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Duetting in the subdesert mesite *Monias benschi*: evidence for acoustic mate defence?

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Abstract Despite numerous hypotheses proposed for the function of duets, there is currently no consensus as to why males and females should coordinate their songs in such a precise way. There is evidence indicating that duets sometimes serve in territory defence, but additional functions are rarely considered. The mate-defence hypothesis proposes that birds sing in response to their partner's song and the resulting duet repels rivals and may prevent desertion of a partner. We investigated this idea in the subdesert mesite *Monias benschi* using playback experiments in which we broadcast recordings of solos and duets to single birds and groups. Two predictions of the hypothesis were met: (1) the solo songs of both sexes incited aggressive responses from paired birds of the same sex; and (2) compared to solo songs, pair duets elicited weaker responses from groups and duetting pairs. However, groups responded to male duets with a vigour equal to that with which they responded to male solos. This indicated that the weaker responses of groups to pair duets compared to male solos was a function of the sex rather than number of vocalising birds. Groups responded more strongly to male solos than to either female solos or pair duets, and females' responses were generally weaker than those of males. This may reflect stronger competition among males for mates, due to a male-biased sex ratio in the population. We conclude that song serves similar functions in each sex and that duets may arise through mutual mate defence.

Keywords Duets · Female song · Mate defence · Playback · Subdesert mesite

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Introduction

In approximately 222 species of mainly tropical bird species (Kunkel 1974; Harcus 1977; Farabaugh 1982) paired birds either overlap or alternate their vocalisations to produce duets, with varying degrees of temporal precision, sex- and pair-specificity (for examples, see Thorpe 1972 and Wickler and Seibt 1982). Traditionally, duets were viewed as cooperative ventures between the male and female of a pair involving the establishment and maintenance of year-round territories (Farabaugh 1982). A recently favoured additional hypothesis proposes that duets are a form of acoustic mate-guarding whereby pair members answer their partner's songs to repel potential rivals that might otherwise be attracted (Sonnenschein and Reyer 1983). Specifically, it proposes that in species in which females initiate the duets (i.e. the majority of duetting species studied so far: Langmore 1998), females sing to attract mates and males respond to deter other males and thereby defend their paternity (e.g. North American quail: Stokes and Williams 1968; bay wrens *Thryothorus nigricapillus*: Levin 1996b). Similarly, in species in which males initiate duets (e.g. laughing kookaburras *Dacelo novaeguineae*: Reyer and Schmidl 1988; mohos *Hypergerus atriceps* and yellow-crowned gonoleks *Laniarius barbartus*: P.J.B. Slater, personal communication), females are hypothesised to reply to their partner's song to ward off rivals and thereby defend their access to male care, which might be compromised should their partner acquire a second mate. In species where both sexes initiate duets, it is proposed that both sexes sing to attract mates and the duet arises through mutual mate-guarding (Sonnenschein and Reyer 1983).

If duets reflect paternity guarding by males, and guarding of male care by females, then males should respond to their mate's solo most strongly during her fertile period whilst female responsiveness should be sustained throughout the period of male care or during the period a rival is fertile (if she is able to discern this). However, this prediction was not met in a recent study of duetting in magpie larks *Grallina cyanoleuca* in which

males were less likely to respond to female solos during the fertile period (Hall and Magrath 2000). Similarly, studies in other species show male responsiveness to female songs declining or remaining constant between the prefertile and fertile periods (e.g. slate-coloured boubous *Laniarius funebris*: Sonnenschein and Reyer 1983; red-winged blackbirds *Agelaius phoeniceus*: Whittingham et al. 1997). It has therefore been proposed that rather than defending paternity, duets defend the partnership: birds sing in response to their partner's song and the duet thus formed not only repels rivals but demonstrates commitment to the partnership to discourage desertion (Zahavi 1977; Smith 1994; Hall 2000). Although this has traditionally been presented as cooperative 'pair bond maintenance' (Farabaugh 1982), it intuitively invokes conflict: pair members are unlikely to have to demonstrate commitment or defend their mate if there is no sexual conflict.

The subdesert mesite *Monias benschi* is a group-living, terrestrial bird endemic to southwest Madagascar (Evans et al. 1996). It belongs to a monotypic genus in ancient gruiform family endemic to Madagascar: Mesitornithidae (Evans et al. 1996). The subdesert mesite lives in groups typically containing 1–2 females and 2–3 males, all of whom cooperate over the defence of permanent, multipurpose territories and in the raising and defending of young (Seddon et al. 2003). Stable groups apparently act as units during territory defence and territories are maintained to access sufficient resources rather than to obtain mates. Indeed, competition for mates occurs within groups rather than between territory holders, and as such territory defence and mate defence are separate issues in this species, with the former setting the stage for the latter. Some mesite groups apparently comprise monogamous pairs with related and unrelated helpers, while others may be polygamous (Seddon 2001). Such variation probably reflects different outcomes of each group member's attempt to maximise inclusive fitness. For example, conflict will arise between parents and offspring over access to breeding positions, and between male and female breeders over the sex of helpers tolerated in the group. In this climate of conflict each pair member may need to rigorously defend their partnership, and for males their paternity, especially against rivals from within the group. Given the low visibility afforded by the dense understorey of this species' habitat (Seddon 2001), it might be difficult for mates to monitor each other's whereabouts visually and acoustic signals may be used instead. That duets might fulfil this role within multi-male and/or multi-female groups of birds was first suggested by Reyer and Schmidl (1988), but no study has hitherto undertaken an experimental investigation.

Subdesert mesites give sexually differentiated solos which they frequently combine to produce relatively simple but precisely timed antiphonal duets (Seddon 2002). Although these duets are produced in a variety of situations, a large proportion are produced in apparently non-territorial contexts and are often initiated by birds

that are out of visual contact with fellow group members. Furthermore, solo songs elicit approaches from birds of the opposite sex, either group members from which the singer has become separated or intruders, and solos given by intruding birds of both sexes apparently provoked approaches from residents of the opposite sex (Seddon 2001). These observations hint that duetting in subdesert mesites may at least partly function in acoustic mate defence.

The observations that females initiate >75% of the duets and that within duets, male syllables follow female syllables after a significantly shorter time interval than the converse (Seddon 2001) suggests that duets could arise through the vocal defence of the dominant female by her mate. Certainly the male sex-ratio bias at the level of the population and group (Seddon et al. 2002) implies that there is likely to be strong selection on males to do so. However, the fact that males also initiate duets raises the possibility that mesite duets arise through mutual mate defence.

We investigated these ideas using a series of playback experiments in which we broadcast recordings of male and female solos and duets to lone birds and groups. If duets function in mutual acoustic mate defence then we predicted that:

1. Solos should attract unpaired members of the opposite sex and repel or incite aggressive responses from paired members of the same sex;
2. Duets should repel unpaired members of the opposite sex and elicit weak responses from paired birds of either sex.

Methods

In this study definitions of the song types and their constituent phrases and syllables follow those given in Seddon (2002). The term 'song' includes solos, duets and choruses and excludes simple contact calls. The experimental protocol employed, together with the methods used to generate replicates, control for pseudo-replication and minimise habituation are described in detail in Seddon (2001). We therefore only provide a summary here.

Study species and sites

This study was conducted as part of a 3-year investigation into the ecology of the subdesert mesite, a cooperatively breeding terrestrial bird endemic to the semi-arid Mikea Forest of southwest Madagascar (Seddon 2001). Fieldwork was carried out at two sites: PK32 (23°04'57"S, 43°37'15"E, 200 ha) and Mangily (23°07'09"S, 43°37'30"E, 120 ha). Descriptions of the habitat and climate of these locations are given in Seddon et al. (2000).

Playback experiments

Experiment 1: responses of lone birds to solos

We opportunistically played recordings of male solos to five lone males and five lone females, and of female solos to two lone males and three lone females. Playbacks were carried out at Mangily, PK32 and along transects north of Manombo in 1997–1999.

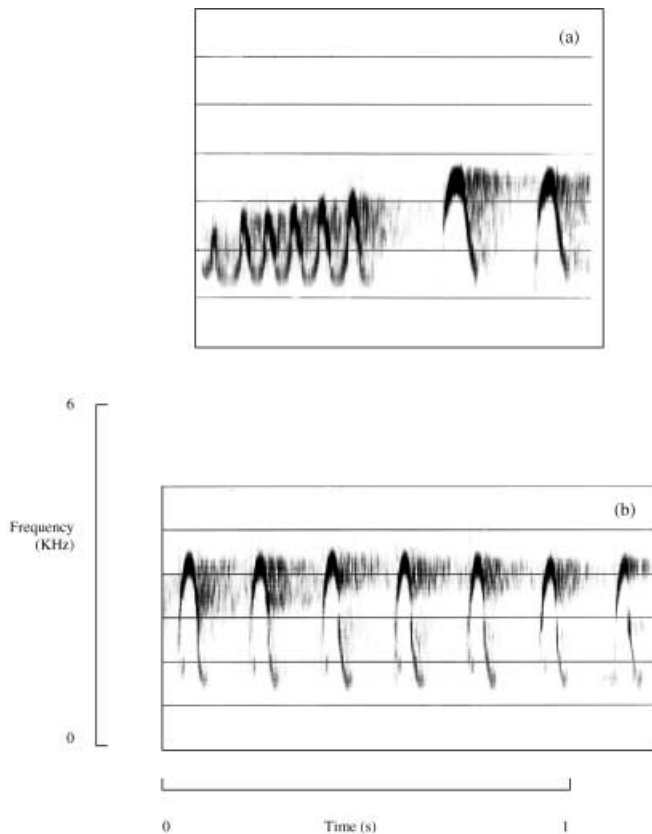
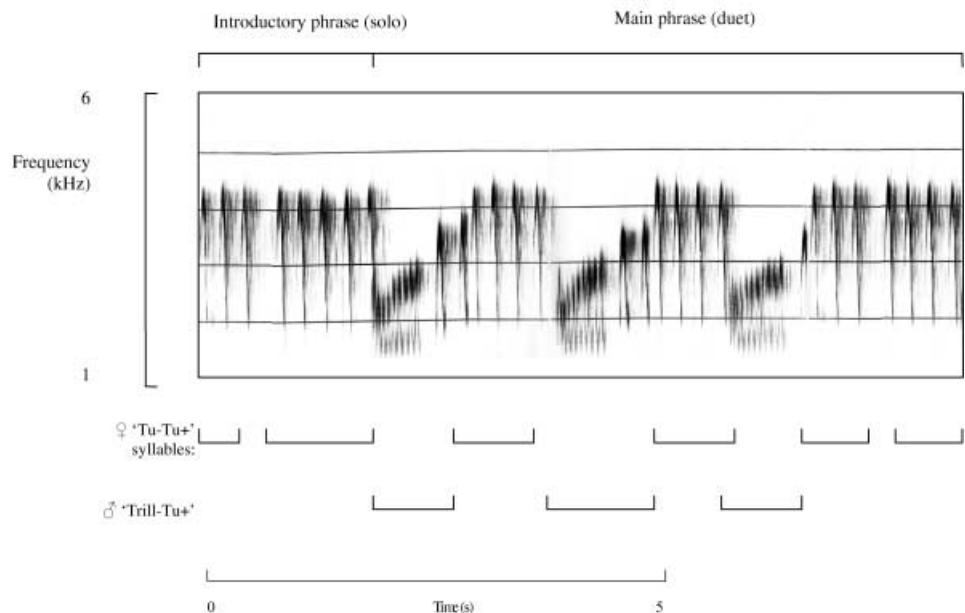


Fig. 1 Sonograms depicting **a** a ‘Trill-Tu+’ syllable taken from a male subdesert mesite *Monias benschi* solo, and **b** a ‘Tu-Tu+’ syllable comprising seven ‘Tu’ elements taken from a female solo

Two factors limited the sample sizes. Firstly, lone birds were very rarely encountered. Secondly, resident groups occasionally responded to either the playback or the subject’s response, which confounded the result; in these cases we do not present the data. It was not possible to ascertain the status of lone birds encountered

Fig. 2 Sonogram of a brief duet given by a pair of subdesert mesites, with annotations showing which syllables were contributed by the male and which by the female



along the transects, but they are likely to have been dispersing birds given the observation that all lone individuals encountered at PK32 and Mangily were unmarked birds intruding upon the territories of resident groups.

Experiment 2: responses of pairs and groups to solos versus duets

In October–December 1998 we gave each of ten colour-marked study groups three different playback treatments: A – male solo (a series of ‘Trill-Tu+’ syllables; Fig. 1a), B – female solo (a series of ‘Tu-Tu+’ syllables; Fig. 1b), and C – pair duets (a series of alternating ‘Trill-Tu+’ and ‘Tu-Tu+’ syllables initiated and terminated by a female; Fig. 2). Under natural conditions, subdesert mesites occasionally gave male duets, which comprised a series of ‘Trill-Tu+’ syllables uttered in alternation by two males as part of a chorus. In order to investigate whether any differences in the responses of groups to duets as compared to solos was a function of the sex rather than number of vocalising birds, we played male duets (i.e. treatment D) to eight of the same study groups.

Experimental design

Experiment 1 involved a single trial, and experiment 2 involved four trials. In each trial we broadcast one 30-s solo or duet to lone birds or groups positioned 15–20 m from a Sony SRS-58 loudspeaker. Sound intensity was adjusted (using amplification in SoundEdit and the volume control on the cassette recorder) to a natural level (Seddon 2001) where a broadcast vocalisation gave a maximum intensity of 65 dB from 15 m in front of the speaker (as measured using a handheld Tandy sound level meter on slow setting). The loudspeaker was placed 0.1–0.2 m above the ground and ca. 15 m from concealed observers.

To avoid problems of pseudoreplication and the potentially confounding influence of recognition of individual songs, each subject or subject group received a different recording of lone birds or pairs of birds made in October–December 1997 from a site 6 km away in the case of PK32 and Mangily, and over 30 km away for the birds encountered along transects north of Manombo. Subjects were located either by chance along forest trails, following a natural vocalisation, or in a minority of cases (16/38 trials) by playing a 30-s subdesert mesite chorus to elicit a vocal response. In all cases, a period of 15 min was left before conducting playback to allow the birds to resume normal non-vocal activities

Table 1 The order in which treatments A–D were played to ten study groups. A Male solos, B female solos, C pair duets, and D male duets

Week starting	Group name and adult composition (males/females)									
	P1 (3/2)	P2 (1/2)	P3 (1/1)	P4 (6/2)	P6 (2/2)	P7 (1/2)	P9 (2/2)	P12 (2/2)	M9 (5/3)	M10 (3/2)
5 Oct 98	–	B	–	A	B	–	–	A	B	A
19 Oct 98	–	C	B	C	A	C	–	B	D	D
26 Oct 98	–	D	A	D	D	B	A	C	A	B
2 Nov 98	A	A	C	B	C	A	B	–	C	C
9 Nov 98	B	–	D	–	–	D	C	–	–	–
16 Nov 98	D	–	–	–	–	–	–	–	–	–
23 Nov 98	C	–	–	–	–	–	–	–	–	–

(foraging and preening). In experiment 2, playback was conducted at least 50 m from the nearest territory boundary. Each group received the treatments A–D in a different order at an interval of 7–10 days between 0600 and 1000 hours (Table 1).

Quantifying responses to playback

In experiment 1, playbacks were conducted opportunistically as it was impossible to predict when or where lone birds would be encountered. Consequently only four basic responses were recorded: the occurrence and type of song given in response, whether or not the subjects approached and the minimum distance to which they approached.

In experiment 2, a variety of behavioural responses was recorded onto a Sanyo dictaphone by one observer, whilst a second observer recorded any vocalisations onto a 60 min metal TDK tape using a WM-D6C Sony Walkman and a Sennheiser ME67 directional microphone. In addition to the aforementioned variables we recorded: latency in seconds to first song, the duration of the first song, the total number of songs given within 5 min of the start of the first playback (where the interval between successive songs was at least 5 s and where no response was scored as zero); and the rate of syllables during the first song (per min). All these responses were considered to be those of the whole group as they were difficult to disentangle from the specific responses of the main duetting pair. However, it was possible to identify a pair whose duet constituted the bulk of the vocal response to each playback treatment. It is likely that this pair were the breeders in each subject group, but as yet there are too few genetic data to clarify this. This pair led the group towards the speaker, often perched alongside one another whilst duetting and one of the pair almost invariably initiated the vocal response. We therefore recorded which pair member initiated the first song, measured the duration of the introductory phrase of this song using Canary 1.2 (Charif et al. 1995) and, where possible, noted which member of the pair approached the speaker the closest. To investigate the vocal contributions of these birds more closely, using a Kay Elemetrics Sonograph DSP Model 5500 (KEDS) we subsequently produced sonagrams from recordings of the first song (filter setting: 300 Hz, bandwidth: 0–8 kHz, time resolution: 4 ms). The recordings used were those given only by pairs positioned such that they were clearly visible to concealed observers, <10 m from the microphone and <0.5 m apart throughout the duet. From these we measured the percentage of syllables (excluding those produced by other group members) given by each pair member in the main phrase (i.e. we excluded syllables produced in the initial solo which would have otherwise elevated the contribution of the initiating sex). From sharply defined sonagrams generated from recordings of duets that were given in response to male and female solos, we additionally counted the number of elements per male ‘Trill-Tu+’ and female ‘Tu-Tu+’ syllable and, using the on-screen cursors on the KEDS, we measured the time interval between the male and female syllables. From each pair, we sampled 15–20 syl-

lables from each of the male and female duet contributions, and measured at least 20 consecutive intervals between male and female syllables. Each pair then provided one mean value for these variables to use in matched comparison tests (see below).

Statistics and sampling

The sample sizes for the first set of experiments were too small to enable a statistical comparison of lone birds’ responses to male and female solos. We therefore simply present these results without further analysis. The analysis of the second set of experiments is based on matched comparisons within 8–10 study groups. In all experiments data from 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 the fact that the habitat is almost identical and contiguous, the two sites being only 6 km apart. The continuous response variables, namely latency, duration, number of songs, and minimum approach distance were found not to be correlated with each other (Seddon 2001). Principal components analysis was therefore inappropriate for this study, and the responses were analysed separately. For matched comparisons within groups, non-parametric tests were used as the sample sizes were small. For Wilcoxon signed-rank tests, the *T* statistic is given with its associated *P*-value calculated using Table V in Rohlf and Sokal (1995). In all these analyses, *N* is taken as the number of groups with each group providing one mean. Sample sizes for the analysis of the syllable structure of responses to playback were reduced because we could only use very high quality recordings made in conjunction with good behavioural observations (see above). All statistical tests are two-tailed, all means are given \pm SE, and all *P* values are corrected for ties.

Results

Experiment 1: responses of lone birds to solos

Table 2 summarises the responses of lone birds to playback of solos. Of the five lone males that received male solos, all approached and all but one vocalised. Two males each produced a series of alternating male ‘Trill-Tu+’ and female ‘Tu-Tu+’ syllables, effectively producing the duet usually given by a pair. Of the five females that received male solos, three approached (including two to within 1 m), and all produced solos. Of particular interest was the observation that one female alternated her song with the recording of a male solo, thereby producing a duet. This indicated that the playback loops

Table 2 Responses of lone subdesert mesites to playback of male and female solos

Subject	Date	Location (site/transect)	Playback	Approach (m)	Song elicited
Male					
1	10 Dec 98	PK32	Male solo	<1	Silent
2	9 Dec 99	Salary–Belitsaka	Male solo	<5	Duet-solo ^a
3	12 Dec 99	Ambatomilo–Andabotoka	Male solo	<5	Duet-solo ^a
4	13 Dec 99	Ambatomilo–Andabotoka	Male solo	<10	Solo
5	13 Dec 99	Ambatomilo–Andabotoka	Male solo	<5	Solo
6	30 Nov 97	Mangily	Female solo	<1	Solo
7	10 Nov 98	PK32	Female solo	<5	Solo
Female					
1	16 Nov 98	Mangily	Male solo	Retreated	Solo
2	10 Nov 98	PK32	Male solo	Retreated	Solo
3	23 Oct 99	PK32	Male solo	<1	Solo
4	13 Dec 99	Ambatomilo–Andabotoka	Male solo	<10	Solo
5	5 Jan 00	PK32	Male solo	<1	Alt.-solo ^b
6	30 Dec 97	Mangily	Female solo	Retreated	Solo
7	30 Dec 98	PK32	Female solo	<5	Solo
8	9 Oct 99	PK32	Female solo	Retreated	Silent

^a Male alternated ‘Trill-Tu+’ and ‘Tu-Tu+’ syllables to produce a duet

^b Female alternated ‘Tu-Tu+’ syllables with male solo playback to produce a duet

Table 3 Comparison of groups’ responses to playback of three different treatments. Values for $\chi^2_2=6.0$ and P derive from Friedman tests; means \pm SE are given and $n=10$ groups

	Male solo	Female solo	Pair duet	χ^2_2	P
Minimum distance (m)	9.9 \pm 2.1	13.3 \pm 1.7	20.6 \pm 2.5	7.00	0.03
Latency to first song (s)	17.5 \pm 4.0	28.9 \pm 5.6	36.2 \pm 8.6	4.20	0.12
Duration of first song (s)	68.1 \pm 11.5	46.2 \pm 4.7	48.4 \pm 7.3	7.40	0.03
Number of participants	2.8 \pm 0.3	2.7 \pm 0.4	2.6 \pm 0.3	0.07	0.97
Rate (syllables min ⁻¹)	69.3 \pm 6.7	71.9 \pm 3.1	67.5 \pm 4.2	2.22	0.33
Number of songs	3.5 \pm 0.5	3.0 \pm 0.5	1.9 \pm 0.4	4.39	0.11

constructed for these experiments were realistic. The two males that received female solos approached and sang, whereas of three females that received female solos two retreated and one approached.

Experiment 2a: responses of groups to solos versus duets

All ten study groups sang following playback of treatments A (male solo), B (female solo) and C (pair duet), but the probability of approach varied: ten groups approached male solos, nine approached female solos and five approached pair duets (Cochran Q -test: $Q=8.4$, $n=10$, $P<0.02$). Groups approached male solos significantly more closely than either female solos or pair duets, and they vocalised for a significantly greater duration in response to male solos than any other treatment. However, there were no significant differences across treatments for the remaining response variables (Table 3).

Overall, groups responded more strongly to male solos than pair duets i.e. they approached more closely and sang for a greater duration in response to playback of male solos compared to pair duets (multiple comparison tests: $P<0.05$). To investigate whether this was a function of the number rather than the sex of the vocalising intruders, we compared groups’ responses to pair duets and male duets. We found that groups approached male

duets more closely than pair duets [11.4 \pm 2.4 versus 20.1 \pm 3.1 m, Wilcoxon signed-rank test: $T=1$, $n=8$ groups (minus 1 tie), $P=0.016$]. Finally, we compared groups’ responses to male solos with their responses to male duets and found no significant differences between them ($n=8$ groups, P values ranged from 0.17–0.60). These results provided some indication that groups differentiated between male-only pairs and male-female pairs, with the former eliciting stronger responses that were equivalent to those evoked by male solos.

Experiment 2b: responses of pairs to solos versus duets

In each group it was possible to identify a pair whose duet constituted the bulk of the song given in response to each playback treatment. Males were more likely than females to initiate songs in response to male solos, while females were more likely than males to initiate songs in response to female solos (Table 4). Males were more likely to initiate responses to male solos than pair duets (paired sign test: $P=0.016$). There was no significant variation across treatments in the likelihood that males or females would approach the closest, and neither sex was more likely than the other to approach the closest to any of the three treatments.

It took significantly more time for a female to respond antiphonally to her partner following playback of

Table 4 Comparisons within and between the sexes as to which member of the duetting pair initiated the first vocal response and approached the three playback treatments. Values for χ^2 and associated P derive from chi-square tests (P^*) and Fisher's exact tests (P^\dagger), and values for Q and associated P derive from Cochran Q -tests (following Siegal and Castellan 1988)

Response	Playback			Q	P
	Male solo	Female solo	Pair duet		
Number of occasions when:					
Male initiated first song response	10	2	3	12.6	<0.01
Female initiated first song response	0	8	7	12.6	<0.01
χ^2_{11}	20.0	7.20	3.20		
P^*_{11}	<0.0001	0.007	0.074		
Male approached closest	5	5	4	0.33	<0.90
Female approached closest	2	2	3	0.44	<0.98
χ^2_{11}	1.98	1.98	0.29		
P^\dagger_{11}	0.35	0.35	0.59		

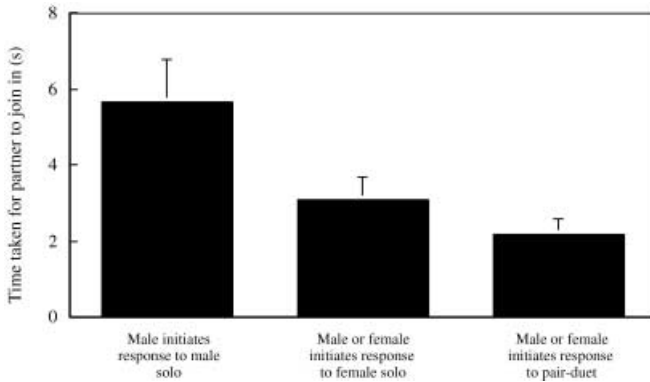


Fig. 3 The effect of three treatments on the time it took either member of the duetting pair to respond to its partner's solo. There was significant variation across treatments (Friedman test: $\chi^2_2=6.0$, $n=10$ groups, $P=0.008$), with females taking significantly longer to respond to their partner's solo following playback of male solos, than it took males or females to respond to their partner's solos elicited by playback of female solos or pair duets (multiple comparison tests: $P<0.05$ in all comparisons)

a male solo than it did for either a male to join his female following playback of a female solo, or for a bird of either sex to respond antiphonally to the initiator of responses to pair duets (Fig. 3). It is possible that, rather than replying to its partner's song, a paired bird is simply showing a delayed response to the playback itself. However, we think this is unlikely for two reasons. Firstly, the duet always comprised male and female syllables interposed with relatively high degrees of temporal precision indicating that the duet is interactive and not independent. Secondly, in natural duets the structure of male and female syllables changed significantly when they were given in concert (e.g. duet syllables were of greater duration, comprised more elements and had a broader bandwidth than solo syllables for both sexes: Seddon 2002).

The percentage of syllables males and females contributed to duets given in responses to playback also varied across treatments (Fig. 4). Females contributed the greatest percentage of syllables in responses to female solos and males contributed the least. Overall, males produced a greater percentage of syllables than females

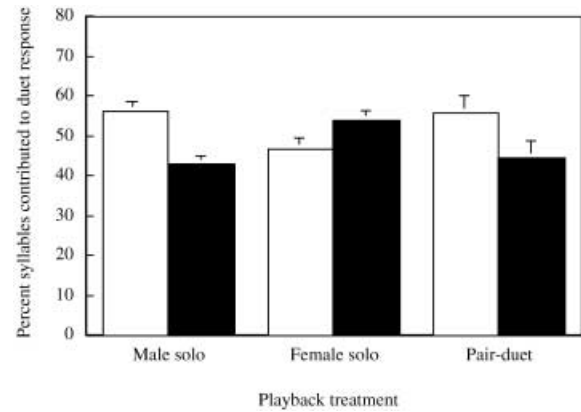


Fig. 4 The effect of experimental treatment on the percentage of syllables contributed by the duetting male (*open bars*) and female (*solid bars*) to the first duet elicited by playback. There was significant variation across treatments in the percentage of syllables contributed by each sex (Friedman test: $\chi^2_2=6.0$, $n=7$ groups, $P=0.049$). Males contributed a significantly greater percentage of syllables than expected if males and females contributed equally to duets given in response to male solos (Wilcoxon signed-rank test: $T=0$, $n=8$ (minus 1 tie), $P=0.008$). As the initiating solo song was eliminated from this analysis this result does not reflect the fact that one sex had a head start in the same-sex playback treatment. However, males and females did not differ significantly in their contribution to duets given in response to playback of female solos ($T=9$, $n=8$, $P>0.5$) or pair-duets solos ($T=7$, $n=7$, $P>0.5$)

in duets given in response to male solos, but males and females contributed equally following playback of female solos and pair duets.

Finally, the time taken for males to answer their partners' syllables was significantly less following playback of male solos (Table 5). Females showed no significant differences between treatments in either the number of elements per syllable nor in the time they took to answer male syllables.

Overall, males and females responded more strongly to same-sex solos than opposite-sex solos, and in terms of likelihood of initiating the response, males also responded more strongly to male solos than to pair duets. To investigate whether this was an effect of number rather than sex of simulated intruders, we compared eight groups' responses to pair duets with their responses to male duets. We found no significant differences between

Table 5 Comparison between two solo playbacks in some aspects of the syllable structure of duets given by main pair. Values for T and P derive from Wilcoxon signed-rank tests; means \pm SE are given, and $n=8$ duets given by unique pairs

Response	Playback		T	P
	Male solo	Female solo		
Number elements in male syllables	2.5 \pm 0.2	1.8 \pm 0.3	4.5	<0.1
Number elements in female syllables	4.3 \pm 0.3	5.2 \pm 0.4	7.0	>0.1
Female-male syllable interval (s)	0.02 \pm 0.03	0.10 \pm 0.02	1.0	<0.02
Male-female syllable interval (s)	0.16 \pm 0.01	0.17 \pm 0.03	18	>0.9

Table 6 Comparisons within and between the sexes as to whether or not members of the main duetting pair from each of eight study groups initiated the first vocal response and approached two different duet treatments. Values for χ^2_1 and P^* derive from Fisher's exact tests, and values for P^\dagger derive from paired sign tests. Note that in the lower left cell, $n=7$ because in one case neither male nor female approached the closest

Response	Playback		P^\dagger
	Pair duet	Male duet	
Number of occasions when:			
Male initiated first vocal response	2	6	0.22
Female initiated first vocal response	6	2	0.22
χ^2_1	4.0		
P^*	0.13		
Male approached closest	4	6	0.63
Female approached closest	3	2	0.99
χ^2_1	0.29		
P^*	0.99		

the treatments within or between the sexes in the likelihood of initiating or approaching, but sample sizes are small (Table 6). However, we found that males produced a significantly greater proportion of syllables in duets given in response to male duets than would be expected if males and females had contributed equally (56.7 \pm 2.2% versus 50 \pm 0%, Wilcoxon signed-rank test: $T=0$, $n=7$, $P=0.016$).

Discussion

Subdesert mesites responded strongly to playback of solos and duets whether as individuals, pairs or groups. Lone birds of either sex approached and almost invariably sang in response to playback of male solos. Female solos appeared to elicit approaches from lone males whilst causing lone females to retreat. It was not possible, using behavioural cues, to distinguish between approaches involving attraction and those involving aggression. However, the observation that on two separate occasions single males gave duets in response to male solos suggests aggression, insofar as these males may have been attempting to exaggerate their number and hence the degree of threat they posed to the intruder. Further, the observation that a lone female responded antiphonally to playback of a male solo is highly indicative of attraction. So although the sample sizes are too small to make any firm conclusions about the function of solo song in either sex, the results of experiment 1 are at least consistent with the first prediction of the mate-defence hypothesis, i.e. 'solos should attract unpaired members of the opposite sex and repel or incite aggressive responses from paired members of the same sex'.

Upon hearing same-sex solos, each member of the main duetting pair was more likely to initiate songs and produce more syllables which, for males, comprised more elements and followed the female syllables more promptly. While females responded to female solos and pair duets with equal vigour, males responded to male solos more strongly than to pair duets. Overall, groups produced stronger responses to male solos than to female solos or pair duets and gave stronger responses to male duets than to pair duets. Furthermore, groups responded to male duets with a strength comparable to that with which they responded to male solos.

Do subdesert mesite duets serve in mate defence?

The sex specificity of responses to playback suggest that solo songs in both sexes function in intra-sexual territorial aggression, but also may attract unpaired birds of the opposite sex. Sex-specific responses to playback have been found in several other duetting species (reviewed in Hall 2000) and have been taken as evidence for duets being the by-product of independent territory defence (Morton 1996; Morton and Derrickson 1996). However, if paired birds sing to repel same-sex rivals, why do paired birds respond to their partner's solos? The alternative explanation for sex-specific responses to playback is that paired birds respond to deter a partner from pairing with a rival and to signal the presence of a mutually defended pair on territory (Hall 2000). The main predictions of this hypothesis are summarised in Table 7.

A key prediction of this hypothesis is that duets repel rivals. However, as the opportunity did not arise to play duets to unpaired birds it was not possible to test this directly. Nonetheless there are two pieces of supportive in-

Table 7 Predictions generated by the mutual mate-defence hypothesis and whether or not they are met in the subdesert mesite

Duet variable	Prediction	Prediction met?
Structure	Comprise sex-specific songs	Yes
Spacing of singers	Out of sight of one another	Sometimes
Main participants	Breeding pair in the group	?
Sex of initiator	Males and females	Yes
Responses to solo playback	Attract unpaired birds of opposite sex	Yes
	Elicit strong response from paired birds of same sex	Yes
Responses to duet playback	Repel unpaired birds of either sex	?
	Elicit weak responses from paired birds of either sex	Yes

direct evidence. Firstly, observations of lone males producing 'pair duets' following playback of male solos indicated that a duet may be a more effective deterrent signal than solo song. Secondly, males produced weaker responses to playback of pair duets compared to male solos. There are at least two possible alternative interpretations. One is that pairs of intruders posed a greater threat to the group and to each pair member and therefore elicited a more cautious response overall. However, this is unlikely as all study groups comprised three or more adults (Seddon et al. 2002) and male duets elicited a response as equally vigorous as that elicited by male solos. The second interpretation is, therefore, that a pair duet represents a less threatening signal than a male solo. For example, if a pair duet signals the intrusion of a mated pair then the threat is to the group overall and is a territorial issue deserving a unified response, rather than a more direct and insidious threat to the paternity of the dominant male or males through displacement or extra-pair copulations.

Is mate defence in subdesert mesites mutual or male only?

There are at least three observations indicating that mate defence is mutual and that both male and female behaviour is important in duet formation: (1) both sexes initiated natural duets and responses to same-sex solos, (2) a female was recorded singing in precise alternation with playback of a male solo, and (3) the structure of both sexes' syllables changed when males and females sang in alternation with their partner (Seddon 2002). Indeed, it is possible that the latter may have evolved to facilitate recognition by intruders that two birds are present and defending their territory and each other.

However, there are several pieces of evidence indicating that mate defence is stronger in males. Firstly, within the main phrase of the natural duets sampled, male syllables followed female syllables more promptly than the converse (Seddon 2002). Secondly, male syllables followed female syllables more promptly after playback of male solos than after playback of female solos. Thirdly, groups responded more strongly to male solos than to either female solos or pair duets. And finally, females' responses to playback were generally weaker than those of

males. Stronger defence of females by males may relate to the male sex-ratio bias found in both the study population and within study groups (Seddon et al. 2002). This bias may mean that males need to defend their paternity against rivals from either within the population or within the group. The need for females to defend their mates is likely to be less than that for males given the asymmetry that males might lose paternity to rivals, but females might at most lose some care at the nest.

Do subdesert mesite duets demonstrate commitment?

Mutual mate defence can explain why paired mesites respond to their partner's solos. However, it cannot alone explain why they should coordinate their songs so precisely. In the 'coyness model' proposed by Wickler (1980) duets are hypothesised to discourage desertion because they represent time-consuming pair-specific investment. Mesites performed duets with new and artificial partners, which indicated that duets do not represent a big investment by either sex. However, mere involvement in a duet involves some partner-specific investment, rapid responses to partner's solos may signal commitment to the partnership (Smith 1994) and the precision with which they alternated their syllables may improve with time and may even facilitate female choice. A detailed and long-term analysis of the relationship between paternity and the temporal characteristics of duets is necessary to investigate this possibility. If duets do facilitate mate choice then as for other sexually selected traits there are a wealth of possibilities as to how this might have evolved and be maintained (Andersson 1994; Bradbury and Vehrencamp 1998).

Does duetting arise through cooperation or conflict?

Duets are usually regarded as either cooperative ventures by a pair over the establishment and maintenance of pair bonds and territories (Farabaugh 1982; Morton 1996; Hall 2000), or as the uneasy resolution of sexual conflict (Levin 1996a; Slater 1997). However, such a dichotomy may be misleading as it is becoming increasingly clear that duets contain elements of both: hypotheses invoking cooperation do not exclude those invoking conflict. In a

recent study of duetting in a socially monogamous species, the Australian magpie lark, Hall (2000) found that duets were more threatening signals than solo songs and suggested that they therefore function in territory defence. She also found that males responded to a greater proportion of their partners' songs in contexts where their partners might desert them and this led her to suggest that duets also served to maintain the pair bond. Although Hall concluded that duets in magpie larks are cooperative endeavours, her results could also be interpreted in terms of conflict: the greater need of the male to defend his partnership can only arise in a climate of conflict. In this study, we found that duets in the subdesert mesite represent a less threatening signal than solo songs and that both males and females show sex-specific territorial responses. Although these results appear at odds with Hall's, we propose that duets ultimately may serve the same function in both species. The fact that they appear more cooperative in one than the other may simply reflect differences between the two species in their mating systems and hence in the costs and benefits of each of the duetting pair in attracting same-sex rivals.

Conclusions

The experimental evidence described in this study suggests that song is used in intra-sexual, territorial aggression with each sex singing to repel same-sex rivals. However, anecdotal observations and experiments carried out on lone birds hinted that solo song may attract members of the opposite sex. This preliminary study of duetting in subdesert mesites has highlighted the role of sexual conflict in an unusual avian vocal display usually held to be a cooperative venture between a mated pair. It provides some suggestive evidence that males and females may sing to guard each other from the attentions of rivals in a dense habitat where visual or direct physical forms of mate defence may be ineffective. However, three lines of further investigation are clearly required before any firm conclusions can be drawn. Firstly, removal experiments are needed to investigate the relative roles of male and female song in mate-attraction. Secondly, experiments in which duets are played to unpaired birds and solo songs are played to a greater number of unpaired individuals are also necessary. And thirdly, a detailed study of the patterns of responsiveness of paired birds to their partner's songs and to playback of solo songs with respect to the fertile period is required to investigate whether duets function to defend paternity as well as to guard alliances. Finally, our observations of single males producing duets usually given by pairs raises the interesting possibility that mesites are able to and may occasionally exaggerate their number in vocal territorial interactions. Further work is needed to investigate the evidence for such 'deceitful' behaviour in this and other duetting birds.

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