

Communal singing in the cooperatively breeding subdesert mesite *Monias benschi*: evidence of numerical assessment?

Nathalie Seddon and Joe A. Tobias

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It has long been suggested that competing groups of social animals assess one another on the basis of communal vocalisations, but so far this has only been demonstrated in mammals. We investigated this idea in the subdesert mesite, a group-living bird that produces communal songs during aggressive territorial interactions with other groups. Where groups compete as units, differences in group size might outweigh inter-individual differences in determining the outcome of contests. Given this species' variable social system, we predicted that the composition of groups would also influence their resource holding potential. Playback experiments showed that the number of simulated intruders significantly influenced the strength of response by defending groups hearing the stimulus: groups were less likely to approach but gave more protracted and more communal vocal responses as the number of vocalising intruders increased. We found that the likelihood of a group approaching playback increased as the ratio between the number of males in the defending group and the number of males in the intruding group increased. Furthermore, the ratio of adult males to females in the defending group significantly affected the probability of approach, with the probability increasing as groups became more male-biased. This finding supports the idea that the social structure of groups may be important in determining the outcome of contests between groups. Overall this study provides some indication in birds of relative numerical assessment based on vocal cues.

N. Seddon (correspondence), Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, U.K. E-mail: ns10003@hermes.cam.ac.uk. J. A. Tobias, 131 Catharine Street, Cambridge, CB1 3AP, UK.

It is becoming apparent that vocal communication in animals is rarely pair-wise and that there are often multiple signallers and receivers forming a communication network (McGregor 1993). Although this has been discussed and tested within the context of eavesdropping in birds (e.g. McGregor and Dabelsteen 1996, Naguib et al. 1999, Tobias and Seddon 2002a), multiple signallers and receivers are most conspicuous in social animals wherein groups of individuals may compete and vocalise as a unit to defend a territory.

The outcome of dyadic interactions is often determined by inter-individual differences in body size and stamina, some aspect of the acoustic display being related to these differences (e.g. roaring in red deer *Cervus elaphus*, Clutton-Brock and Albon 1979). However, where groups compete as units, differences in the

number of individuals per group might outweigh inter-individual differences in determining the outcome of a contest (McComb 1992). In group-territorial animals, acoustic signals are likely to contain information about the number of individuals in the group and groups may assess their rivals on the basis of this information.

Indeed, group-vocalisation occurs in numerous social mammals, especially primates (e.g. Bornean gibbons *Hylobates muelleri*, Mitani 1984) and carnivores (e.g. wolves *Canis lupus*, Harrington and Mech 1979) and it has long been suggested that competing groups assess one another on the basis of these vocalisations (Sekulic 1982, Harrington 1989). However, so far this has only been demonstrated in lions *Panthera leo* (McComb 1992, McComb et al. 1994). Many group-living birds also produce communal vocalisations, ranging from

uncoordinated 'shouting matches' (e.g. yellow-rumped caciques *Cacicus cela*, Robinson 1985) to coordinated pair-duets (e.g. stripe-backed wrens *Campylorhynchus nuchalis*, Wiley and Wiley 1977) and choruses involving three or more birds singing simultaneously (e.g. Australian magpies *Gymnorhina tibicen*, Brown and Farabaugh 1991). Whilst duetting has received some attention (Farabaugh 1982, Levin 1996a, b, Langmore 1998, Hall 2000), detailed studies of chorusing have so far been limited to the laughing kookaburra *Dacelo novaeguineae* (Reyer and Schmidl 1988), the Australian magpie (Brown and Farabaugh 1991) and the white-browed sparrow-weaver *Plocepasser mahali* (Wingfield and Lewis 1993). Although these studies all demonstrated that the choruses were involved in territorial aggression, none investigated the possibility that communal vocal displays functioned in assessment of the size and hence potential threat posed by an intruding group.

The subdesert mesite *Monias benschi* is a terrestrial, group-living bird that cooperates over reproduction and territory defence (Seddon et al. 2003). It produces sex-specific vocal syllables that it combines into a variety of communal songs, ranging from coordinated pair-duets to choruses of five birds singing simultaneously (Seddon 2002). Communal songs therefore contain information about the number and sex of the birds producing them, and it is possible that mesites are capable of perceiving and responding to this information. Certainly, neighbouring groups often vocally respond to each other's communal songs over large distances. Moreover, direct encounters between neighbouring groups almost invariably involve prolonged bouts of chorusing in conjunction with group-aggression. The question that arises is: can groups of mesites assess each other's size and hence 'resource holding potential' (RHP, Parker 1974) on the basis of these communal songs?

If subdesert mesites are capable of such assessment, the tendency of groups to approach intruding rivals should vary in relation to the ratio between the size of the opposing group and that of the defending group, as demonstrated in lions (McComb et al. 1994). Furthermore, given the probable existence in this species of strong within-group conflicts over reproduction (Seddon et al. 2003), group composition should also influence the likelihood that a group approaches intruders. For example, in groups where males outnumber females, strong male-male competition may increase the probability of approach, whether to repel male rivals and/or to assess breeding opportunities in the intruding group.

We investigated these ideas using a series of experiments in which territorial intrusions involving groups of varying sizes were simulated using call-playback. If communal songs function in assessment of RHP, we predict that: (1) groups' responses to playback will vary

with the number of intruders, and (2) groups will adjust their agonistic response to playback in relation to the size and composition of their own group.

Methods

Study species and sites

This study was conducted as part of a three-year investigation into the ecology of the subdesert mesite, a group-living insectivorous gruiform endemic to the semi-arid Mikea Forest south-west Madagascar (Seddon 2001). Subdesert mesites are anatomically adapted to flight (Lowe 1924), but are largely terrestrial, only flying to elevated roost sites or as an anti-predator response. They are medium-sized birds (30–32 cm long) with a distinctly horizontal carriage, and while the breast and throat of females is rufous, that of males is white with black crescents (Evans et al. 1996). They live in stable groups typically containing 1–2 females and 2–3 males, all of whom cooperate over defence of permanent, multipurpose territories and the raising of 1–2 annual broods of 1–2 precocial young (Seddon et al. 2003). Some groups apparently comprise monogamous pairs with related and unrelated helpers, while others may be polygamous (Seddon 2001). Aggressive interactions between resident groups and intruders include bouts of communal singing typically involving up to five group members, of which 1–3 usually perch at 0.1–0.5 m above the ground. Songs are usually interspersed with short scurrying chases between members of the opposing groups.

A group was defined as a cohesive collection of individuals that cooperated over territory defence and reproduction. There was some change in group size and composition between seasons; groups were defined as unique if different individuals accounted for more than half of the group.

Fieldwork was carried out at two sites: PK32 (23°04'57S, 43°37'15E, 200 ha), Mangily (23°07'09S, 43°37'30E, 120 ha) and along nine transects in the Mikea Forest north of Manombo (see Tobias and Seddon 2002b). Detailed descriptions of the vegetation and climate of these sites are given in Seddon et al. (2000).

Experimental design

Effect of numbers of intruders: do groups distinguish between playback of songs involving different numbers of birds?

Experiment 1: male solo versus pair-duet versus small chorus. We gave each of ten colour-marked study groups at PK32 three different playback treatments: A:

male solo, B: pair-duet (a series of alternating male and female song syllables, initiated and terminated by a female), and C: small chorus (a series of non-overlapping, alternating male and female song syllables given by two males and one female, initiated and terminated by a female). Each group received these treatments in the orders given in Table 1 at an interval of 7–10 days in September–October 1998. For definitions and sonagrams of subdesert mesite song types see Seddon (2002). The term ‘song’ includes solos, duets and choruses.

Experiment 2: The power of experiment 1 to detect a treatment effect may have been reduced by changes between treatments in the breeding condition of groups (i.e. whether or not they were nest-building, incubating etc.) and/or the value of the patch of the habitat where playback was conducted. The possible effects of these factors were spread across subjects by giving groups two treatments separated by a 3 min interval: a male solo and a large chorus (i.e. a series of alternating male and female song syllables given by three males and one female, initiated and terminated by a female). This experiment was conducted on nine colour-marked groups and 11 unmarked groups along the PK32 – Mikoboka Plateau transect. The possible effects of order of treatment on the results were distributed across groups by giving nine groups the male solo first and the remainder the large chorus first.

Effect of number of defenders: does group size and composition influence response to playback?

In Experiment 3 we played recordings of 1–4 intruders to a total of 104 groups of known size and composition. Of these groups, 13 were located along the Tsifota–Ankililoaka transect on 4 January 1999, 69 were located along eight transects north of Manombo between 28 November and 13 December 1999 and 22 were located along the PK32–Mikoboka Plateau transect on 25 November 1999 (Tobias and Seddon 2002b). We used the responses of these groups to playback to investigate whether group size, the number of males, the number of females, the number of males per female per group (‘sex ratio’) or the number of defenders relative to the number of intruders (‘odds ratio’) influenced the likelihood that a group approached playback.

We used multivariate statistics in order to partition out the relative effects of these variables on likelihood of approach.

Experimental procedure

Each treatment consisted of broadcasting a 30 s recording of continuous singing through a Sony SRS-58 loudspeaker; 30 s being close to the mean duration of natural, unstimulated solos and duets. In experiments 1 and 2, the loudspeaker was placed at 0.1–0.2 m above the ground and positioned facing the group, c. 15 m from concealed observers. Although an array of speakers arranged in natural positions and a multi-track playback system would have been ideal, setting this up in dense undergrowth is likely to have caused subject groups to move > 25 m from the loudspeaker and out of sight of observers. However, given that mesites often sang when < 1 m apart, the use of one speaker was not unrealistic. Behavioural responses were recorded onto a Sanyo Dictaphone by one observer, while a second observer recorded vocal responses using a WMD6C Sony Walkman and a Sennheiser ME67 directional microphone. In experiment 3, groups were located by their vocal responses to a 30 s male solo broadcast through the loudspeaker held at c. 1 m and slowly and evenly rotated through 360 degrees (starting and ending at north). When a group responded, it was located as quickly as possible. Once some or all of the group was in view, a period of 3 min was allowed before a recording of 1–4 birds was broadcast through a loudspeaker placed on the ground at the survey point facing the group. The observer with the group noted if there was an approach towards the speaker within 5 min of the start of playback and then ascertained the size and composition of the group.

We constructed playback loops by editing recordings of songs made < 10 m from vocalising birds and which produced sharp sonagrams on a Kay Elemetrics Co. Digital Sonagraph DSP Model 5500 (settings: 300 Hz filter, 4 ms time resolution, 0–8 kHz bandwidth). Noise below 2 and above 9 kHz was filtered out using SoundEdit 16 version 2f. The sound pressure level (SPL) of natural songs varied from c. 65 dB for solos to c. 70 dB for duets and choruses at 15 m (Seddon 2001).

Table 1. The order in which treatments A–C were presented to subject groups in Experiment 1.

Week starting	Group									
	1	2	3	4	5	6	7	8	9	10
07 Sep 98	–	A	–	A	–	–	–	C	–	–
14 Sep 98	–	B	C	C	B	–	C	B	–	B
21 Sep 98	–	C	A	B	A	–	B	A	B	C
28 Sep 98	A	–	B	–	C	C	A	–	C	A
05 Oct 98	B	–	–	–	–	A	–	–	A	–
19 Oct 98	C	–	–	–	–	B	–	–	–	–

Using amplification in SoundEdit and the volume control on the cassette recorder, each recording was broadcast at a c. 65 dB at 15 m in front of the loudspeaker, verified using a Tandy sound level meter at the beginning of each playback. To ensure that across treatments groups were subject to approximately the same amount of sound, we only constructed playback loops from cuts in which syllables were given at a rate of c. 80 per min.

To avoid pseudoreplication, groups received different replicates. For all study groups and half of the transect groups, these replicates were constructed from recordings made from different groups. The rest of the transect groups were given replicates that had been constructed from different recordings of the same groups made at different times of the day or month. In other words, all the replicates used in these experiments were different, but not all involved different groups. To ensure that the groups were unfamiliar with the songs, replicates used at one site were made from recordings made at another site. This avoided the potentially confounding effects of individuals recognising opponents and associating with them some preconceived value of RHP (see McComb 1992).

Playback was carried out in calm conditions in mid-September to mid-December between 06.00–10.00, thereby avoiding the first hour after dawn when birds are foraging most vigorously. Natural rates of singing remained relatively constant throughout the day and the season (Seddon 2002) so it is unlikely that responsiveness to playback will have varied significantly between treatments.

Playbacks on study groups were carried out from > 50 m within territory boundaries. Groups were located by following tracks, by listening for vocalisations, and by chance encounters along forest trails. If the group detected the observers, a period of 15 mins was left before playback to allow the group to resume normal behaviour. Groups were required to be silent (except for contact and alarm calls) for at least 5 mins before the start of playback. In experiment 3, territory location was not controlled for, but as territories were large the likelihood of any playback point being well within a territory was high.

In experiments 1 and 2 groups were 20–25 m away at the start of playback, but in experiment 3 playbacks were conducted at varying initial distances (10–300 m). The methods used for estimating initial distances of these groups are described elsewhere (Tobias and Seddon 2002b). Initial distance had no significant effect on the likelihood of approaching playback of any type (logistic likelihood ratio test, $\chi^2_1 = 2.60$, $P = 0.11$, $n = 104$). Furthermore, there was no significant difference between treatments in the variance of the groups' initial distances (ANOVA, $F_{3,100} = 1.01$, $P = 0.39$). Therefore, when comparing approach response between treatments, the possible effects of distance on the results were distributed across groups.

Quantifying responses to playback

For the purpose of the present study, only the responses of the group as a unit were documented. We gathered as much of the following information as possible: (i) whether or not a song was given by the group within 5 mins of the start of playback; (ii) whether any member of the group approached the speaker within 5 mins of the start of playback, where an approach constituted any movement of at least 0.5 m towards the speaker; (iii) minimum distance (in m) of any group member to the speaker during the experiment (accurate estimation was made possible by the conspicuous tracks left in the sandy substrate); (iv) time from start of playback to start of first song (latency in seconds); (v) duration in seconds of the initial phrase of the first song given in response to playback; (vi) total duration in seconds of the first song given in response to playback; and (vii) maximum number of birds singing (and hence the percentage of the group singing).

In experiment 3 it was vital that the size and composition of transect groups was ascertained. As a result, groups were occasionally accidentally disturbed during their vocal responses to the second playback as we attempted to obtain clear views of them in the dense undergrowth. For this reason, in this experiment we only recorded if playback elicited an approach.

Statistics and sampling

We used MINITAB version 10.5 to generate correlation matrices for standardised response variables (iii)–(vii) for experiments 1 and 2. We found that the responses were only weakly correlated: in no experiment did the proportion of correlation coefficients > 0.3 exceed 50%, and the correlation matrices did not differ significantly from an identity matrix in which all variables were completely unrelated (Bartlett's test of sphericity, P -values: 0.24–0.93). The data were thus unsuitable for principal components analysis and we present and analyse the responses to the different playback treatments separately. The analyses for experiments 1 and 2 are based on matched comparisons within study groups. Cochran Q -tests were used to test the effect of treatments on the nominal response measure 'approach'; Friedman tests were used to investigate the effect of three treatments on continuous response measures, and multiple comparison tests were used to ascertain if there were significant differences between pairs of treatments (Siegel and Castellan 1988). In experiment 2, Wilcoxon-signed rank tests were used; as $n < 16$ the T statistic is given with its associated P value (calculated using Table V on p. 136–138 in Rohlf and Sokal 1995). In experiment 3 we used STATVIEW version 5 to generate multiple logistic regression models to investigate whether group size and composition

influenced the probability that a group approached playback.

In experiment 1, data from study groups at PK32 were pooled with those at Mangily. Sample sizes were too small to test for differences in vocal responses to playback between the sites, but pooling of these data was justified given that the habitat is almost identical and contiguous, the two sites being only 6 km apart. In experiment 3 data are pooled across 138 different survey points located along a total of nine transects. Although playback for this experiment was therefore conducted in a variety of slightly different dry forest habitat types (see Tobias and Seddon 2002b) we hope that the variety encompassed by the relatively large sample controls for any effects of habitat on response to playback. In experiment 3, data from January 1999 are pooled with those from November–December 1999. This is unlikely to have influenced the results given the lack of differences in natural song structure between field seasons and the apparent lack of seasonality in vocal behaviour (Seddon 2002). In all analyses, n is taken as the number of groups. All statistical tests are two-tailed and all means are given \pm SE. P-values are corrected for ties and, following the methodology in Rice (1989), sequential Bonferroni corrections are applied where appropriate.

Results

Behavioural responses to simulated intrusion

Upon hearing playback, group members became alert and congregated from scattered foraging positions to form a cohesive unit. This was often accompanied by much 'Nak' and 'Purr'-calling (Seddon 2002), pronounced tail-flicking and a distinctive ruffling of breast feathers. Either during or shortly after playback, a single bird of either sex sang for up to 30 s to produce the 'introductory phrase' of the vocal response. Once the group had assembled, up to four additional group members sang.

Playback experiments

Effect of numbers of intruders: do groups distinguish between playback of vocalisations involving different numbers of birds?

Experiment 1: male solo versus pair duet versus small chorus. All ten subject-groups vocally responded to playback of male solos, duets and small choruses. However, whilst all ten approached playback of male solos, only four approached playback of duets and six approached playback of small choruses. This variation was significant (Cochran Q-test: $Q = 9.3$, $P < 0.01$). The

distance to which groups approached also varied significantly across treatments (see Fig. 1a), with groups approaching more closely to male solos than to duets or small choruses. Whilst groups produced their vocal responses more promptly following playback of solo song (Fig. 1b) it took significantly longer for other group members to join a solo initiator to produce a communal song following a male solo (6.0 ± 1.3 s) than following a duet (2.2 ± 0.4 s) or small chorus (2.1 ± 0.5 ; Friedman test: $\chi^2_2 = 12.4$, $n = 10$, $P = 0.002$; multiple

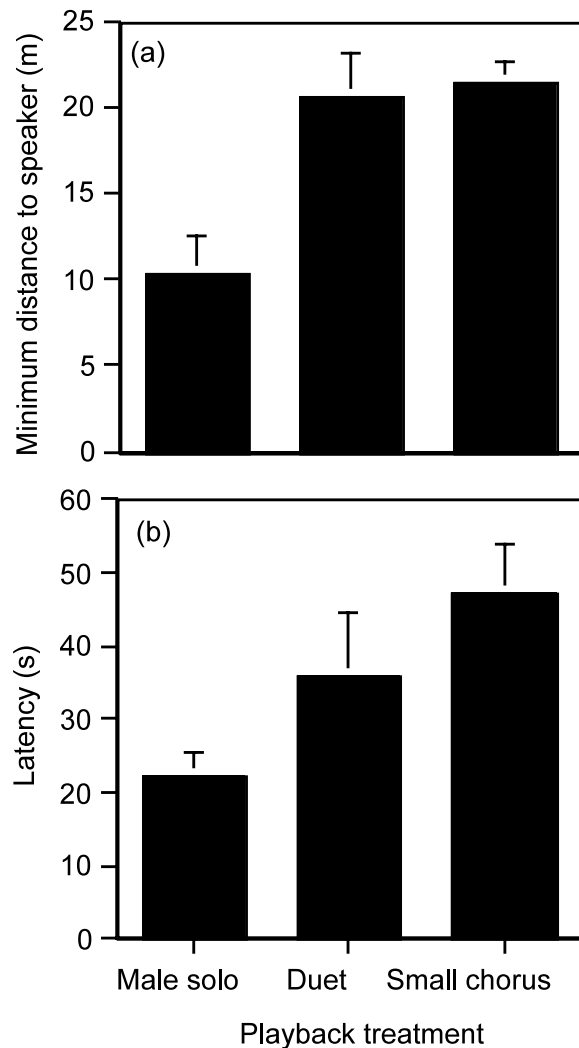


Fig. 1. Responses of ten groups to playback of male solos, duets and small choruses. (a) The distance to which they approached the speaker varied significantly across treatments (Friedman test, $\chi^2_2 = 11.0$, $P = 0.004$), with groups approaching significantly more closely to male solos than to small choruses (multiple comparisons tests, $P < 0.05$). (b) The latency of groups' vocal responses varied significantly across treatments ($\chi^2_2 = 9.0$, $P = 0.011$), and groups took significantly more time to sing in response to playback of both duets and small choruses than to male solos (multiple comparisons tests: $P < 0.05$ in both comparisons). All results are significant after Bonferroni corrections. Bars show mean \pm SE; $n = 10$ groups.

comparison tests: $P < 0.05$). In 9/10 cases, songs given in response to male solos were initiated by males, whilst males vocally initiated only four out of ten responses to both duets and small choruses. There was no significant variation across treatments in the mean duration of groups' responses to playback (64.1 ± 12.1 s versus 48.3 ± 7.3 s versus 44.2 ± 10.6 s; $\chi^2_2 = 1.90$, $n = 10$, $P = 0.39$), nor in the number of birds singing (2.30 ± 0.2 s vs. 2.60 ± 0.3 s vs. 2.80 ± 0.3 s, $\chi^2_2 = 3.92$, $n = 10$, $P = 0.14$).

Experiment 2: male solo versus large chorus. There was no significant difference between treatments in the latency to first song given in response to playback (Wilcoxon signed-rank test, $T = 5.0$, $n = 7$, $P > 0.1$).

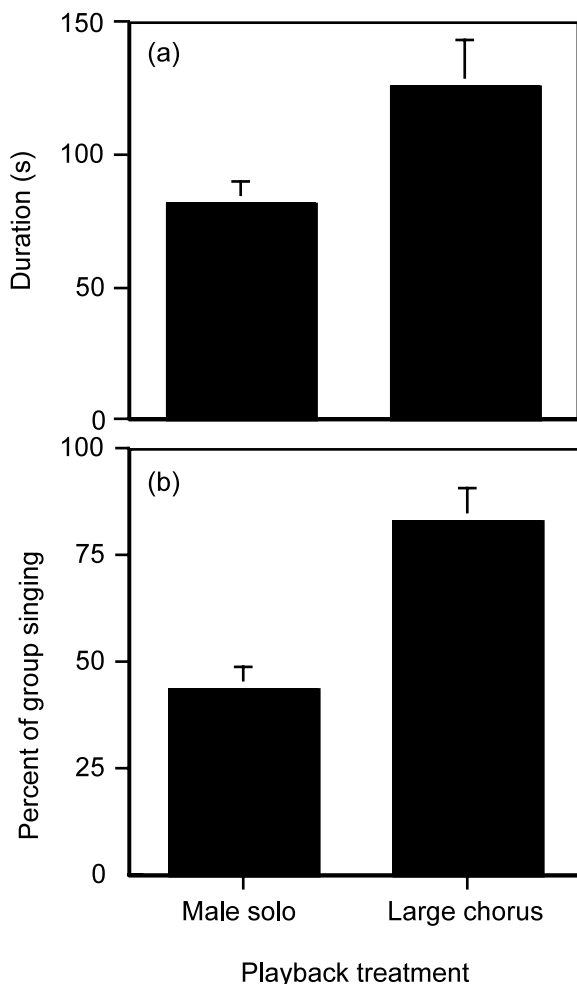


Fig. 2. Responses of groups to playback of male solo songs followed by large choruses: (a) the duration of the first song given in response to the large chorus was greater than that given in response to male solo song ($T = 0$, $P = 0.016$); and (b) a greater percentage of the group sang in response to the large chorus ($T = 0$, $P = 0.016$). Neither of these results were significant after Bonferroni corrections where $\alpha = 0.013$. As only seven groups sang in response to both treatments, $n = 7$ in all comparisons. Bars show mean \pm SE.

However, songs evoked by playback of large choruses were of a greater duration and involved a greater proportion of the group than those elicited by male solos (Fig. 2). Further, groups were more likely to approach playback of male solos (Table 2), whilst tending to retreat on hearing a large chorus three minutes after a male solo (Fig. 3).

There were no significant effects of treatment order on the likelihood of singing or approaching (Table 2) or on the minimum distance to which groups approached (Fig. 3; Mann–Whitney U-tests, male solo: $U = 40.5$, $n_1 = 9$, $n_2 = 11$, $P = 0.48$; large chorus: $U = 44.5$, $P = 0.70$). As only five groups vocally responded to large

Table 2. Comparisons of response to playback for different orders of treatments within study groups. Values for P derive from chi-square tests and for P* from paired sign tests.

Order of treatment	Vocal response/no vocal response		P*
	Male solo	Large chorus	
Male solo/large chorus	9/0	7/2	0.50
Large chorus/male solo	10/1	5/6	0.06
χ^2_1	0.86	2.2	
P	0.35	0.14	
	Approach/no approach		
	Male solo	Large chorus	
Male solo/large chorus	8/1	4/5	0.06
Large chorus/male solo	8/3	2/9	0.03
χ^2_1	0.81	1.6	
P	0.37	0.20	

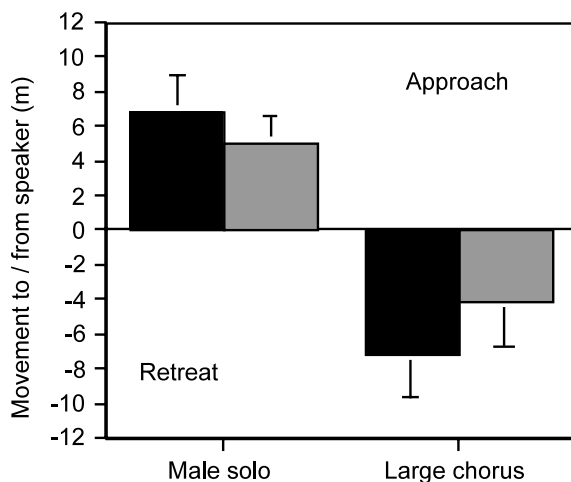


Fig. 3. Responses of groups to playback of male solo songs followed by large choruses: groups tended to approach the speaker following playback of male solos and tended to retreat in response to large choruses (Wilcoxon signed-rank tests, male solo first: $T = 3.0$, $n = 9$, $P = 0.02$; large chorus first: $T = 13$, $n = 11$, $P = 0.08$). Bars show mean values \pm SE.

Table 3. Approach data arranged with respect to relative sizes of defending and intruding groups.

Number of intruders	Number of defenders								
	Approach/no approach								
	1	2	3	4	5	6	7	8	9
1	2/0	7/1	6/2	8/2	11/1	6/2	3/1	2/0	1/0
2	1/0	2/0	4/0	2/0	1/1	1/0	1/0	1/0	1/0
3	–	2/1	1/1	2/0	2/1	2/0	2/0	1/0	–
4	0/2	1/1	0/2	2/1	3/0	1/0	0/1	–	–

Table 4. Data showing whether or not playback of 1–4 intruders elicited an approach from groups with varying numbers of males per female.

Number of intruders	Number of males per female in defending group													
	Approach/ no approach													
	0:1	1:0	1:1	1:2	1:3	2:1	2:3	3:1	3:2	3:4	4:1	5:2	5:3	6:1
1	2/0	–	13/1	4/1	0/1	9/3	1/1	4/0	7/1	1/0	4/0	2/0	1/0	–
2	–	1/0	3/0	2/0	–	2/0	–	1/0	0/2	–	1/0	2/0	1/0	–
3	–	–	4/1	–	–	1/0	0/1	1/0	2/1	1/0	2/0	1/0	–	–
4	0/1	0/1	1/2	0/1	–	0/1	–	2/0	1/0	–	2/0	0/1	–	1/0

chorus playbacks when they were played first, it was not possible to compare statistically the latency, duration and percent of group singing between ‘order-treatments’.

Effect of number of defenders: does group size and composition influence response to playback?

In support of the forgoing results, we found that across the 104 groups located along transects, the number of intruders significantly influenced likelihood of approach (Tables 3–5). When number of intruders was controlled for using a multiple logistic regression, counter to the original prediction, total group size had no effect on the likelihood of approach. The number of defenders was divided by the number of intruders to produce a single variable ‘overall odds ratio’: a rough measure of relative RHP. Counter to our prediction, this variable had no effect on the likelihood of a group approaching the loudspeaker (Table 5). However, when only males were considered, we found that relative number of males exerted a significant effect: a defending group was more likely to approach the loudspeaker if it contained more males than the intruding group. Overall, the variable best predicting the probability of approach was the number of males relative to number of females in the defending group.

Discussion

What is the evidence for numerical assessment?

Experiment 1 indicated that groups of subdesert mesites distinguished between one and two or more simulated intruders. Groups were more likely to sing and ap-

proach playback of male solos than duets or small choruses. Furthermore, groups approached more closely and initiated songs more promptly following playback of a single versus pairs or small groups of intruders. However, we also found that group members took significantly longer to join a solo initiator in response to a single male singing in their territory. In Experiment 2, when large choruses and male solos were played to groups within three minutes of each other, we found the former tended to incite a retreat but that songs evoked by playback involved more group members and were sustained for a significantly greater duration. Overall, it therefore appears that groups’ response to two or more intruders was more collective and cautious than that to single intruders.

Subdesert mesites appeared to distinguish between one and two or more intruders using vocal cues. However, as we cannot know what those cues are it is not possible to ascertain if actual ‘counting’ occurs. For

Table 5. Summary of results of a logistic regression analysis to determine parameters affecting the binary variable approach = 1, no approach = 0. All variables relating to the defending group (except ‘odds ratios’) control for number of intruders. Values for chi-square and P are derived from logistic likelihood ratio tests; df = 1 in all cases. R² = coefficients of determination, rc = regression coefficients; n = 104.

Variable	R ²	rc	χ ₁ ²	P
Number of intruders	0.05	–0.48	5.45	0.02
Number of defenders	0.06	0.12	0.87	0.35
Number of males	0.09	0.36	3.90	0.05
Number of females	0.06	–0.37	1.61	0.20
Overall odds ratio	0.02	0.18	2.23	0.15
Male odds ratio	0.06	0.48	6.01	0.01
Number of males per female	0.11	0.76	6.85	0.01

example, the cue may be variation in individual syllable output, which invariably declines as the number of birds singing increases; mesites might respond to a change in signal intensity. To test this further experiments are required including the use of different playback treatments in which the amount of sound produced per individual is kept constant (a somewhat unnatural simulation).

Do subdesert mesite groups adjust their agonistic responses relative to the number of individuals in their own group?

In their study of roaring and numerical assessment in lions, McComb et al. (1994) found that the ratio of number of defenders to number of intruders predicted 60.4% of the deviance in probability of approach (McComb et al. 1994). In contrast, in subdesert mesites, we found that the overall 'odds ratio' exerted no significant effect. Instead the number of males in the defending group relative to the number of males in the intruding group affected the probability of approach. Furthermore, the number of males per female in a group had a strong effect on the likelihood of a group approaching the speaker. Higher probability of approach by larger groups of males and by male-dominated groups may reflect a more aggressive role by males in territorial interactions. This possibility is supported by the finding that in this species territory size is positively correlated with number of males but not overall group size (Seddon et al. 2003). It is possible therefore that RHP is more adequately reflected in the number of males in this species.

The variability in reproductive success within groups of cooperatively breeding subdesert mesites may mean that intra-group conflict within and between the sexes over reproduction might interfere with and override inter-group conflict. For example, direct, visual assessment between opposing groups may be important, especially for non-breeding adults that may use these interactions as a means of assessing the potential for breeding in other groups. This may also be true for another communally breeding, terrestrial gruiform bird, the pale-winged trumpeter *Psophia leucoptera*, in which subordinate males frequently defect to neighbouring groups after territorial conflicts apparently in pursuit of better breeding opportunities (Sherman 1995). Observations of mesites over three years showed that both adult male and female mesites dispersed to adjacent groups, and that during direct territorial disputes with intruders, songs were accompanied by visual signalling. It is therefore possible that direct contact between groups is important for information exchange. The observation that group 'sex ratio' influenced the probability of approaching the loudspeaker accords with this idea: the more male-biased the group the greater the potential

within-group conflict over reproduction. For example, a group with a surplus of males might always approach intruders: with the non-breeding males approaching to assess alternative breeding opportunities, and the dominant pair approaching to expel the group to which valuable group members may defect.

A further explanation as to why 'odds ratio' was found to have no significant effect may be that response to intruders and hence the outcomes of contests are simply not decided on the basis of RHP. Instead, asymmetries in payoff, where one contestant has more to gain from winning, may also be important. Payoff asymmetries have been postulated as the principal determinant of the outcome of territorial disputes between Tasmanian native hens *Gallinula mortierii* in which the initiator of contests almost invariably wins (Putland and Goldizen 1998). In subdesert mesites, it is possible that the outcome is determined by asymmetries in territorial ownership (as in speckled wood butterflies *Pararge aegeria*, Davies 1978, and robins *Erithacus rubecula*, Tobias 1997). One observation of a pair expelling a group of five from its territory indicated that ownership might supersede group size in this species. If so, territory owners should always approach and respond aggressively towards intruders irrespective of relative group size because they are most likely to win.

Finally, the methods adopted in this study may have been inadequate to show an effect of relative group size. The considerable logistic challenges posed by the dense habitat and nervousness of the study species limited the degree to which groups' responses to playback could be quantified. Other variables such as the sex and status of the individual that approached the closest, the relative vocal contributions of different individuals and the speed with which birds approached may all have been important and may have shown significant differences in relation to group size. By measuring only one aspect of the response, it is possible that more subtle variations in responses relative to group size may simply not have been detected. Further work, ideally involving video recording and/or a more easily observable study species, is required in order to gather more detailed data. Only in this way can we determine the relative importance of within-group and between-group conflicts determining the outcome of contests.

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