



Chorus-call classification in the southern pied babbler: multiple call types given in overlapping contexts

K.A. Golabek* and A.N. Radford

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

*Corresponding author's current address: Botswana Predator Conservation Trust,
Private Bag 13, Maun, Botswana, e-mail: kagolabek@gmail.com

Accepted 1 March 2013

Abstract

Individuals of many species communicate with one another using a range of vocalisations and there is often variation in the use and structure of these calls depending on sex, status and context. In social species, two or more group members may also combine their vocalisations to produce duets or choruses. While the function of duets and the different contributions of males and females have received considerable research attention, less is known about the different calls used by group members in choruses. Southern pied babblers (*Turdoides bicolor*) are cooperatively breeding birds of Southern Africa that live in permanent stable groups. In addition to a variety of calls given by individuals, group members frequently combine to produce raucous choruses which include several different call types. Here we describe these different call types for the first time and explore their usage, with respect to the sex and dominance status of callers, production of the call alone or as part of a chorus, and the social context. Eight out of nine possible calls used in choruses on some occasions were found to be statistically distinct. As expected from the variation shown in individual calls, some of those call types included in choruses were sex-specific and some were used more by dominants than subordinates. Moreover, there was variation in the use of different call types as solos and within choruses, as well as their occurrence in different contexts. We discuss what might be concluded about the functions of the different call types from their patterns of usage.

Keywords

vocal communication, chorus-calling, call classification, repertoire, call function, *Turdoides bicolor*.

1. Introduction

In many animal species, individuals produce a repertoire of different vocalisations (see, for example, reviews on primates by McComb & Semple

(2005) and on oscine birds by Devoogd et al. (1993)). Each vocalisation type is likely to have evolved to serve a different function or functions. Individuals in numerous species from a variety of taxa use discrete calls to signal, for example, the location of food (e.g., Dittus, 1984; Elgar, 1986), the presence of predators (e.g., Seyfarth et al., 1980; Manser, 2001; Leavesley & Magrath, 2005), their current nutritional state (e.g., Bengtsson & Ryden, 1983; Leonard & Horn, 1996) and their imminent departure from the area (e.g., Stewart & Harcourt, 1994; Radford, 2004a). The same vocalisation types may also serve more than one function in the same species, as is the case with the songs of some passerine birds that are used both to attract mates and to defend territories (Catchpole & Slater, 2008).

In addition to the use of several different call types, there is often intraspecific variation in the use of the same call type. Some calls are only emitted by certain individuals within the population. For example, there are calls given between mother and infant dyads that are not produced by adult males (e.g., Whitham et al., 2007) and it is often the case that calls with an important mating function are given exclusively by one sex (e.g., McComb, 1991; Gerhardt, 1994). Alternatively, all individuals may produce a particular call, but its frequency of use may differ within a population. For example, when calls are used to signal size or competitive strength, they are likely to be given at greater rates by higher ranking individuals (e.g., Kitchen et al., 2003). Moreover, a particular call may be graded depending on the circumstance. For instance, changes in the rate or pitch of production may indicate the level of threat urgency (e.g., Leavesley & Magrath, 2005; Bell et al., 2009) or satiation of the individual (Bengtsson & Ryden, 1983; Leonard & Horn, 1996).

In many species, individuals do not just give vocalisations alone, but also in combination with others to form duets or choruses (Catchpole & Slater, 2008). Considerable research effort has been devoted to assessing the potential functions of duets (see Hall, 2004) and in investigating the types of vocalisations that form the duet, which individuals produce them and the variation involved (Stokes & Williams, 1968; Langmore, 1998; Appleby et al., 1999). Choruses, which include contributions by three or more group members, are less common and harder to analyse than duets (Catchpole & Slater, 2008). As such, although some studies have investigated their potential function (e.g., Seddon, 2002; Radford, 2003, 2005; Radford & du Plessis,

2004), detailed assessments of the contributions by group members of different sex and status and of the different vocalisations making up the chorus are rare (but see Brown & Farabaugh, 1991; Voigt et al., 2006).

Pied babblers (*Turdoides bicolor*) are group-living birds of southern Africa that produce a variety of vocalisations, although they do not sing (Hockey et al., 2005). Individuals produce several different call types when foraging (Radford & Ridley, 2006, 2008), when acting as a sentinel (Hollén et al., 2008) and to warn of danger (Golabek, unpublished data). Some of these calls can serve several functions. For example, the low-amplitude ‘chuck’ calls produced by foraging individuals can mediate spacing between potential competitors (Radford & Ridley, 2008), provide information about group size and individual position and, thus, the need for personal vigilance (Radford & Ridley, 2007), indicate the current nutritional state of the forager (Radford & Ridley, 2008; Bell et al., 2010) and form the basis of negotiation over sentinel duty (Bell et al., 2010). Likewise, the ‘watchman’s song’ of sentinels provides information about their presence (Hollén et al., 2008), height (Radford et al., 2009) and current level of risk in the area (Bell et al., 2009), as well as playing a role in negotiating this cooperative activity (Bell et al., 2010). These calls produced by individuals alone often vary in their structure and rate (see, for example, Radford & Ridley, 2008; Bell et al., 2009) and their usage can differ between group members of different sex and status (see, for example, Radford & Ridley, 2006).

In addition to this repertoire of calls given by individuals alone, pied babbler group members frequently vocalise together to produce raucous choruses during a variety of intra-group and inter-group contexts. These conspicuous displays involve individuals converging in a tree or on the ground, and each producing one or more loud, atonal call types repetitively in combination with others (Figure 1 and the audio clips that are a part of the online version of the article, which can be accessed via <http://booksandjournals.brillonline.com/content/1568539x>). Call types used within choruses can also be given as solo calling bouts. Here, we present the first classification of these different call types which are used by pied babblers within choruses and explore their patterns of use. Specifically, we investigate if each call type is given equally in choruses and by birds calling alone, whether all call types are given by all group members of different sex and dominance status, and in what contexts different calls are used.

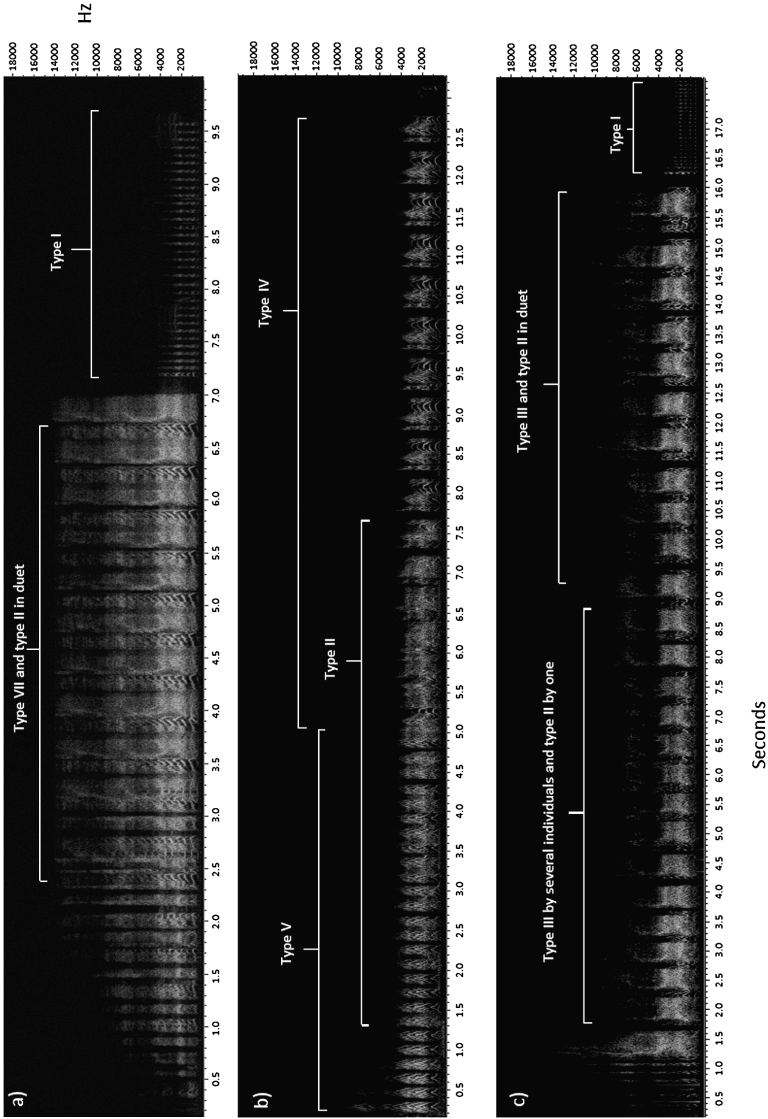


Figure 1. Spectrograms and waveforms of call types during choruses. (a) A duet by a breeding pair, male using type VII and female type II, (b) one individual changes from call type V to type IV during the chorus, with call type II in the background, (c) multiple individuals chorusing at the start, with breeding pair in a duet using call types III and II after other group member stop, and chorus ending with call type I.

2. Materials and methods

2.1. Study site and population

Data were collected from nine habituated pied babbler groups on the Kuruman River Reserve, South Africa (26°58'S, 21°49'E) between December 2006 and August 2009. The study site consists of semi-arid Kalahari scrubland with a strong seasonal trend in rainfall (for a detailed description of vegetation and climate see Clutton-Brock et al., 1999 and Ridley & Raihani, 2007).

Pied babblers live in stable, cooperatively breeding groups, consisting of a dominant breeding-pair, that are the parents of ca. 95% of the offspring (Nelson-Flower et al., 2011), and sexually mature subordinate helpers. The dominant pair is identifiable by agonistic interactions towards other group members, extended preening together, and investment in incubation and nest building (Ridley & Raihani, 2008). Subordinates are identified by submissive responses, including bill-gaping, crouching, looking away and fleeing (Raihani, 2008). Group size in the study period ranged from 2 to 13 (mean \pm SD 6.1 \pm 2.6) adults (individuals > 365 days old). Birds were sexed using DNA from blood collected when ringing (for capture details, see Radford & Ridley, 2008) using the technique described in Griffiths et al. (1998). Groups defend year-round territories (Golabek et al., 2012) and move around these as a tight unit throughout the day. All birds were individually colour-ringed for identification and groups were habituated to human presence at <3 m. This enabled clear observations of which bird(s) were calling and close-proximity audio recordings.

2.2. Data collection

Each group was visited approximately three times per week. Calls made by identified individuals were recorded ad libitum using a Sennheiser ME66 shotgun microphone (frequency response 40 Hz–20 kHz \pm 2.5 dB), with a K6 power module (2004 Sennheiser). They were digitally transformed through a Marantz PMD660 solid-state recorder (frequency response 20 Hz–16 kHz, –0.5 dB tolerance; 2008 D&M Holdings), at a sample rate of 48 kHz, 32-bit, and stored directly onto a Compact Flash media card in WAVE file format. After calling ceased, the identity of caller(s) that could be confidently assigned, whether the vocalisation was given alone or as part of a chorus, and the context (intra or inter-group) was spoken into the microphone. Inter-group contexts involved any visual/vocal interaction with

non-group members (a group, roving coalition or single intruder) and all other contexts were considered intra-group. During choruses, there are occasions when only one bird is vocalising, either at the start or the end or due to a break in participation from the others. For example, X_1 calling at the start of a chorus involving X_1 , X_2 , X_3 , with a break in the middle when X_2 called alone, and the chorus ended with X_1 calling alone again. Such situations enabled the isolation of calls from within a chorus for known individuals in some circumstances. Overall, the database for analysis included 324 calling occasions from 107 days, from which information on 617 individual calling bouts were recorded; 50 adults (14 dominant females (DF), 13 dominant males (DM), 14 subordinate females (SF) and nine subordinate males (SM)) were identified clearly whilst calling.

2.3. Call classification

Calls that could be identified to a specific individual were used in call classification. Calls were initially classified by eye into 9 types (see Figure 2). In many cases, there was only one call type from an individual that had excellent audio quality (low noise-to-call ratio and with no overlap with other individuals calling), so a single-factorial design was used. Where multiple calls per individual were available the call used was selected at random. The sample sizes (N = individuals) were as follows: call type I, N = 11; type II, N = 8; type III, N = 7; type IV, N = 7; type V, N = 10; type VI, N = 10; type VII, N = 10; type VIII, N = 15 and type IX, N = 10.

The acoustic parameters of each call were measured by hand using AVISOFT-SAS Lab Pro 4.52 (R. Specht, Berlin, Germany) with a fast Fourier transformation of 1024-point, 100% frame size, 96.87% overlap, viewed in a Hamming window. The parameters extracted from each sonogram were: call duration; inter-call interval; distance from the start of the call to the point of maximum amplitude; the number of visible harmonic bars below 5 kHz; the frequency gap between harmonic one and two, and between harmonic two and three; and the frequency on the first harmonic bar at the start, maximum frequency point (hereafter, peak1Har) and the end point. Entropy was also measured across the whole call at four equally spaced intervals to estimate call linearity. The time between the start and the peak1Har, and the relative location of the peak1Har (i.e., 0.5 would be exactly in the middle), were calculated, along with the frequency difference between the start and end point, the peak1Har and start, and the peak1Har and end. The

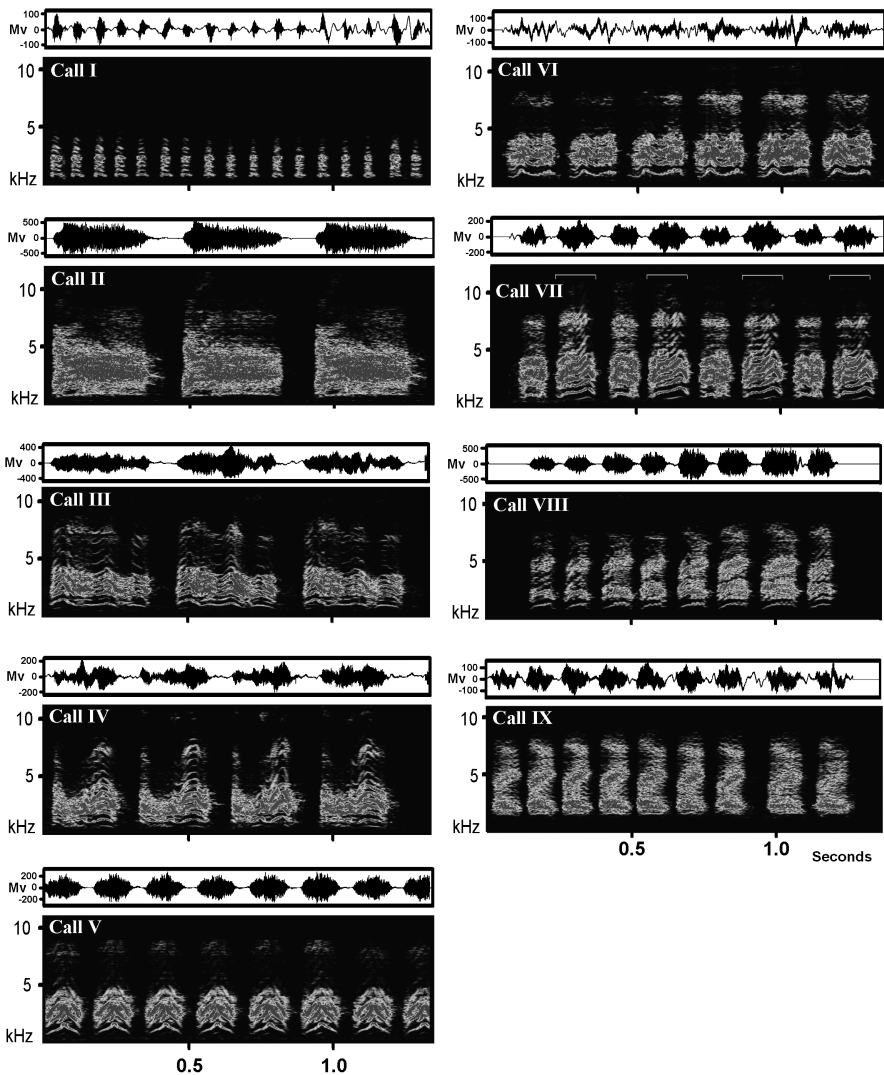


Figure 2. Spectrograms and waveforms of call types produced by pied babblers during choruses. Call type I, high purr; call type II, noisy atonal call; call type III, 3-syllable modulated call, contains three descending sub-elements; call type IV, 2-syllable modulated call, contains two ascending sub-elements; call type V, v-shaped chatter; a distinct upside-down v shape; call type VI, extended v-shaped chatter, an extended end to a softer v shape; call type VII, double syllable ascending call, the first note is highly variable, but the second has a consistent rise and dip at the end; call type VIII, tonal chatter, clear harmonic; call type IX, atonal chatter, high noise and no harmonic structure.

measured and calculated parameters were targeted specifically to describe the rise or fall of the calls, their harmonic structure and the symmetry of the call.

Call types appeared to differ considerably in duration, so a Kruskal–Wallis test was performed and calls were then grouped according to call duration. Multivariate analyses were then performed on the two resulting groups of call types. To test the initial eye-based classification, we used discriminant function analysis (DFA), having first used a principal components (PCs) correlation matrix to condense the information from the multiple parameters measured on each call. All PCs with eigenvalues > 1 were included in the DFA.

2.4. Call type and individual contributions

To explore patterns in use of call type by different sex and dominance categories (DF, DM, SF, SM), only call types with excellent ($\geq 80\%$) DFA cross-validated classification were used, because they could be assigned by eye with confidence. Only calls given by a clearly identified individual were used, resulting in sample sizes ($N =$ individuals) as follows: call type I, $N = 17$; type II, $N = 18$; type III, $N = 11$; type IV, $N = 12$; type V, $N = 11$; type VI, $N = 12$; type VII, $N = 11$; and type IX, $N = 21$. Chi-squared tests, with Yates corrections when counts were < 5 , were used to examine differences between the observed use of different call types and that expected by chance, given the available population and assuming equal use of the call types by all individuals. Expected values were calculated from the total number of individuals in each social category present across all groups at the times when recordings were made: DF = 15, DM = 17, SF = 46, SM = 28.

2.5. Call type and context relationships

To investigate if there were any contextual patterns in the use of different call types, again only those call types that showed excellent ($\geq 80\%$) cross-validation and, thus, could be confidently assigned by eye were used. First, the likelihood of a particular call type being used within a chorus ($N = 339$) compared to being produced as a solo ($N = 270$) was considered. Within a calling bout, birds can either use a single call type in a continuous sequence or they can switch between call types (see Figure 1). To look for patterns of use of particular call types, position in the chorus (at the start or the end only, or throughout the whole bout) was examined. Finally, the use of the different call types between intra- and inter-group contexts was investigated.

In all cases, Chi-squared tests were used to compare the observed distributions to that expected by chance given the number of occasions the particular behaviour/context was recorded, using Yates' continuity correction for all samples < 5 . Contributions to the Chi-squared value are quoted when one or two categories alone contributed heavily, showing they are important to any variation found.

2.6. Multiple testing

Every recorded call was tested under several possible hypotheses: (i) who made the call, (ii) was it as a solo or as part of a chorus, (iii) where was it given if in a sequence and (iv) in what context. To control for this exploratory multiple testing on the same dataset of calls, we used the Dunn–Šidák correction, $\beta = 1 - (1 - \alpha)^{1/N}$, β = new significance threshold, $\alpha = 0.05$ the significance threshold for the whole series of tests. Due to the exploratory nature of these analyses, tests were ranked by significance (most to least) and their significance threshold adjusted appropriately; test 1 $\beta = 0.05$, test 2 $\beta = 0.0253$, test 3 $\beta = 0.0170$, test 4 $\beta = 0.0127$, test 5 $\beta = 0.0102$. Where appropriate the test number is reported by the significance predictor p in subscript.

3. Results

3.1. Call classification

Call types differed significantly in duration (Kruskal–Wallis test: $\chi_8^2 = 80.84$, $p < 0.001$). Type I, the high purr, was significantly shorter than all other call types, while the remainder clustered into two distinct groups: types II, III and IV (group 1) were significantly longer than the others; types V, VI, VII, VIII and IX (group 2) all had intermediate durations with a degree of overlap between them (Figure 3).

Calls classified by eye as types II, III and IV (group 1) showed excellent classification by DFA, with 100% of the original calls and 95.2% of cross-validated calls being assigned to the correct call type. Specifically, 85.7% of calls assigned by eye as call type II and 100% assigned by eye as types III and IV were correct according to the cross-validation. All three call types were, therefore, used for subsequent analyses. The first two discriminant function (DF_{*i*}) scores described 100% of the variation from the first seven principal

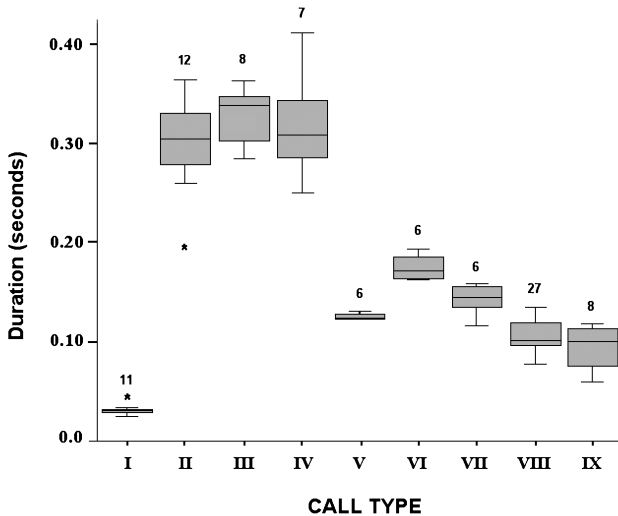


Figure 3. Median and inter-quartile range for call-duration of different call types. Number of individuals is shown above bars.

components and were used in the analysis of the group 1 call types; DF_1 describing 73.4% and DF_2 describing 26.6% of the variation (Figure 4a).

Calls classified by eye as types V, VI, VII, VIII and IX (group 2) also showed excellent classification by DFA, with 94.5% of the original calls and 83.6% of cross-validated calls being assigned to the correct call type. Specifically, 80% of calls assigned by eye as call type V, 100% assigned as types VI and VII, and 90% assigned as type IX were correct according to the cross-validation. These calls (all $\geq 80\%$ correctly cross-validated) were used in subsequent analyses. Call type VIII had only 60% correctly cross-validated classification and was, therefore, not included in subsequent analysis. The first four discriminant function (DF_i) scores described all of the variation from the first six principal components and were used in the analysis of the group 2 call types; DF_1 describing 63.6%, DF_2 describing 25.1%, DF_3 describing 8.4% and DF_4 describing 3% of variation (Figure 4b).

3.2. Call type and individual contributions

Three calls types showed strict sex specificity: call type II, the noisy atonal call, was only ever recorded from females; and call types III, the 3-syllable modulated call, and IV, the 2-syllable modulated call, were only ever recorded from males (Figure 5). Female-specific call type II was given sig-

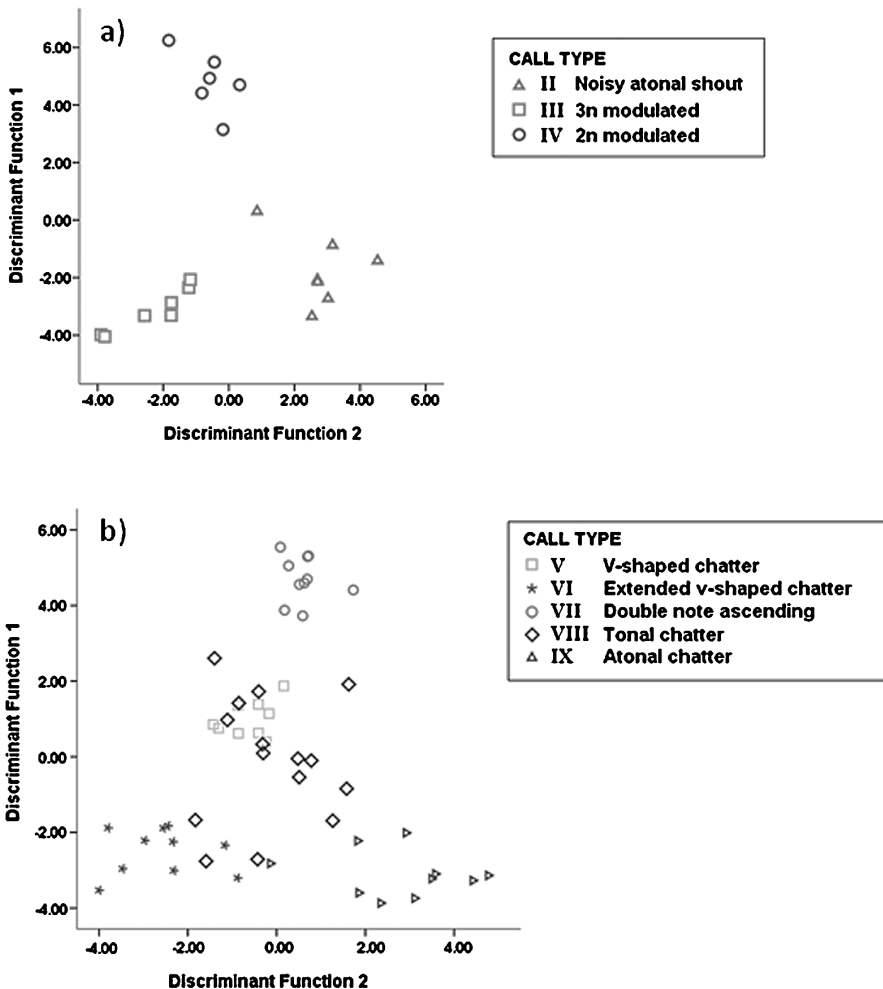


Figure 4. Discriminant function plots for call types II to IX. (a) Discriminant function scores 1 and 2 describing 100% of the total variation between call types II, III and IV (group 1) and (b) discriminant function scores 1 and 2 describing 88.7% of the total variation between call types V, VI, VII, VIII and IX (group 2).

nificantly more than expected by dominant individuals and less than expected by subordinates ($\chi_1^2 = 17.19$, $p_1 < 0.001$; contributions to chi-squared value: $\chi_{DF} = 12.96$, $\chi_{SF} = 4.23$). Likewise, male-specific call types III ($\chi_1^2 = 7.30$, $p_3 = 0.007$, $\chi_{DM} = 4.54$, $\chi_{SM} = 2.76$) and IV ($\chi_1^2 = 12.62$, $p_1 < 0.001$, $\chi_{DM} = 7.85$, $\chi_{SM} = 4.76$) were given significantly more than expected by dominant individuals and less than expected by subordinates.

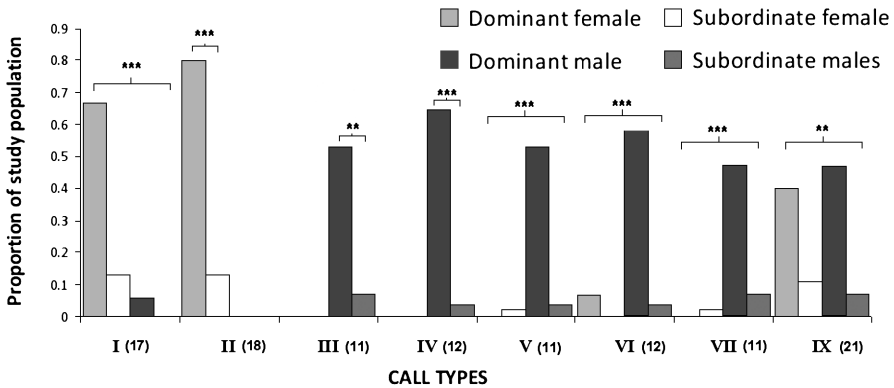


Figure 5. Proportion of adult population recorded giving each call type. Total number of individuals recorded in parentheses. Observed frequencies of calling were compared to expected frequencies given the known population ratio. ** $p < 0.01$; *** $p < 0.001$.

Call types I, V, VI, VII and IX were given by both sexes, but showed significant differences between the observed and expected counts recorded in all social categories (Figure 5). Call type I was given significantly more than expected by dominant females and less than expected by all other categories ($\chi^2_3 = 25.12$, $p_1 < 0.001$, $\chi_{DF} = 20.90$). Call types V, the v-shaped chatter ($\chi^2_3 = 29.36$, $p_1 < 0.001$, $\chi_{DM} = 25.72$), VI, the extended v-shaped chatter ($\chi^2_3 = 34.98$, $p_1 < 0.001$, $\chi_{DM} = 29.82$), and VII, the double syllable ascending call ($\chi^2_3 = 21.67$, $p_1 < 0.001$, $\chi_{DM} = 29.82$), were given significantly more than expected by dominant males and less than expected by all other categories. Call type IX, the atonal chatter, was given significantly more than expected by dominant birds and less than expected by subordinate birds ($\chi^2_3 = 13.58$, $p_4 = 0.004$, $\chi_{DM} = 6.37$, $\chi_{DF} = 3.08$).

3.3. Call type and context relationships

Although all call types were used within choruses, most differed significantly in their likelihood of being used as solo calls or within a chorus (Figure 6). Call types I ($\chi^2_1 = 10.97$, $p_2 < 0.001$), II ($\chi^2_1 = 38.58$, $p_2 < 0.001$), III ($\chi^2_1 = 21.29$, $p_1 < 0.001$) and IV ($\chi^2_1 = 32.21$, $p_2 < 0.001$) were significantly more likely to occur within a chorus and less likely as a solo than expected by chance. In contrast, call types VI ($\chi^2_1 = 10.31$, $p_2 = 0.001$), VII ($\chi^2_1 = 8.46$, $p_3 = 0.004$) and IX ($\chi^2_1 = 26.17$, $p_1 < 0.001$) were significantly more likely to occur as solos and less likely to be used during choruses than expected by chance. Call type V was no more likely to occur as a solo than within a chorus ($\chi^2_1 = 3.27$, $p_3 = 0.07$).

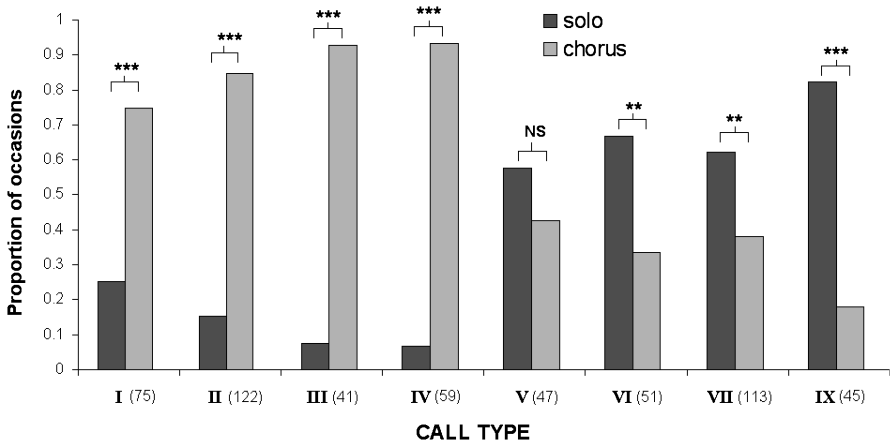


Figure 6. Use of different call types as a solo or in a chorus. Sample sizes in parentheses. Observed distributions were compared to that expected by chance given the number of occasions calls were recorded. NS, not significant; ** $p < 0.01$; *** $p < 0.001$.

When given as part of a chorus, some calls showed distinct patterns in where they occurred within a sequence (Figure 7). Call type I was given exclusively at the end of a chorus on all 56 occasions it was recorded, whereas call types II ($\chi^2_2 = 133.90$, $p_3 < 0.001$, $\chi_{\text{whole}} = 89.76$), III ($\chi^2_2 = 46.80$,

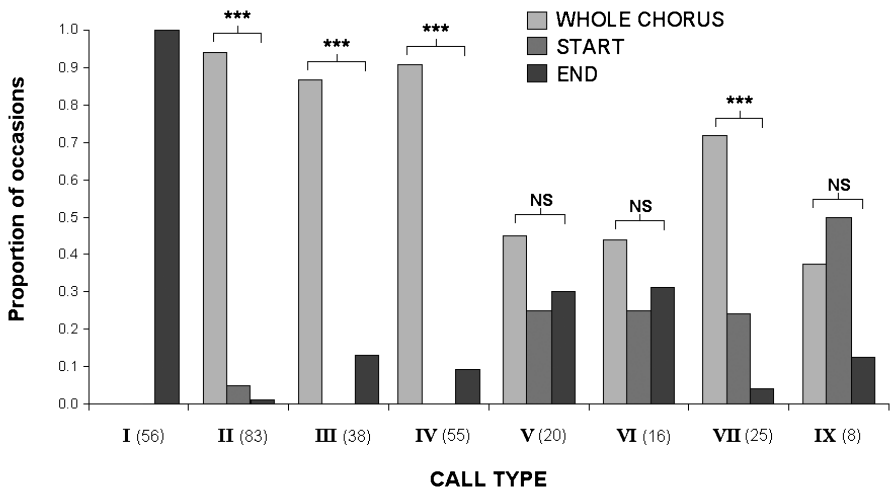


Figure 7. Use of different call types at specific periods within a choruses. Sample sizes in parentheses. Observed distributions were compared to that expected by chance given the number of occasions that calls were recorded. NS, not significant; *** $p < 0.001$.

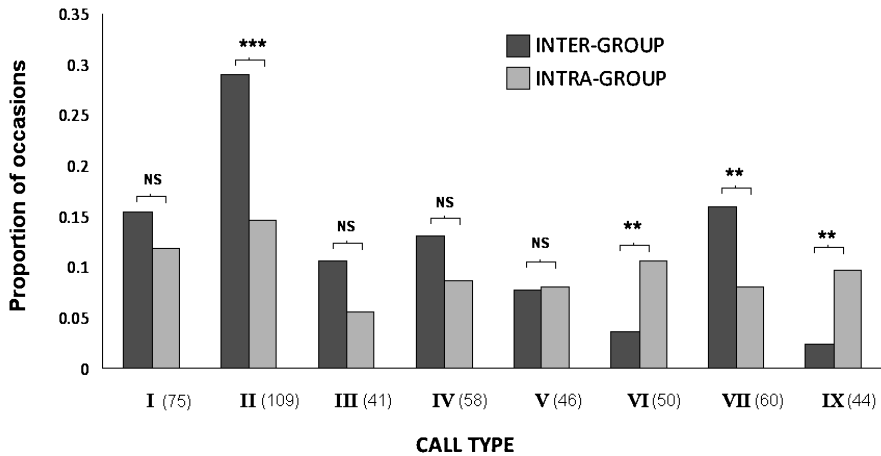


Figure 8. Use of different call types in intra-group and inter-group contexts. Sample sizes in parentheses. Observed distributions were compared to that expected by chance given the number of occasions calls were recorded. NS, not significant; ** $p < 0.01$; *** $p < 0.001$.

$p_2 < 0.001$, $\chi_{\text{whole}} = 31.05$), IV ($\chi_2^2 = 79.31$, $p_3 < 0.001$, $\chi_{\text{whole}} = 52.98$) and VII ($\chi_2^2 = 16.09$, $p_2 < 0.001$, $\chi_{\text{whole}} = 10.08$) were more likely to occur throughout the whole chorus than just at the start or the end. Call types V ($\chi_2^2 = 0.71$, $p_4 = 0.700$), VI ($\chi_2^2 = 0.39$, $p_5 = 0.823$) and IX ($\chi_2^2 = 0.78$, $p_5 = 0.677$) were equally likely to be produced at the beginning, throughout the whole chorus or just at the end.

The likelihood of calls being used in different social (intra- and inter-group) contexts differed significantly for some calls, but not for others (Figure 8). Call types II ($\chi_1^2 = 13.40$, $p_4 < 0.001$, $\chi_{\text{inter}} = 9.1$) and VII ($\chi_1^2 = 7.42$, $p_4 = 0.006$, $\chi_{\text{inter}} = 5.26$) were given significantly more during inter-group interactions and less during intra-group contexts than expected by chance. In contrast, call types VI ($\chi_1^2 = 7.05$, $p_3 = 0.008$, $\chi_{\text{intra}} = 5.00$) and IX ($\chi_1^2 = 7.56$, $p_3 = 0.006$, $\chi_{\text{intra}} = 5.36$) were given significantly more in intra-group contexts and less in inter-group contexts than expected by chance. Call types I ($\chi_1^2 = 1.15$, $p_4 = 0.283$), III ($\chi_1^2 = 4.40$, $p_4 = 0.036$), IV ($\chi_1^2 = 2.226$, $p_5 = 0.136$) and V ($\chi_1^2 = 0.01$, $p_5 = 0.908$) showed no significant difference between use in intra- and inter-group contexts.

4. Discussion

Of the nine possible call types that were considered, eight were found to be statistically distinct calls used by pied babblers in group choruses; these call

Table 1.

Summary of call types and their use depending on caller sex and dominance status, the context and position in a chorus sequence.

Call type	Call name	Sex specific	Commonest caller	Solo or chorus	Location in chorus	Intra or inter-specific context
I	High purr	>DF	67% DF	>chorus	* end	NS pattern
II	Noisy atonal	* Female	80% DF	>chorus	>whole	>inter-group
III	3-syllable modulated	* Male	53% DM	>chorus	>whole	NS pattern
IV	2-syllable modulated	* Male	65% DM	>chorus	>whole	NS pattern
V	v-chatter	>DM	53% DM	NS pattern	NS pattern	NS pattern
VI	Extended v-chatter	>DM	59% DM	>solo	NS pattern	>intra-group
VII	Double syllable ascending	>DM	47% DM	>solo	>whole	>inter-group
VIII	Tonal chatter			Not classified		
IX	Atonal chatter	no	47% DM, 40% DF	>solo	NS pattern	>intra-group

NS, not significant; DM, dominant male; DF, dominant female. >denotes when a behaviour is more significant, * denotes exclusive use or behaviour.

types also occurred as solo bouts, and varied in their usage depending on the sex and dominance status of callers and the context (Table 1). One call type (II) was given only by females, and two types (III and IV) were male specific. Half of the call types (I, II, III and IV) were more common to choruses, while others (VI, VIII and IX) were heard more commonly as solo bouts. Calling bouts could involve one call type throughout or switching between types. Type I was exclusively given at the end of a chorus, types V, VI and IX could occur at any point in a bout, whereas types II, III, IV and VII were typically given throughout a chorus. Some call types also showed clear variation with respect to the context in which they were emitted: types II and VII were more common during inter-group encounters, whereas types VI and IX were more regularly produced in intra-group situations.

4.1. Sex-specific signalling

Three of the call types used by pied babblers in choruses are sex-specific: call type II is given only by females, while call types III and IV are given only by males. Sex-specific calls can arise in two ways. Each sex can give unique call

types, produced by one sex and not the other (e.g., roaring by male red deer (*Cervus elaphus*); McComb, 1991); such calls are commonly used in sexual advertisement. Alternatively, both sexes can produce the same call type, but calls contain sex-specific features in their structure (e.g., pheasant coucal (*Centropus phasianinus*) long calls (Maurer et al., 2008), green woodhoopoe (*Phoeniculus purpureus*) vocal rallies (Radford, 2003, 2004b)); such differences are largely thought to be the result of inter-individual differences in anatomy. Pied babbler sex-specific calls are structurally distinct and, therefore, unlikely to be the result of anatomical differences; they may instead be the result of selection to serve discrete functions in signalling between the sexes.

Sex-specific call types in many duetting bird species are suggested to have evolved to mediate conflict between members of a mated pair (Levin, 1996; Seddon, 2002). They may, for example, function in mate/paternity guarding by repelling competitors or be used to advertise continued presence (Hall, 2004). Alternatively, they could be important in reducing any possibility of misdirected aggression towards their own mate during territorial interactions (Farabaugh, 1982). Sex-specific calls are also associated with breeding behaviours that are restricted to one or other sex, such as male-specific notes in song that facilitate mate choice (Catchpole & Slater, 2008), or female copulation calls in non-human primates that improve post-copulatory mate-guarding by high ranking males (Maestriperi et al., 2005). Where both males and females call together and give discrete call types, their calling may, therefore, also serve similar functions (see Seddon, 2002; Hale, 2006; Bradley & Mennill, 2009). In many ways, pied babbler sex-specific calls are similar to the duets of other monogamous species, as they are given most commonly as part of a chorus, rarely alone, and are typically given continuously throughout the chorus. The pied babbler female sex-specific call type II, a noisy atonal call, is most commonly used in inter-group interactions when interacting with other groups or non-group members. This call could function either in mate/paternity guarding by repelling competitors or to advertise continued presence of a dominant female and avoid intrusion. Male call types III and IV are given commonly in both intra and inter-group interactions, so may serve an alternative function such as signalling of status.

4.2. Dominance status

All pied babbler call types used in choruses were recorded being performed more by dominant birds than subordinates; two types were given signifi-

cantly more by dominant females (type I and II), five types significantly more by dominant males (type III, IV, V, VI and VII), and one by both (type IX). There are a number of reasons why dominant individuals may use some calls more often than other group members. For example, in many non-human primates, high-ranking males give loud calls that are thought ultimately to mediate male–male competition (see Waser, 1982). High-ranking individuals may also simply call more because they are bigger and such calls are honest signals of strength (e.g., chacma baboons (*Papio ursinus*); Kitchen et al. (2003)). Such high-ranking individuals are also likely to have the most to lose, such as their breeding monopoly, and so may invest more in calling, if such calls are involved in mate-defence (e.g., Kitchen & Beehner, 2007). Alternatively, the calls of lower ranking males may actually be suppressed if they are punished by dominants for calling (see Enquist et al., 1985).

In pied babblers, both the dominant male and female receive high reproductive fitness with extra-group paternity never recorded to date (Nelson-Flower et al., 2011). However, dominant females risk losing their breeding position through forced eviction by non-group members (Raihani et al., 2008, 2010). Dominant female pied babblers would, therefore, benefit by advertising their presence to any potential rivals, and perhaps call types I and II, as mentioned above, act as a signal in this way. The high purr (type I) is given more during choruses than as a solo and when used in a chorus this call exclusively appeared at the end, and was used in both intra and inter-group contexts. Therefore, such a call is likely also to have a within-group function, for example possibly being used as a vocal display of dominance, such as signalling her presence and strength to the group (see Reyer & Schmidl, 1988; Seddon, 2002). The noisy atonal call (type II) as discussed above may be a direct signal targeting opposite-sex rivals as it occurs most commonly in inter-group interactions.

Dominant male pied babblers in our study population have never been observed to lose their breeding position to another male, and there is no evidence of extra-group paternity (Nelson-Flower et al., 2011), so signalling to same-sex competitors (Sekulic, 1982; Grinnell & McComb, 2001; Kitchen & Beehner, 2007) is unlikely. An alternative possibility for the evolution of dominant-male call types is that they act as a signal to opposite sex individuals, possibly their dominant partner, as males run the risk of being divorced (A.R. Ridley, unpublished data), or any potential non-group mates that are

able to overthrow the current dominant partner and prove a better breeding partner. Call type III and IV are male specific and most commonly used by the dominant male, and as discussed above are used in both social contexts, so may function as a signal to both the female mate but also potential dispersers that may be attracted to this call. The other call types are not sex-specific but are commonly used by the dominant male bird.

Call type V appears to have great plasticity in its use, and is given equally in both choruses and solo bouts, during both social contexts and when in a chorus used at various times throughout the bout, so perhaps serves multiple functions. Whereas call types VI and VII were more commonly given as solo bouts, type VI was used more commonly in intra-group contexts and type VII in inter-group contexts. Calls may also function in various cooperative functions, such as resource defence. Signals during such inter-group interactions, such as call type VII, may act as a display of strength to non-group member that may reduce the likelihood of a fight (Maynard-Smith & Parker, 1976) and calling together with the dominant female in a cooperative display of territory defence will benefit both the dominant pair. In contrast, a call used primarily in a within-group context, such as call VI, may serve to reassert a dominance rank and maintain the social hierarchy (see Reyer & Schmidl, 1988; Seddon, 2002).

4.3. Conclusions

In summary, we found eight acoustically distinct call types given by pied babblers at least some of the time during choruses. The occurrence of so many distinct call types is to our knowledge rarely found in coordinated vocal displays, except those described as song. Given our findings and patterns in call use we suggest that, unlike song, each call-type has been selected to serve a discrete function, although further investigation and experimental manipulation is required to confirm this.

Acknowledgements

We are extremely grateful to Amanda Ridley and the Pied Babbler Research Project for allowing us to conduct work on the habituated study population. Nichola Raihani and Martha Nelson-Flower assisted with the habituation, and Martha also conducted the molecular sexing. We also thank the Cambridge Kalahari Meerkat Project and Tim Clutton-Brock and Marta Manser

for permission to work on their land and for providing infrastructural support. Permits were granted by the Northern Cape Authority and clearance given by the University of Bristol Ethics committee. Two anonymous referees provided valuable comments on an earlier version of the manuscript and Neil Jordan for contributions to early drafts. Funding for this work was provided by the Natural Environment Research Council in a studentship awarded to K.G.

References

- Appleby, B.M., Yamaguchi, N., Johnson, P.J. & MacDonald, D.W. (1999). Sex specific territorial responses in tawny owls *Strix aluco*. — Ibis 141: 91-99.
- Bell, M.B.V., Radford, A.N., Rose, R., Wade, H.M. & Ridley, A.R. (2009). The value of constant surveillance in a risky environment. — Proc. Roy. Soc. Lond. B: Biol. 276: 2997-3005.
- Bell, M.B.V., Radford, A.N., Smith, R.A., Thompson, A.M. & Ridley, A.R. (2010). Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. — Proc. Roy. Soc. Lond. B: Biol. 277: 3223-3228.
- Bengtsson, H. & Ryden, O. (1983). Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major* — an experimental study. — Behav. Ecol. Sociobiol. 12: 243-251.
- Bradley, D.W. & Mennill, D.J. (2009). Solos, duets and choruses: vocal behaviour of the rufous-naped wren (*Campylorhynchus rufinucha*), a cooperatively breeding neotropical songbird. — J. Ornithol. 150: 743-753.
- Brown, E.D. & Farabaugh, S.M. (1991). Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. 3. Sex specificity and individual specificity of vocal parts in communal chorus and duet songs. — Behaviour 118: 244-274.
- Catchpole, C.K. & Slater, J.B. (2008). Bird song: biological themes and variations. — Cambridge University Press, Cambridge.
- Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (1999). Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. — J. Anim. Ecol. 68: 672-683.
- Devoogd, T.J., Krebs, J.R., Healy, S.D. & Purvis, A. (1993). Relations between song repertoire size and the volume of brain nuclei related to song — comparative evolutionary analyses amongst oscine birds. — Proc. Roy. Soc. Lond. B: Biol. 254: 75-82.
- Dittus, W.P.J. (1984). Toque macaque food calls — semantic communication concerning food distribution in the environment. — Anim. Behav. 32: 470-477.
- Elgar, M.A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. — Anim. Behav. 34: 169-174.
- Enquist, M., Plane, E. & Roed, J. (1985). Aggressive communication in fulmars (*Fulmarus glacialis*) competing for food. — Anim. Behav. 33: 1007-1020.

- Farabaugh, S.M. (1982). The ecological and social significance of duetting. — In: Communication and behaviour an interdisciplinary series (Kroodsma, D.E., Miller, E.H. & Ouellet, H., eds). Academic Press, New York, NY, p. 85-124.
- Gerhardt, H.C. (1994). The evolution of vocalizations in frogs and toads. — *Annu. Rev. Ecol. Syst.* 25: 293-324.
- Golabek, K.A., Ridley, A.R. & Radford, A.N. (2012). Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. — *Anim. Behav.* 83: 613-619.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998). A DNA test to sex most birds. — *Mol. Ecol.* 7: 1071-1075.
- Grinnell, J. & McComb, K. (2001). Roaring and social communication in African lions: the limitations imposed by listeners. — *Anim. Behav.* 62: 93-98.
- Hale, A.M. (2006). The structure, context and functions of group singing in blackbreasted wood-quail (*Odontophorus leucolaemus*). — *Behaviour* 143: 511-533.
- Hall, M.L. (2004). A review of hypotheses for the functions of avian duetting. — *Behav. Ecol. Sociobiol.* 55: 415-430.
- Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (2005). Roberts birds of Southern Africa, 7th edn. — Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Hollén, L.I., Bell, M.B.V. & Radford, A.N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. — *Curr. Biol.* 18: 576-579.
- Kitchen, D.M. & Beehner, J.C. (2007). Factors affecting individual participation in group-level aggression among non-human primates. — *Behaviour* 144: 1551-1581.
- Kitchen, D.M., Seyfarth, R.M., Fischer, J. & Cheney, D.L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). — *Behav. Ecol. Sociobiol.* 53: 374-384.
- Langmore, N.E. (1998). Functions of duet and solo songs of female birds. — *Trends Ecol. Evol.* 13: 136-140.
- Leavesley, A.J. & Magrath, R.D. (2005). Communicating about danger: urgency alarm calling in a bird. — *Anim. Behav.* 70: 365-373.
- Leonard, M. & Horn, A. (1996). Provisioning rules in tree swallows. — *Behav. Ecol. Sociobiol.* 38: 341-347.
- Levin, R.N. (1996). Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. 1. Removal experiments. — *Anim. Behav.* 52: 1093-1106.
- Maestriperieri, D., Leoni, M., Raza, S.S., Hirsch, E.J. & Whitham, J.C. (2005). Female copulation calls in guinea baboons: evidence for postcopulatory female choice? — *Int. J. Primatol.* 26: 737-758.
- Manser, M.B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. — *Proc. Roy. Soc. Lond. B: Biol.* 268: 2315-2324.
- Maurer, G., Smith, C., Susser, M. & Magrath, R.D. (2008). Solo and duet calling in the pheasant coucal: sex and individual call differences in a nesting cuckoo with reversed size dimorphism. — *Aust. J. Zool.* 56: 143-149.
- Maynard-Smith, J. & Parker, G.A. (1976). Logic of asymmetric contest. — *Anim. Behav.* 24: 159-175.

- McComb, K. & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. — *Biol. Lett.* 1: 381-385.
- McComb, K.E. (1991). Female choice for high roaring rates in red deer, *Cervus elaphus*. — *Anim. Behav.* 41: 79-88.
- Nelson-Flower, M.J., Hockey, P.A.R., O’Ryan, C., Raihani, N.J., du Plessis, M.A. & Ridley, A.R. (2011). Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. — *Behav. Ecol.* 22: 559-565.
- Radford, A.N. (2003). Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. — *Anim. Behav.* 66: 1035-1044.
- Radford, A.N. (2004a). Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). — *Ethology* 110: 11-20.
- Radford, A.N. (2004b). Voice breaking in males results in sexual dimorphism of green woodhoopoe calls. — *Behaviour* 141: 555-569.
- Radford, A.N. (2005). Group-specific vocal signatures and neighbour-stranger discrimination in the cooperatively breeding green woodhoopoe. — *Anim. Behav.* 70: 1227-1234.
- Radford, A.N. & du Plessis, M.A. (2004). Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. — *Anim. Behav.* 68: 803-810.
- Radford, A.N. & Ridley, A.R. (2006). Recruitment calling: a novel form of extended parental care in an altricial species. — *Curr. Biol.* 16: 1700-1704.
- Radford, A.N. & Ridley, A.R. (2007). Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance. — *Biol. Lett.* 3: 249-252.
- Radford, A.N. & Ridley, A.R. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. — *Anim. Behav.* 75: 519-527.
- Radford, A.N., Hollén, L.I. & Bell, M.B.V. (2009). The higher the better: sentinel height influences foraging success in a social bird. — *Proc. Roy. Soc. Lond. B: Biol.* 276: 2437-2442.
- Raihani, N.J. (2008). Cooperation and conflict in pied babblers. — PhD thesis, University of Cambridge, Cambridge.
- Raihani, N.J., Ridley, A.R., Browning, L.E., Nelson-Flower, M.J. & Knowles, S. (2008). Juvenile female aggression in cooperatively breeding pied babblers: causes and contexts. — *Ethology* 114: 452-458.
- Raihani, N.J., Nelson-Flower, M.J., Golabek, K.A. & Ridley, A.R. (2010). Routes to breeding in cooperatively breeding pied babblers, *Turdoides bicolor*. — *J. Avian Biol.* 41: 681-686.
- Reyer, H.U. & Schmidl, D. (1988). Helpers have little to laugh about — group-structure and vocalization in the laughing kookaburra *Dacelo novaeguineae*. — *Emu* 88: 150-160.
- Ridley, A.R. & Raihani, N.J. (2007). Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. — *Behav. Ecol.* 18: 324-330.
- Ridley, A.R. & Raihani, N.J. (2008). Task partitioning increases reproductive output in a cooperative bird. — *Behav. Ecol.* 19: 1136-1142.
- Seddon, N. (2002). The structure, context and possible functions of solos, duets and choruses in the subdesert mesite (*Monias benschi*). — *Behaviour* 139: 645-676.
- Sekulic, R. (1982). The function of howling in red howler monkeys (*Alouatta seniculus*). — *Behaviour* 81: 38-54.

- Seyfarth, R.M., Cheney, D.L. & Marler, P. (1980). Vervet monkey alarm calls — semantic communication in a free-ranging primate. — *Anim. Behav.* 28: 1070-1094.
- Stewart, K.J. & Harcourt, A.H. (1994). Gorilla vocalizations during rest periods — signals of impending departure. — *Behaviour* 130: 29-40.
- Stokes, A.W. & Williams, H.W. (1968). Antiphonal calling in quail. — *Auk* 85: 83-89.
- Voigt, C., Leitner, S. & Gahr, M. (2006). Repertoire and structure of duet and solo songs in cooperatively breeding white-browed sparrow weavers. — *Behaviour* 143: 159-182.
- Waser, P.M. (1982). The evolution of male loud calls among mangabeys and baboons. — In: *Primate communication* (Snowdon, C.T., Brown, C.H. & Petersen, M.R., eds). Cambridge University Press, Cambridge, p. 117-143.
- Whitham, J.C., Gerald, M.S. & Maestripieri, D. (2007). Intended receivers and functional significance of grunt and girney vocalizations in free-ranging female rhesus macaques. — *Ethology* 113: 862-874.