others. In cooperatively signalling species, communication could have two distinct types of receiver: an 'audience' addressed by the cooperative signal, and 'co-signallers' with whom an individual cooperates to form the joint signal. Additionally, if a signal is multimodal, each component could have its own target audience (Partan & Marler, 2005). Experimental study of multimodal signalling in cooperatively signalling species is therefore challenging because there could be multiple receivers and messages.

We tested whether the visual and acoustic components of Australian magpie-lark, *Grallina cyanoleuca*, duetting displays communicate equivalent or different messages, and analysed the relationship between components within the cooperative display. In many bird species, mated pairs produce acoustic duets, and some also coordinate their songs with movements to form cooperative audiovisual displays (Hall, 2009; Malacarne, Cucco, & Camanni, 1991; Todt & Fiebelkorn, 1980; Von Seibt & Wickler, 1977; Zimmer, Whittaker, & Oren, 2001). Nevertheless, such multimodal cooperative behaviours have not been broken down experimentally into their constituent parts. Magpie-lark partners produce antiphonal duets, often with a high level of coordination between partners, and these are used to defend the territory (Hall, 2000; Hall & Magrath, 2007). Birds also produce visual displays, including alternating wing movements, but their function has never been studied.

We documented how vocal and visual components are combined within magpie-lark cooperative displays, and experimentally tested their function. We used taxidermic robotic birds that produced wing movements, which we synchronized with acoustic playbacks to test the function of signal components and to analyse the integration of components from different sensory channels. The acoustic component is known to have a territorial function, so we measured behaviours used in territorial defence. In magpie-larks, playback of acoustic duets elicits a territorial defence syndrome consisting of both singing, with more duets compared to solo songs, and flying (Hall, 2000). Therefore, if the visual component transfers the same message as the acoustic one, then visual and acoustic playbacks should prompt the same territorial syndrome from focal pairs, which is likely also to be similar to the multimodal playback. Responses to multimodal signal components may differ in intensity but as long as the syndrome is maintained, the components are redundant. If, however, components prompt different responses from focal pairs, it would mean that they are nonredundant. In this case, the multimodal playback may elicit (1) a new response, a behaviour qualitatively different from either unimodal playback; (2) the same response as one of the unimodal components, meaning that one component dominates the message; (3) or a response that is a combination of behaviours given to unimodal playbacks. An additional complexity in cooperative signallers is that the partner is also a potential target, so that different components may address different receivers.

METHODS

Study Population and Species

We studied a colour-banded population of magpie-larks in and near the Australian National University in Canberra. Magpie-larks are endemic to Australia, where they commonly inhabit open woodland and suburban parks and gardens (Mulder et al., 2003; Peter, Cowling, & Higgins, 2006). Pairs defend territories throughout the year (Hall & Magrath, 2000), and the sexes are easily distinguishable by plumage differences (Disney, 1974).

Males and females each produce solo songs, and together can combine songs to form antiphonal duets. Solo songs consist of a series of short units, called motifs, which are 300–600 ms long and given at a tempo of about 1 motif/s. Individuals have a repertoire of about three to six different song types, each composed of a single, repeated motif, and an earlier study found nine motifs in the study population, but with only two used by all birds (Hall, 2006). In duets, partners alternate their motifs on average six or seven times. Each bird uses the same motif throughout a duet, but it is rare for pairs to sing a duet in which each bird uses the same motif type (Hall, 2006). Coordination is often precise, with perfect alternation of motifs and a regular tempo of about 1 motif/bird per s. Pairs that have been together longer are more likely to produce well-coordinated duets, which are a more threatening territorial signal (Hall & Magrath, 2007).

In addition to the vocal display, magpie-lark duets are typically accompanied by synchronized body movements (Hall & Magrath, 2007; Peter et al., 2006; Tingay, 1974). Most often, the movements consist of wing spreading or raising of folded wings ('shoulder' raising), but sometimes the whole body bends forward (Supplementary Videos S1–S3, respectively). Although most duets entail both a vocal and visual component, magpie-larks can give purely vocal or visual duets (P. Reş, personal observation). However, unimodal duets are relatively rare, and in our experimental sample of 188 duets only three were purely vocal and none purely visual (see Results).

Ethical Note

The use of the animals adhered to ethical guidelines for animal research in Australia (Australian Bird and Bat Banding Scheme, Environment ACT) as well as all the institutional guidelines of the Australian National University (A2014/17). Although the procedures we applied might cause temporary distress to birds, we minimized the number of recordings and playbacks consistent with experimental goals, and always kept the rate of playback below natural rates.

Robotic Models

We used a male–female pair of taxidermic robotic magpie-larks during the playback experiment (Supplementary Video S4). Each bird contained two servo motors (Power HD, Analog Micro Servo HD-1440A) that were attached to the humeri of the wings, which enabled the outstretched wings to be moved up and down. This movement corresponded to the 'wing spreading' movement, which is the most common visual display of magpie larks (76% of 370 movements observed during this study). The servo motors from one bird had a single circuit, so that the two wings moved in synchrony, while the motors of the male and female were controlled independently, so that they could be moved in alternation. Model birds were attached to a perch next to each other facing the same direction, so that they resembled a duetting pair. Movements of robotic birds were controlled together with acoustic playbacks

(below) from a custom-designed circuit-board based on the Arduino platform (Arduino Micro; <http://www.arduino.cc>). This controller enabled us to precisely manipulate wing movements and vocalizations. To protect models against attack by magpie-larks and other birds, they were enclosed in a cage (1 × 0.4 m and 0.4 m high) covered with a very fine, black fabric netting.

Our playbacks were aimed at reproducing the natural temporal distribution of movements and songs within a pair of robotic birds (Tingay, 1974). In a natural display, male and female movements and songs alternate. This means that when the amplitude of one bird's movement reaches its maximum the partner's movement is close to its minimum, and when one bird finishes a motif, the partner starts the next. The timeline of acoustic and visual events may differ depending on the movement and motif used; however, reaction times of males and females in both modalities are highly regular, and motifs of well-coordinated duets do not overlap (Hall & Magrath, 2007). In the model's displays, the movement started a few milliseconds before the acoustic playback of the initiator and continued for 0.5 s up and 0.5 s down. The initiator's motif finished before the end of its wing movement but the length of this gap depended on the length of the motif used. The responder started its wing movement when the initiator's wings reached the top level and continued the movement up and down and with its song identical to the initiator's. This sequence continued three times, for a total of six motifs.

Acoustic playbacks were broadcast from a Mipro MA-101A amplified loudspeaker (45 W, frequency range 60–15 000 Hz) placed near the robotic models. Playback was at natural amplitudes of 66–70 dBA SPL at 10 m, measured by a RadioShack Sound Level Meter from seven individuals (see also Mulder et al., 2003). We used recordings of antiphonal duets from 18 local pairs unfamiliar with the subjects. These local pairs and subject pairs were different sets of birds. We chose three full duets from each pair, one for each treatment in playbacks to a different pair. We used only well-coordinated duets without overlapping of male and female songs, and chose a pair of motifs to synthesize a duet with standardized timing. The consecutive motifs of partners started at 0, 0.5, 1, 1.5, 2, 2.5 s, with male and female motifs alternating as in natural duets. The total duration of each playback lasted for about 3.0 s. The male and female models' motifs came originally from males and females, respectively, because song structure appears to differ between the sexes (Mulder et al., 2003). The playbacks were prepared from recordings taken with a Sennheiser ME64 cardioid microphone connected to a Canon XA20 HD Camcorder, recording wav files at 48 kHz and 16 bits, and subsequently edited using Adobe Audition (Adobe Systems Inc., San Jose, CA, U.S.A.) and Avisoft-SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) software.

Field Playback Methods and Response Variables

We used the robotic models to test how magpie-larks respond to complete duets and to their acoustic and visual components. Each of 18 experimental pairs were exposed to three treatments on the same day: an acoustic duet (A), consisting of an acoustic playback of a pair of magpie-larks; a visual duet (V), consisting of wing movements of a pair of robotic magpie-larks; and an audiovisual duet (AV), consisting of synchronized acoustic and visual stimuli (Supplementary Video S4). The playbacks consisted of three pairs of male and female motifs (A), three pairs of wing movements (V) or both (AV). The order of treatments was balanced by design, including having half starting with each sex. The experiment was carried out in February 2015, with nine pairs tested in the morning (0630–0900 hours) and nine in the evening (1700–1930 hours), which were the two distinct peaks of activity. We conducted one or two trials each morning and evening. We avoided testing

neighbouring pairs on the same morning and evening, to reduce any risk that previous playbacks to other pairs could influence the response.

A full experiment consisted of three 5 min treatments separated by two approximately 5 min breaks. The first treatment was preceded by a 5 min baseline period of observation followed by a 1 min period during which birds were attracted to the vicinity of models. All playbacks were presented from the territory centre, and were carried out only if partners were together and not interacting with neighbours during the last minute before each playback. Birds were attracted to the vicinity of the models to avoid the potential problem that visual signals may be more easily overlooked, so reducing apparent response to the visual component of a multimodal signal. We broadcast magpie-lark juvenile begging calls to attract the birds' attention to the location of robot birds prior to the first treatment, and only started playbacks when the focal birds were within 25 m of the models. In a pilot experiment, birds subjected to begging calls approached the speaker but did not sing. After the playback of begging calls we waited for 10–30 s before starting the treatment. During each treatment playback, birds received 10 playbacks, which by default started at 0, 20, 40, 60, 90, 120, 150, 180, 210, 240 s, but we delayed initiating a playback if birds were singing at these times. We presented the model pair in all treatments, including purely acoustic, to control for the effect of presence of birds independently of the mode of display.

We quantified the response to playback by measuring in the baseline and playback periods the number of songs produced, including duets and solos, and flights performed over the 5 min sampling periods. These behaviours together, and duets specifically, provide a measure of the strength of territorial defence (Hall, 2000). We counted only flights longer than 2 s because most of the shorter flights were simply movements between branches, whereas longer flights were stereotypical behaviours, usually performed by partners simultaneously and often associated with singing. We quantified responses from audiovisual recordings if possible (quality of files: AVCHD, 28 Mb/s, 1920 × 1080 @ 59.94p; PCM, 48 kHz, 16 bits), but scored the number of flights directly if the video recording could not capture both birds in the field of view. Direct scoring was only required for 44 of the total of 487 flights.

Observation of Displays

To analyse the structure of multimodal duets, we compared motif and movement types used by the duetting males and females during experiments. We selected only duets with full information about male and female vocalizations and movements, recorded up to 5 min prior to and during the treatments. We categorized motifs into the nine distinct classes described for the study population (Hall, 2006). Movements were categorized into three distinct classes: wing spreading, shoulder raising and body flicking (Supplementary Videos S1–S3, respectively). These categorizations meant that we could classify duets based on whether partners used the same or different motifs and movements. In two cases where birds gave a vocal duet but only one bird gave a visual display, we classified displays as having different movements, but we excluded three duets, from a total of 188 observed duets, in which neither bird gave a visual display.

Data Analysis and Statistics

To compare the responses of males and females in acoustic, visual and audiovisual treatments we used generalized estimating equations (GEE). This procedure is appropriate for repeated measures data (Hardin & Hilbe, 2002), which enabled us to account for the relationships between the male and female within a pair, and

responses of the same individuals to multiple treatments. We fitted the data using a negative binomial distribution because our count data were strongly skewed, and this distribution is especially useful for discrete data over an unbounded positive range whose sample variance exceeds the sample mean (McCullagh & Nelder, 1989). To compare the intensity of responses in treatments we separately analysed songs (solos plus duets) and flights as dependent variables, with sex of the responder and treatment (A, V, AV) as independent factors. To analyse the type of responses in treatments we first compared the numbers of duets and solos produced by pairs in treatments. We then compared the relationships between duetting and flying within pairs, to test for the territorial defence syndrome of increased duetting and flying. In this analysis, the number of duets was the dependent variable, the number of flights was the covariate and treatments were the independent factor. Fisher's LSD method was used in GEE analyses to create confidence intervals for differences between treatment means. We used the SPSS v. 22 software (IBM, Armonk, NY, U.S.A.) for statistical analyses. All *P* values were two tailed and, if not stated otherwise, means \pm SE are given.

RESULTS

Response to Audiovisual Playbacks

Birds responded to all treatments by increasing the number of songs and flights compared to the baseline period before playbacks (Fig. 1; $P < 0.001$ for all comparisons; song baseline = 1.19 ± 0.18 per individual; flight baseline = 0.11 ± 0.06 , only five birds flew in the baseline period, with a total of five flights). Males and females produced similar numbers of songs and performed similar number of flights per trial (Table 1; songs: males 31.83 ± 4.68 , females 29.78 ± 4.65 ; flights: males 13.72 ± 1.74 , females 13.33 ± 1.80). Overall, birds responded even to purely visual duets, and males and females responded similarly to treatments.

Although purely visual duets did prompt a response, there were far fewer songs and flights than to the other treatments (Table 1, Fig. 1), and only multimodal and acoustic duets prompted a typical territorial response (Table 2, Fig. 2). Birds produced a high proportion of duets in response to acoustic and multimodal duets, consistent with a strong territorial response, but a much lower proportion of duets in response to visual-only playbacks (Table 2, Fig. 2). Furthermore, there was a strong association between increased flying and increased duetting among individuals only in response to acoustic and multimodal playbacks, and not visual playbacks (Fig. 3; a linear regression of duet number on flight number: acoustic: $B = 0.587$, Wald $\chi^2 = 14.71$, $P = 0.0001$; multimodal: $B = 0.529$, Wald $\chi^2 = 6.03$, $P = 0.014$; visual: $B = 0.059$, Wald $\chi^2 = 0.06$, $P = 0.804$; interaction: GEE: Wald $\chi^2_3 = 18.05$, $P = 0.0004$). Again, this suggests that only the acoustic and multimodal playbacks prompted strong territorial defence, while the visual playback led to a generalized increase in singing and flying.

Structure of Multimodal Duets

Individual birds had a repertoire of movement and song motif types, and the type of visual display could be combined with any type of song motif. We classified the types of movements and motif types of both partners in the 185 multimodal displays for which we could score both movement and song (Table 3). Within our sample, pairs gave on average 2.67 ± 0.18 (range 1–3) different types of movements and produced on average 2.94 ± 0.19 (range 2–4) different types of motifs. Across the population males and females combined movements and motifs in all possible combinations when forming duets. Pairs produced on average 5.06 ± 0.66

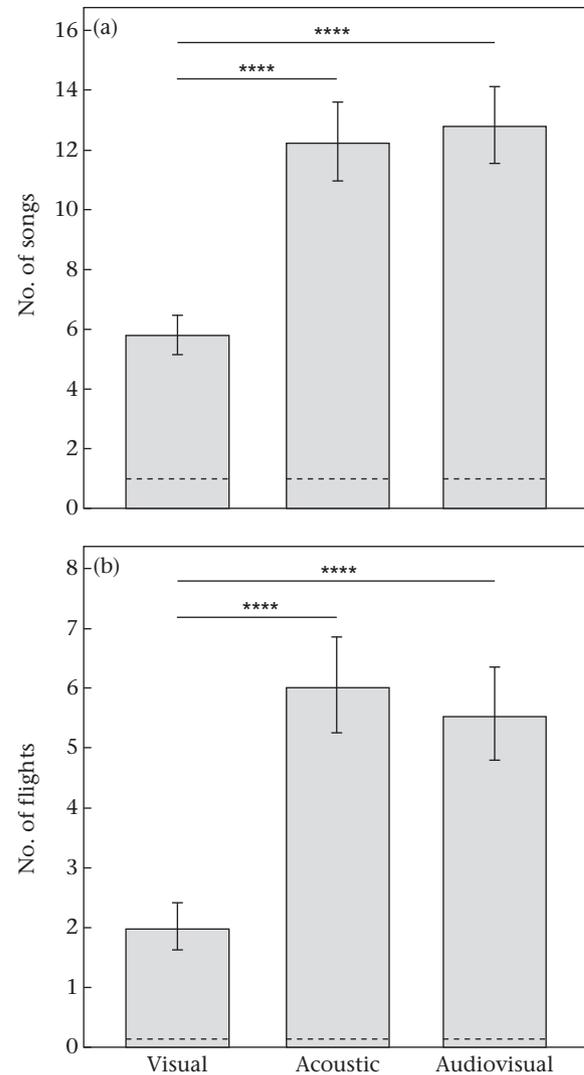


Figure 1. Numbers of (a) songs and (b) flights performed in 5 min by males and females during three treatments: acoustic, visual and audiovisual, and in 5 min prior to playbacks (the dashed lines). Significant differences are indicated with thick black lines (*** $P < 0.001$). The boxes show means \pm SE.

different combinations of movements and motifs, and the number of combinations was strongly correlated with the number of displays observed ($r_{16} = 0.96$, $P < 0.0001$) and the number of different motif types sung by a pair ($r_{16} = 0.89$, $P < 0.0001$). The strong association with sample size suggests that the number of combinations is high for all individual pairs.

Table 1

The effects of sex and treatment on the intensity of magpie-larks' responses

| | Wald χ^2 | df | <i>P</i> |
|----------------------|---------------|----|----------|
| Songs | | | |
| Intercept | 41.59 | 1 | <0.001 |
| Sex (M, F) | 0.64 | 1 | 0.425 |
| Treatment (A, V, AV) | 10.08 | 2 | 0.006 |
| Sex * Treatment | 0.86 | 2 | 0.650 |
| Flights | | | |
| Intercept | 111.30 | 1 | <0.001 |
| Sex (M, F) | 1.03 | 1 | 0.309 |
| Treatment (A, V, AV) | 21.92 | 2 | <0.001 |
| Sex * Treatment | 2.45 | 2 | 0.293 |

Treatments consisted of an acoustic (A), visual (V) or audiovisual (AV) playback.

Table 2
The use of solos or duets by pairs in treatments

| | Wald χ^2 | df | P |
|-------------------------|---------------|----|--------|
| Intercept | 55.32 | 1 | <0.001 |
| Treatment (A, V, AV) | 87.69 | 2 | <0.001 |
| Song usage (Solo, Duet) | 6.76 | 1 | 0.009 |
| Treatment * Song type | 10.16 | 2 | 0.006 |

Treatments consisted of an acoustic (A), visual (V) or audiovisual (AV) playback. Fig. 2 displays the results.

Despite producing multiple types of movements and motifs, partners almost always used the same type of movement within a duet, yet almost never used the same motifs within a duet (Tables 3, 4). Over the whole sample of 185 duets, birds used the same movement in 96% of cases, yet used the same motif in only 1.6% of cases (Table 3). Such a pattern could come about because birds actively chose movements and motifs, or simply by chance if all birds used the same movement almost all the time, yet have a very large repertoire of motifs. To test statistically between these alternatives, we created a random subsample of data in which each pair contributed only a single datum for a given initiating movement or motif type. Both birds in 15 of the 18 pairs in the study produced all three types of movement (Table 3). Therefore, for each movement type of the bird that initiated movement in a duet, we randomly sampled one duet. If the responding bird actively chose to match the movement type, then the ‘answering’ movement would match the initiator regardless of the initiating movement. If they did not actively choose the matching type, then the probability of the three ‘answering’ movements would remain constant regardless of the initiating movement. We carried out the same sampling strategy on the eight pairs in which each bird sang the three most common motif types, to see if they actively avoided matching motifs. The results show that birds do match movement types, yet avoid matching motif types (Tables 4, 5; Fisher’s exact test: $P < 0.001$ for both movement and motif type association). Another possible cause of association of movement and motif type between partners is that the playback type itself prompted specific behaviour, independently of their partner’s behaviour. However, we can reject that possibility because the pattern of using the same movement but a different motif type also occurred during the 5 min period before playback. All 27 duets from 14 pairs consisted of the same type of movement yet different types of motif; the sample included 22 wing-spreading movements, three ‘shoulder’-

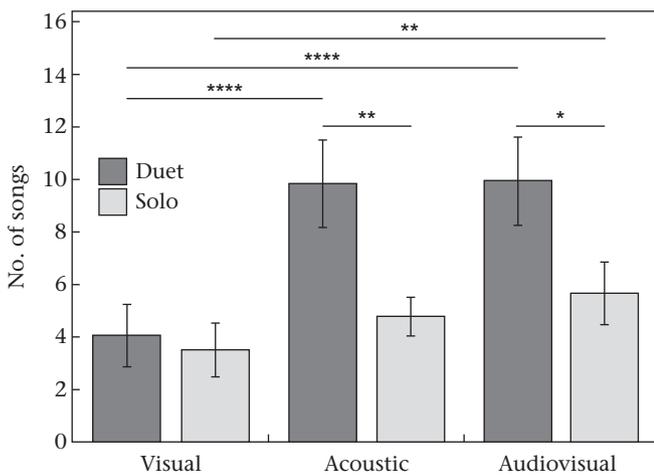


Figure 2. Numbers of duets and solo songs performed by pairs in 5 min during three treatments: acoustic, visual and audiovisual. Significant differences are indicated with thick black lines (**** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$). The boxes show means \pm SE.

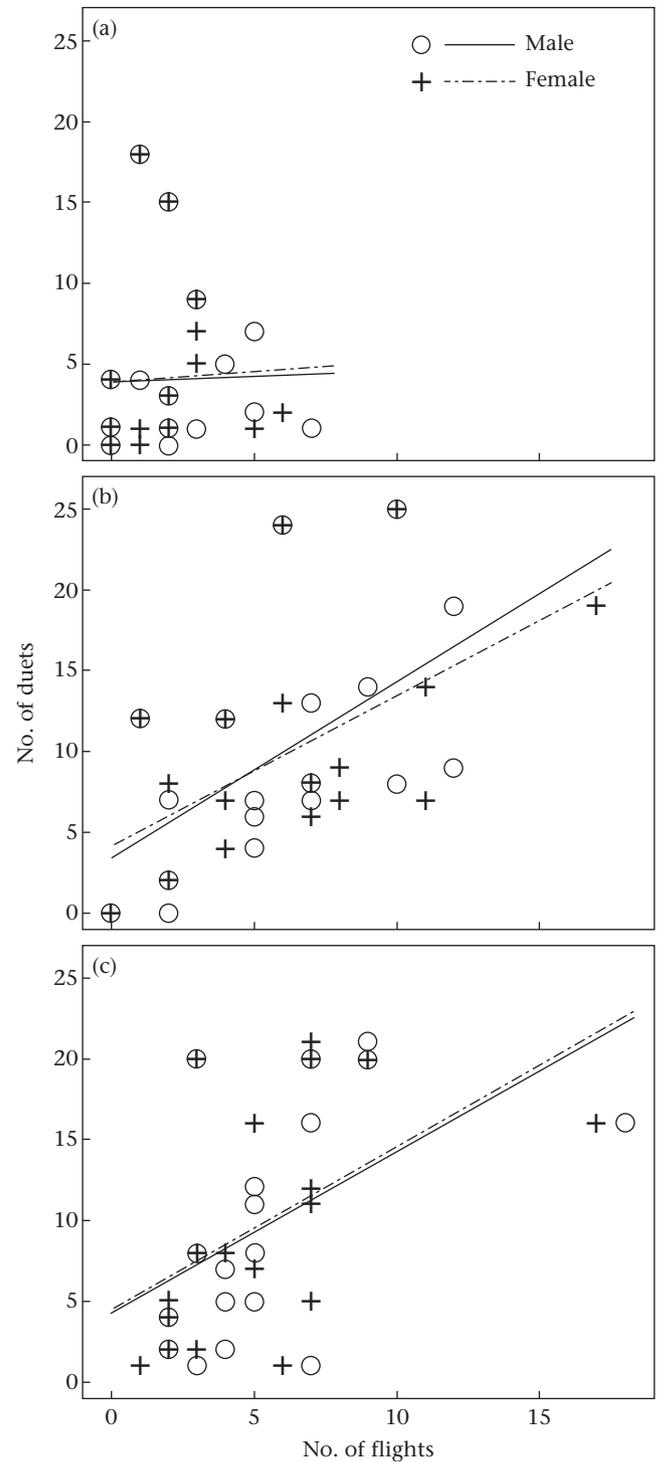


Figure 3. Relationship between duetting and flying in (a) visual, (b) acoustic and (c) audiovisual treatments. The points show the number of duets and flights performed in a 5 min period. Plots show estimated linear trends for each sex separately.

raising movements and two body-flicking movements. Overall, birds actively matched their partner’s movement in a duet, but avoided using the same motif.

DISCUSSION

Acoustic and visual components of the magpie-lark bimodal display appear to convey different messages, potentially targeting

Table 3
The organization of multimodal duets according to the types of motifs and movements used by pairs

| Pair | No. of multimodal displays | Motif types ¹ | Motif matching combinations ² | Motif nonmatching combinations | Male movements ¹ | Female movements ¹ | Movement matching combinations | Movement nonmatching combinations ² | Motif-movement combinations |
|------|----------------------------|--------------------------|--|--------------------------------|-----------------------------|-------------------------------|--------------------------------|--|-----------------------------|
| 1. | 7 | 3 | 0 | 2 | 5W 1F 1S | 5W 1F 1S | 3 | 0 | 4 |
| 2. | 3 | 2 | 0 | 1 | 3W | 3W | 1 | 0 | 1 |
| 3. | 5 | 2 | 0 | 1 | 2W 2F 1S | 2W 2F 1S | 3 | 0 | 3 |
| 4. | 1 | 2 | 0 | 1 | 1W | 1W | 1 | 0 | 1 |
| 5. | 13 | 3 | 0 | 3 | 10W 1F 2S | 9W 2F 2S | 3 | 1 | 7 |
| 6. | 21 | 4 | 0 | 4 | 17W 2F 2S | 16W 3F 2S | 3 | 1 | 9 |
| 7. | 17 | 4 | 0 | 4 | 14W 1F 2S | 15W 1F 1S | 3 | 1 | 9 |
| 8. | 13 | 3 | 1 | 2 | 11W 1F 1S | 11W 1F 1S | 3 | 0 | 7 |
| 9. | 14 | 4 | 1 | 2 | 10W 3F 1S | 10W 3F 1S | 3 | 0 | 7 |
| 10. | 19 | 4 | 0 | 3 | 15W 3F 1S | 14W 4F 1S | 3 | 1 | 8 |
| 11. | 9 | 3 | 0 | 2 | 6W 1F 2S | 5W 1F 3S | 3 | 1 | 5 |
| 12. | 2 | 2 | 0 | 1 | 2W | 2W | 1 | 0 | 1 |
| 13. | 24 | 4 | 0 | 4 | 20W 1F 3S | 19W 2F 3S | 3 | 1 | 9 |
| 14. | 6 | 2 | 0 | 1 | 4W 1F 1S | 4W 1F 1S | 3 | 0 | 3 |
| 15. | 8 | 2 | 0 | 1 | 5W 1F 2S | 5W 2F 1S | 3 | 1 | 4 |
| 16. | 11 | 3 | 1 | 2 | 9W 1F 1S | 9W 1F 1S | 3 | 0 | 6 |
| 17. | 8 | 3 | 0 | 2 | 6W 1F 1S | 6W 1F 1S | 3 | 0 | 4 |
| 18. | 4 | 3 | 0 | 2 | 1W 1F 2S | 1W 1F 2S | 3 | 0 | 3 |

The table lists only motifs for which males and females were observed ($N = 185$). Matching and nonmatching combinations pertain, respectively, to duets with the same and different types of motifs or movements.

¹ Nine distinct types of motifs and three distinct types of movements were identified (W: wing spreading; S: 'shoulder' raising; F: body flicking).

² Each matching combination for motifs, and each nonmatching combination for movements, was observed only once.

Table 4
The frequency of movement types given by duet initiators and responders

| Duet initiator | Duet responder | | |
|--------------------|----------------|--------------------|---------------|
| | Wing spreading | 'Shoulder' raising | Body flicking |
| Wing spreading | 15 | 0 | 0 |
| 'Shoulder' raising | 0 | 15 | 0 |
| Body flicking | 0 | 0 | 15 |

The table lists movements within a random sample of 45 duets from 15 pairs. Observations falling on the diagonal show that responding birds match the movement type of their partner.

different receivers (Partan & Marler, 2005). Focal pairs showed a similar and strong territorial response only to purely acoustic and multimodal playbacks, implying that only the acoustic component provoked territorial aggression. This territorial response included a disproportionate increase in duetting compared to solo song, a known response to territorial challenge, and a correlated increase in both duetting and flying. By contrast, although purely visual playbacks prompted a small increase in song and flight, there was not a disproportionate increase in duetting, and there was no correlation between duetting and flight. The role of the visual component of bimodal duets is therefore unresolved, but the coordination of movements implies that partners look at each other to choose their display, suggesting that the signal might primarily be addressed to partners, perhaps as a way to coordinate acoustic duets.

Table 5
The frequency of three most common motif types given by duet initiators and responders

| Duet initiator | Duet responder | | |
|----------------|----------------|---------|---------|
| | Motif 1 | Motif 2 | Motif 3 |
| Motif 1 | 0 | 1 | 7 |
| Motif 2 | 6 | 0 | 2 |
| Motif 3 | 3 | 5 | 0 |

The table lists motifs within a random sample of 24 duets from eight pairs. The absence of observations on the diagonal shows that responding birds avoid matching their partner's motif type.

Acoustic and bimodal playbacks, but not purely visual playbacks, prompted a typical territorial response. This territorial response, previously described after acoustic playbacks, consists of an overall increase in singing, with a disproportionate increase in duetting, combined with an increase in the number of flights (Hall, 2000; Mulder et al., 2003; Rogers et al., 2004). In our study, focal pairs produced twice as many songs and three times as many flights to acoustic and bimodal playbacks than to purely visual playbacks. Furthermore, although even the visual treatment did prompt some singing and flying, responses to treatments differed in the use of song, and not merely the magnitude of response. First, the proportion of duets increased only for acoustic and bimodal playbacks, and not visual playbacks. Second, variation in the intensity of response among individuals was consistent with variation in the intensity of territorial response only to acoustic and bimodal playbacks. For these two treatments, an increase in the number of flights was accompanied by an increase in the number of duets, but there was no such association in response to visual playback alone. In other words, comparisons both between and within birds show that a visual display alone does not provoke the territorial syndrome of increased duetting and flight. Overall, our results imply that the addition of a visual component to the bimodal display does not affect the perceived territorial threat of the display.

The pattern of territorial response to playback means that males and females were more likely to cooperate after hearing vocal and bimodal playbacks than solely visual duets. Cooperative territorial defence is a fundamental function of duetting (Sonnenschein & Reyer, 1983; Wickler, 1980). In magpie-larks, duets function to maintain the territory, and duets are more threatening territorial signals than solo songs (Hall, 2000). What is more, precise temporal coordination of songs between partners increases the perceived threat of these cooperative territorial displays (Hall, 2000; Hall & Magrath, 2007). In this study, the purely visual playback prompted much less cooperative display by focal pairs despite a similar number of solo songs. This difference in cooperation again suggests that visual and acoustic components of magpie-lark displays are targeted at different receivers.

One explanation for why the visual display had a lesser and different effect on the response of focal birds was that it was

difficult to detect compared to the vocal signal (Partan & Marler, 2005). However, we think this is unlikely. First, magpie-larks live in open habitat with scattered trees, so their striking black and white plumage and conspicuous visual signals are likely to be easily detectable. Second, although they did not respond with typical territorial behaviour to purely visual displays, the birds none the less responded with increased song and flight, showing that they had seen the models. Third, we attracted attention to the location of the taxonomic robots by first broadcasting magpie-lark begging calls, and only starting the playback after the focal birds were within 25 m. Finally, during bimodal playbacks, the acoustic duet would make the location of the robot birds yet more conspicuous, and probably impossible to miss. However, the response to multimodal playbacks was the same as to purely acoustic ones, showing that the visual component did not increase the response even when given with conspicuous calls.

A lesser effect of the visual display might also result from a lower realism of robotic model movements compared with acoustic playbacks (Klein, Stein, & Taylor, 2012). Clearly our models were not identical to live birds, and these differences might affect the behaviour of focal birds, by either reducing or increasing the intensity of response compared with live birds. However, model realism seems unlikely to explain the key results, for two main reasons. First, models of varying realism have been used successfully in many studies of both birds and mammals; models can standardize key attributes, allow controlled experiments and circumvent ethical problems. For example, stationary taxidermic models and painted wooden models have been used successfully to simulate perched predators or brood parasites (e.g. Curio, 1993; Davies & Welbergen, 2008; Grim, 2008; Krams & Krama, 2002). Similarly, controlled presentation of painted gliders, model aeroplanes, hats, sticks and simple video shapes can all prompt responses specific to raptors, without exposing animals to danger (e.g. Evans, Macedonia, & Marler, 1993; Goodale, Kotagama, & Holberton, 2005; Magrath, Haff, McLachlan, & Igic, 2015; Thompson & Hare, 2010). Our models used taxidermic skins, so that the colour, pattern and surface texture were realistic, and these can be key attributes that prompt responses (Curio, 1975; Němec et al., 2014). Similarly, the timing and alternating pattern of movement were based on the natural timing of multimodal duets, and yet had the advantage of being constant between treatments. The appearance of models will also vary with the distance, viewing perspective and lighting, which should emphasize major features like pattern and movement. These same general comments about the realism of experimental stimuli also apply, although to a lesser extent, to acoustic playbacks of natural calls. Recordings are never perfect, because of limitations of equipment and recording conditions, and playback adds imperfection because of technical constraints on sound reproduction and use of equipment during experiments. Second, a lack of realism seems unlikely to explain the qualitative differences in response by magpie-larks between acoustic and visual treatments. Birds did respond to visual-only duets, but in a different way rather than simply with lower intensity. Furthermore, the response to multimodal playbacks was the same as to purely acoustic ones, showing that the visual component did not affect the response. If the lower response to visual-only duets was due solely to realism, then one would expect that the multimodal duet would provoke a greater response, either because of an additive effect or because visual display appears more realistic when accompanied by conspicuous calls. It is valuable to assess realism of treatments in any experiment, and this will be particularly challenging in studies of multimodal communication, where it will be difficult to assess the relative realism of stimuli affecting different senses.

Instead of being a display to rivals, an individual's visual display might be targeted at its duetting partner and have a role of coordinating the bimodal display. Although pairs produced multiple types of movements and motifs, partners almost always used the same movements yet different motifs in the same joint display. This pattern did not arise because individuals always used the same combination of movement and motif; in fact, movement and motif type were used in all combinations. Therefore, the use of similar movements within a duet implies that birds look at their partner at least some of the time to choose their visual display. This in turn suggests that the visual display might have a role in coordinating vocal duets within pairs, analogous to a conductor's baton, and so have a different audience from the acoustic duet, which is a territorial signal directed at neighbours (Hall, 2000). Currently we are unable to test this possibility, in part because acoustic duets are rarely given without accompanying visual displays.

Although the visual component of duets might be directed at the partner and have a role in coordinating the display, another possibility is that it increases the effectiveness of the cooperative display when signalling over a long distance or in poor conditions for acoustic communication. Magpie-larks live in open habitat, with scattered trees, so can be visible from hundreds of metres. In such open habitats, the visual display may help distant birds localize the display and direct attention to specific signallers, and enhance the intensity of the message, as suggested for the wing display of duetting spotted palm thrushes, *Cichladsa guttata* (Todt & Fiebelkorn, 1980). In our study all playbacks were given close to focal birds, so we were unlikely to see any benefit of enhanced localization of the bimodal compared to purely vocal display, yet such an advantage could appear at long distances. Indeed, body movements can aid the localization of multimodal signals in other species. In the blue-black grassquit, *Volatinia jacarina*, for example, males leap out of the grass while vocalizing, allowing receivers to better localize the acoustic signal (Wilczynski, Ryan, & Brenowitz, 1989), and in Túngara frogs, *Physalaemus pustulosus*, receivers compare the arrival time of simultaneously emitted sounds and ripples on the water surface created during sound production, and so obtain information on relative distance to a source (Halfwerk, Page, Taylor, Wilson, & Ryan, 2014). Visual signalling might also enhance vocal communication in areas exposed to high ambient noise, allowing detection of pairs that are duetting, or facilitating separation of motifs from background noise and division between successive events (Todt & Fiebelkorn, 1980). This possibility has not been tested explicitly, but in noisy conditions bottlenose dolphins, *Tursiops truncatus*, increase whistle repetition, speed of swimming and tend to gather, humpback whales, *Megaptera novaeangliae*, switch from primarily vocal to primarily surface-generated signals, such as breaching, and foot-flagging frogs, *Staurois latopalmitatus*, give specific visual displays (Buckstaff, 2004; Dunlop, Cato, & Noad, 2010; Nowacek, Wells, & Solow, 2001; Preininger, Boeckle, & Hödl, 2009). These behaviours might be effective ways to compensate for vocal signal masking.

Our results suggest that assessing the function of components of multimodal signals can be difficult when examining suites of behaviour rather than different categories of behaviour. Magpie-larks increased the number of both songs and flights in response to visual and acoustic components of display, but with a greater number in response to acoustic and multimodal displays. This might suggest that the components of display are simply redundant, and merely affect the intensity of response. However, birds used their songs and flights differently in response to visual and acoustic components, with only the latter showing a strong territorial response consisting of a disproportionate number of duets, and a correlation in the number of duets and flights. This difference in use shows that the components of magpie-lark displays provoke

different types of response and so are, at least in part, nonredundant. We therefore suggest that it is necessary to examine suites of behaviour when assessing the role of multimodal signal components.

In conclusion, we suggest that the visual and acoustic components of the magpie-lark's duetting display could convey independent messages, with the acoustic component important in territorial defence and the visual component possibly coordinating vocal duets within pairs. It is also possible that, in this open-habitat species, the visual display enhances the multimodal signal at long distances or in conditions difficult for receiving acoustic signals. Multimodal, cooperative displays like magpie-lark duets have received little experimental study, and offer rich opportunities for dissecting the roles of signal function and cooperation.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.04.024>.

References

- Buckstaff, K. C. (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, 20(4), 709–725.
- Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews*, 78(4), 575–595.
- Curio, E. (1975). The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. *Animal Behaviour*, 23(1), 1–115.
- Curio, E. (1993). Proximate and developmental aspects of antipredator behavior. *Advances in the Study of Behavior*, 22, 135–238.
- Davies, N. B., & Welbergen, J. A. (2008). Cuckoo–hawk mimicry? An experimental test. *Proceedings of the Royal Society B: Biological Sciences*, 275(1644), 1817–1822.
- Disney, H. J. d. S. (1974). *Bird in the hand*. Sydney, Australia: Bird Bander's Association of Australia.
- Dunlop, R. A., Cato, D. H., & Noad, M. J. (2010). Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*). *Proceedings of the Royal Society B: Biological Sciences*, 277(1693), 2521–2529.
- Evans, C. S., Macedonia, J. M., & Marler, P. (1993). Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. *Animal Behaviour*, 46(1), 1–11.
- Goodale, E., Kotagama, S. W., & Holberton, R. L. (2005). Alarm calling in Sri Lankan mixed-species bird flocks. *Auk*, 122(1), 108–120.
- Grim, T. (2008). Are Blackcaps (*Sylvia atricapilla*) defending their nests also calling for help from their neighbours? *Journal of Ornithology*, 149(2), 169–180.
- Halfwerk, W., Page, R. A., Taylor, R. C., Wilson, P. S., & Ryan, M. J. (2014). Crossmodal comparisons of signal components allow for relative-distance assessment. *Current Biology*, 24(15), 1751–1755.
- Hall, M. L. (2000). The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Animal Behaviour*, 60(5), 667–677.
- Hall, M. L. (2006). Convergent vocal strategies of males and females are consistent with a cooperative function of duetting in Australian magpie-larks. *Behaviour*, 143(4), 425–449.
- Hall, M. L. (2009). A review of vocal duetting in birds. *Advances in the Study of Behavior*, 40, 67–121.
- Hall, M. L., & Magrath, R. D. (2000). Duetting and mate-guarding in Australian magpie-larks (*Grallina cyanoleuca*). *Behavioral Ecology and Sociobiology*, 47(3), 180–187.
- Hall, M. L., & Magrath, R. D. (2007). Temporal coordination signals coalition quality. *Current Biology*, 17(11), R406–R407.
- Hardin, J. W., & Hilbe, J. M. (2002). *Generalized estimating equations*. Boca Raton, FL: Chapman and Hall/CRC.
- Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, 57(3), 197–214.
- Johnstone, R. A. (1997). The evolution of animal signals. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 155–178). Oxford, U.K.: Blackwell.
- Klein, B. A., Stein, J., & Taylor, R. C. (2012). Robots in the service of animal behavior. *Communicative & Integrative Biology*, 5(5), 466–472.
- Krakauer, D. C., & Johnstone, R. A. (1995). The evolution of exploitation and honesty in animal communication: a model using artificial neural networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 348(1325), 355–361.
- Krams, I., & Krama, T. (2002). Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. *Proceedings of the Royal Society B: Biological Sciences*, 269(1507), 2345–2350.
- Leonard, A. S., & Hedrick, A. V. (2010). Long-distance signals influence assessment of close range mating displays in the field cricket, *Gryllus integer*. *Biological Journal of the Linnean Society*, 100(4), 856–865.
- Magrath, R. D., Haff, T. M., McLachlan, J. R., & Igc, B. (2015). Wild birds learn to eavesdrop on heterospecific alarm calls. *Current Biology*, 25(15), 2047–2050.
- Malacarne, G., Cucco, M., & Camanni, S. (1991). Coordinated visual displays and vocal duetting in different ecological situations among Western Palearctic non-passerine birds. *Ethology Ecology & Evolution*, 3(3), 207–219.
- McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (2nd ed.). London, U.K.: Chapman and Hall.
- Møller, A. P., & Pomianowski, A. (1993). Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, 32, 167–176.
- Mulder, R. A., Bishop, H., Cooper, M., Dennis, S., Koetsveld, M., Marshall, J., et al. (2003). Alternate functions for duet and solo songs in magpie-larks, *Grallina cyanoleuca*. *Australian Journal of Zoology*, 51(1), 25–30.
- Nowacek, S. M., Wells, R. S., & Solow, A. R. (2001). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, 17(4), 673–688.
- Némec, M., Syrová, M., Dokoupilová, L., Veselý, P., Šmilauer, P., Landová, E., et al. (2014). Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. *Animal Cognition*, 18(1), 259–268.
- Partan, S. R. (2013). Ten unanswered questions in multimodal communication. *Behavioral Ecology and Sociobiology*, 67(9), 1523–1539.
- Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *American Naturalist*, 166(2), 231–245.
- Peter, J. M., Cowling, S. J., & Higgins, P. J. (2006). Handbook of Australian, New Zealand & Antarctic birds. In *Boatbill to starlings* (Vol. 7). Melbourne, Australia: Oxford University Press.
- Preininger, D., Boeckle, M., Freudmann, A., Starnberger, I., Sztatecsny, M., & Hödl, W. (2013). Multimodal signaling in the small torrent frog (*Micrixalus saxicola*) in a complex acoustic environment. *Behavioral Ecology and Sociobiology*, 67(9), 1449–1456.
- Preininger, D., Boeckle, M., & Hödl, W. (2009). Communication in noisy environments II: visual signaling behavior of male foot-flagging frogs stauroids *Latopalmatus*. *Herpetologica*, 65(2), 166–173.
- Ratcliffe, J. M., & Nydam, M. L. (2008). Multimodal warning signals for a multiple predator world. *Nature*, 455(7209), 96–99.
- Rogers, A., Ferguson, J., Harrington, H., McDowell, S., Miller, A., & Panagos, J. (2004). Use of stereo duet playback to investigate traditional duet playback methods and mechanisms of cooperative territorial defence in Magpie-larks. *Behaviour*, 141(6), 741–753.
- Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, 58(5), 921–931.
- Rypstra, A. L., Schlosser, A. M., Sutton, P. L., & Persons, M. H. (2009). Multimodal signalling: the relative importance of chemical and visual cues from females to the behaviour of male wolf spiders (Lycosidae). *Animal Behaviour*, 77(4), 937–947.
- Smith, C. L., & Evans, C. S. (2008). Multimodal signaling in fowl, *Gallus gallus*. *Journal of Experimental Biology*, 211(13), 2052–2057.
- Sonnenschein, E., & Reyer, H.-U. (1983). Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarius funebris*). *Zeitschrift für Tierpsychologie*, 63(2–3), 112–140.
- Stevens, M. (2013). *Sensory ecology, behaviour, and evolution*. Oxford, U.K.: Oxford University Press.
- Thompson, A. B., & Hare, J. F. (2010). Neighbourhood watch: multiple alarm callers communicate directional predator movement in Richardson's ground squirrels, *Spermophilus richardsonii*. *Animal Behaviour*, 80(2), 269–275.
- Tingay, S. (1974). Antiphonal song of the magpie lark. *Emu*, 74(1), 11–17.
- Todt, D., & Fiebelkorn, A. (1980). Display, timing and function of wing movements accompanying antiphonal duets of *Cichladas guttata*. *Behaviour*, 72, 82–106.
- Von Seibt, U., & Wickler, W. (1977). Duettieren als revier-anzeige bei vögeln. *Zeitschrift für Tierpsychologie*, 43(2), 180–187.
- Wickler, W. (1980). Vocal duetting and the pair bond. I. Coyness and partner commitment. A hypothesis. *Zeitschrift für Tierpsychologie*, 52(2), 201–209.
- Wilczynski, W., Ryan, M. J., & Brenowitz, E. A. (1989). The display of the Blue-black grassquit: the acoustic advantage of getting high. *Ethology*, 80(1–4), 218–222.
- Zimmer, K. J., Whittaker, A., & Oren, D. C. (2001). A cryptic new species of flycatcher (Tyrannidae: Suiriri) from the cerrado region of central South America. *Auk*, 118(1), 56–78.