



Yelling for sex: harem males compete for female access in bronze-winged jacanas

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Sperm competition in sex-role reversed, polyandrous jacanas is intense because females copulate with multiple male mates before laying each clutch. These males may be unable to attempt to maximize their share of copulations by mate guarding or forcing copulations. Instead, males in polyandrous harems may compete for sexual access to the female by giving a call, termed the 'yell', to attract her. Male bronze-winged jacanas, *Metopidius indicus*, yelled at higher rates in larger harems, and when the female was further from the yeller or on a comate's territory. Half of all yells were given at mating platforms where all copulations occurred. Males that received the clutch yelled at lower rates during the incubation and chick care periods. Yells attracted the female when she was far from the yeller or with a comate. When the yell of a polyandrous male was broadcast from his territory, the female was more likely to fly to his territory during playback than during control periods. Within polyandrous harems the males that yelled at the highest rates received the most copulations, and three out of four females gave clutches to the male that gave the longest and most frequent yells, so females may have used yells to assess male quality. Intrusions by females, but not males, increased during yell playbacks, and tended to be more frequent on the territories of males with high yell rates. Females may therefore respond to their mates' yells because yells may attract female intruders which may attempt to take over the territory.

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Sperm competition arises when females mate with more than one male during a single reproductive cycle (Parker 1984; Birkhead & Møller 1992). Sperm competition is likely to be intense in classically polyandrous bird species in which a single female mates and provides clutches for multiple males (Oring 1986; Birkhead et al. 1987; Birkhead & Møller 1993). In sex-role reversed, polyandrous jacanas, females defend territories containing those of up to four males, and may copulate with all available males before laying each clutch (Jenni & Collier 1972; Tarboton 1992; Butchart, *in press*). In such species how do males compete with the other males in the harem (termed comates) to maximize their share of copulations with the female? In bronze-winged jacanas, *Metopidius indicus*, the conventional paternity guards used in most bird species, mate guarding and frequent copulations (Birkhead & Møller 1992), seem unlikely to be effective. Males are unlikely to be able to monopolize their mates

through physically preventing them from visiting comates' territories, because females are on average 60% heavier (Butchart, *in press*). Nor are they able to defend their paternity through territoriality, because comates defend exclusive territories within the female territory (Butchart et al., *in press*). Furthermore, copulation frequency is dependent on both male and female behaviour in jacanas, because females are larger and can easily terminate mounts before a successful copulation is achieved, so males cannot force copulations with their mates (Butchart 1998).

Here we propose that males may attempt to increase their share of copulations by competing for sexual access to a female and using a particular call to attract her. We refer to this call as the 'yell' following the terminology used for wattled jacana, *Jacana jacana*, vocalizations (S. T. Emlen & P. H. Wrege, unpublished data). Using removal experiments, playback experiments, and observations of the contexts of natural yelling behaviour and the responses of females to their male's yells, we tested the idea that the main function of the yell call is to attract females. Furthermore, we tested whether males that yelled at higher rates received more copulations.

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METHODS

We carried out fieldwork on a colour-ringed population varying between 41 and 62 bronze-winged jacanas at Vembanur, an 18-ha freshwater lake located at 9°11'N 77°23'E in Kanyakumari district, in the state of Tamil Nadu at the southern tip of India. Between 85% (in 1995) and 98% (in 1997) of the lake was covered in floating and rooted vegetation (Butchart, *in press*). The water level of the lake, and hence the density of the vegetation, was influenced naturally by rainfall and artificially by control of sluice gates to let out water for irrigation. Fieldwork was carried out for three breeding seasons between mid-May and mid-October 1995–1997. Each year we captured 72–90% of the jacana population in 10-cm mesh nylon mist nets erected above the water from canoes. We gave each bird an individual combination of two to four coloured plastic leg rings, and distinguished its sex unambiguously using bill length and mass (Butchart 1998). We sexed unringed birds by estimating their size relative to ringed birds of known sex, and by noting unequivocal sex-specific calls and sexual behaviour (Butchart 1998). We determined breeding status, territory ownership and the composition of breeding groups by recording the contexts and details of sexual interactions, calls, nesting behaviour and aggressive interactions.

Focal Watches

We recorded the rates of sexual interactions, yells and intrusions by other jacanas during 2353 h of focal watches (range: 16.5–139.5 h per individual). These were carried out on resident birds at least every few days from the raised bank of the lake, or from a canoe, from dawn (ca. 0645 hours) until at least 0930 hours and from 1530 hours to dusk (ca. 1900 hours). Data were recorded continuously on to worksheets. For polyandrous groups, two fieldworkers collected data simultaneously on different comates, and the data for the female's behaviour on different territories were subsequently combined. As it was usually possible to observe focal individuals almost continuously (except for short periods when they foraged in dense vegetation), the data collected on behavioural interactions were fairly comprehensive.

For each yell we recorded the location of the female and her distance to the male (<5 m, 5–20 m, or >20 m), and for a subset of 411 focal h we also recorded (in the field) the number of individual syllables in each yell, the context in which it was given (e.g. at a mating platform, in response to an intrusion into the territory by another jacana, in response to a comate's yell, etc.), and the female's response (e.g. whether she flew to the male, copulated, etc.). We tape-recorded a subset of yells using a Sennheiser ME80/K3U directional microphone and a Sony WMD6C cassette recorder, and then measured the duration of the yell to the nearest 0.5 s using a stopwatch. For sexual interactions we noted whether the male yelled during the 60 s prior to the first solicit, and whether the interaction culminated in a copulation. For intrusions by other jacanas we recorded the responses of territory

owners, whether they yelled, and whether their female mates responded by helping to evict the intruder.

When a polyandrous female flew from one male's territory to another's, we recorded the rate of yells given by these males during the 60 s preceding the female's departure, during the period whilst she flew and during the 60 s after she landed. We recorded whether the first male followed the female towards the territory border with his comate and whether he attempted to intercept her as she left (characterized by flying within 1 m of the female, and sometimes actually making contact with her in mid-air).

Removal Experiments

To investigate male yelling behaviour when a female disappeared from her territory and was replaced by a new female, we carried out removal experiments on six females. We trapped these individuals in mist nets and then released them at a lake with similar habitat and a resident jacana population at Padmanabapuram 13 km to the northwest of Vembanur. All removals were carried out on pairs or polyandrous groups which did not include any males caring for clutches or chicks. We carried out focal watches on the removed female's territory in order to record the rates of yells given by her male mates (1) during the week prior to removal of the female, (2) from the day of removal up to and including the first 2 days in which a new female intruded on to the vacancy, and (3) during the period 1–2 weeks after take-over by the new female or by the original female who returned to her territory. Five of the removed females returned within 2–11 days, but the other female was not resighted despite fortnightly searches at the release site. Four of the returning females took over their old territories within 1–8 days, whilst the fifth remained a floater for the rest of the season (Butchart *et al.*, *in press*).

Playback Experiments

We carried out a series of playback experiments to investigate the responses of polyandrous females and comates to the yell of one of the males in a polyandrous group. Playbacks were carried out on polyandrous groups in which all males were sexually interacting with the female, and were available to receive a clutch. Experimental trials began at 0600–0700 hours and 1500–1600 hours under calm, dry weather conditions during July–September (the breeding season). We carried out 30 trials on six polyandrous groups, using playback of yells of two males per group (three trials were carried out for each of six males in 1996, and two trials were carried out for each of another six males in 1997). At least 24 h were allowed between trials on the same male.

Each trial consisted of three 30-min periods: silent control, dove control, and yell playback, with the dove and yell periods alternated in consecutive trials to control for order effects. Each male's yell was recorded, and we constructed playback spools by editing the original recordings using SoundEdit on a Macintosh computer.

We filtered out background noise below 2 kHz, and edited the clearest track to produce 10 s of yelling. This was copied and repeated every 30 s for 30 min (a realistic yell duration and frequency: mean natural yell duration was 12.5 s, and exceptionally up to 72 yells were given in a 30-min period). Sound intensity of all recordings was adjusted (using amplification in SoundEdit and the volume control on the cassette recorder) to give an amplitude of 55–60 dB at 20 m, matching that of natural yells (S. H. M. Butchart, unpublished data). Each male's yell was broadcast from his territory through a Panasonic RP-SP70 loudspeaker on a small floating platform positioned in approximately the centre of the territory. This was connected with audio cable to a cassette recorder which was operated from a canoe at least 30 m away or from a raised bank at the lake shore. The dove control was carried out to eliminate the possibility that jacanas simply responded to noise from a loudspeaker, and involved broadcasting the call of a spotted dove, *Streptopelia chinensis*, a common and highly vocal species in the habitat surrounding the lake. We recorded dove calls (a series of repeated 'coos') at Vembanur, and copied and repeated these on to a playback spool to give 10-s calls every 30 s.

In some trials the female was on the playback territory at the start of some periods, but for each female there were at least some occasions when she was off the playback territory at the beginning of each of the three periods and therefore had the opportunity to fly to the playback territory during that period. Two observers recorded the responses of the female and comates during each period, noting yell rates, percentage time alert (characterized by the bird adopting an upright posture, not foraging or showing any sexual behaviour, and often alarm calling), flights between territories, and frequency of intrusions by other males and females. For females we calculated the percentage of trials when they were on a comate's territory at the start of the period and flew to the playback territory during that period, and the latency of their response during the playback period. Each female's mean response produced one data point in the analysis. All statistical tests were two-tailed and corrected for ties where appropriate. Means are presented \pm 1 SE.

RESULTS

Attempted Mate Guarding

When a polyandrous female flew off one male's territory on to a comate's territory, the male she left flew after her in $21.2 \pm 5.3\%$ of cases, and attempted to intercept her in $9.4 \pm 4.5\%$ of cases (means for six females, 16 males, 207 flights). Occasionally the male actually made contact with the female in mid-air, and on three out of 195 occasions (1.5%) a male succeeded in forcing the female to land near the territory border; but in each of these cases the female immediately took off and continued flying to the comate's territory.

Males did not usually intrude into the territories of their comates, but occasionally they carried out distinctive intrusion flights during which they flew out over the middle of a comate's territory, looped round and then

returned to their own territory. We recorded this behaviour nine times by four males during 2353 h focal watches. In all cases, the female had flown to the comate's territory within the previous 15 min, and all cases occurred during the period when the female was mating with multiple comates from 5 days before the first egg of a clutch was laid until the day the second egg was laid. The comates who experienced these intrusions responded by giving alarm calls and carrying out hover-flights, but in no case did the female immediately return to the intruding male's territory. We never observed any instances of males intruding in this way on to the neighbouring territories of nonharem members.

Male Calls

Males gave three types of calls: alarm calls, chick calls and yells. Alarm calls and chick calls had a stuttering cadence composed of repeated groups of 3–10 rapidly repeated syllables (5–10 syllables/s). Alarm calls were louder and were given in response to potential predators, or to sudden disturbances such as loud noises. Chick calls were softer and were given when accompanying chicks. The yell call was distinctly different and consisted of short stereotyped syllables repeated at a regular rate up to 145 times. The mean duration was 23.6 ± 2.2 syllables ($N=16$ males, 641 yells) which were given at a mean rate of 1.9 ± 0.1 syllables/s ($N=10$ males, 106 yells). A continuous series of syllables was defined as one yell if it was separated from the next series of syllables by at least 2 s. **Figure 1** shows a sonagram of a typical yell. In $54.9 \pm 9.1\%$ of cases ($N=16$ males, 641 yells) the male adopted a posture in which the neck was stretched out and the wings were held half open whilst yelling.

The number of syllables per yell varied significantly between males (ANOVA: $F_{11,323}=3.01$, $P=0.0008$), and variation in the syllable rate was marginally significant ($F_{8,63}=2.09$, $P=0.049$). However, when the female was off the territory, the mean number of syllables per yell was significantly positively correlated with the mean yell rate (Spearman rank correlation: $r_s=0.69$, $N=12$, $P=0.022$), and not with the mean syllable rate, although the sample size was small ($r_s=-0.26$, $N=6$, $P=0.56$). Therefore, we used the rate at which yells were given when the female was off the territory as a measure of yelling effort in most of the following analyses. We were unable to test whether the frequency range of yell syllables varied between males or in different contexts.

Contexts of Yells

Almost half of all yells ($49.2 \pm 7.4\%$, $N=16$ males, 641 yells) from throughout the breeding season were given by males at their mating platforms (where all copulations occurred and where the female laid the clutch). Small proportions of yells were given in response to the female flying off the territory ($6.1 \pm 1.9\%$), comates' yells ($2.6 \pm 1.0\%$), or intrusions by other bronze-winged jacanas ($3.6 \pm 1.0\%$) or pheasant-tailed jacanas, *Hydrophasianus chirurgus* ($5.0 \pm 2.4\%$). We could not detect any obvious stimuli for the remaining yells.

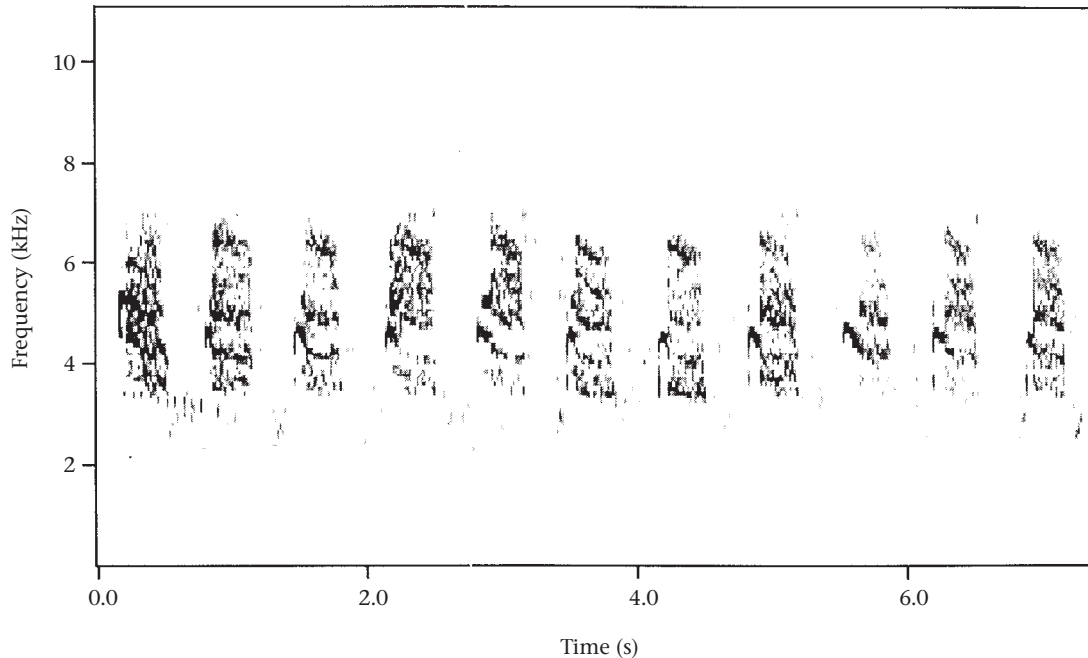


Figure 1. Sonagram of male bronze-winged jacana 'yell' call comprising 11 syllables.

The majority of yells were given when males were not incubating or caring for chicks (see below), so these breeding stages are excluded from the following analyses. Polyandrous males yelled at significantly higher rates when their female mate was on a comate's territory than when she was on the yelling male's territory (Wilcoxon signed-ranks test: $Z = -3.29$, $N=17$, $P=0.001$; Fig. 2a), and monogamous males tended to yell at higher rates on the rare occasions when the female left their territory to forage off the lake, although not significantly so ($Z = -1.69$, $N=8$, $P=0.09$; Fig. 2b). Floaters that settled on territory vacancies or on newly flooded habitat yelled at significantly higher rates before they paired with a female than when the female was off their territory after pairing ($Z = -2.03$, $N=7$, $P=0.042$; Fig. 2c; paired status was defined as when a female consistently foraged with a male, defended his territory, and persistently interacted sexually with him).

When a polyandrous female was on a male's territory, he yelled at significantly higher rates when the female was further away from him (Friedman test: $\chi^2_2=12.9$, $P=0.002$; Fig. 3a). When the female was on a comate's territory, males yelled at significantly higher rates when she was closer to the comate ($\chi^2_2=6.9$, $P=0.032$; Fig. 3b). Presumably males could see how close the female was to comates on adjacent territories because of the relatively two-dimensional nature of the habitat.

Considering all instances when a polyandrous female flew from the territory of one of her mates (male 1) to another's (male 2), male 2 was significantly more likely to yell in the minute before she flew than male 1 (Wilcoxon signed-ranks test: $Z = -2.37$, $N=7$, $P=0.018$; Fig. 4). Male 2 was significantly less likely to yell once the female had arrived on his territory than before she flew ($Z = -2.37$,

$N=7$, $P=0.018$; Fig. 4), and male 1 was significantly more likely to yell than male 2 during the minute after the female landed ($Z = -2.02$, $N=7$, $P=0.043$; Fig. 4).

Males in larger harems yelled at significantly higher rates (Kruskal-Wallis test: $H_2=6.47$, $P=0.039$; Fig. 5). Matched comparisons of males that occurred in more than one size of harem showed that individual males yelled at significantly higher rates in larger harems (Wilcoxon signed-ranks test: $Z = -2.50$, $N=10$, $P=0.013$).

Males that received the clutch ('receivers') yelled at significantly lower rates when they were incubating eggs or caring for chicks (up to 70 days after hatching) than during the prelaying and laying periods (Wilcoxon signed-ranks test: $Z = -1.99$, $N=6$, $P=0.046$), whereas the comates ('nonreceivers') showed no difference in yell rates during these periods ($Z = -0.27$, $N=6$, $P=0.78$), and yelled at significantly higher rates than receivers during the egg and chick periods ($Z = -2.80$, $N=12$ receivers, 6 nonreceivers, $P=0.0051$).

The rate at which males yelled when the female was off their territory, the mean duration of yells and the number of syllables/s were not significantly positively correlated with body mass (Spearman rank correlations: $N=23$ males for yell rates, 16 males for yell duration and syllable frequency, $P_s=0.30-0.83$, data from incubation and chick care stages were excluded). However, as yelling behaviour was related to breeding stage and harem size, these may be confounding variables. In tests on a restricted sample of polyandrous males during the period from day -10 to day $+2$ (when yells were given at the highest rates; day 0 is the day the first egg was laid) the rate at which yells were given when the female was off the territory tended to increase with body mass, although not significantly so (Spearman rank correlation: $r_s=0.67$, $N=8$, $P=0.078$), and

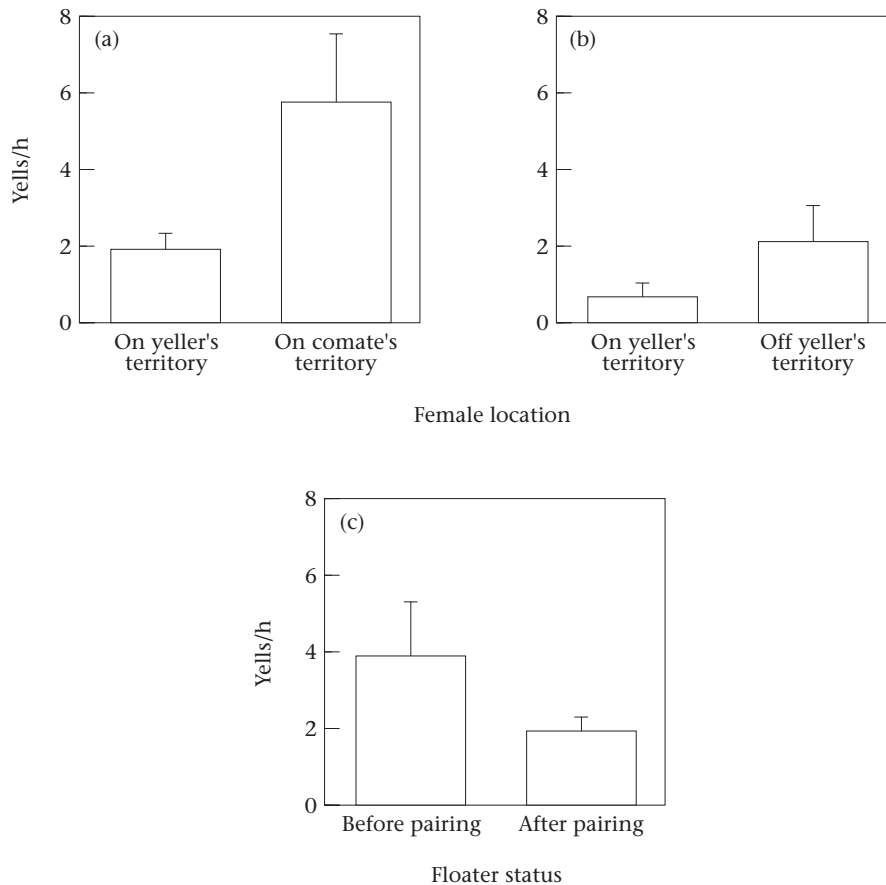


Figure 2. Rates of yells given by (a) polyandrous males when their female mate was on the yeller's or a comate's territory ($N=17$ males), (b) monogamous males when the female was on or off the yeller's territory ($N=8$ males), and (c) settling floaters before pairing with a female and after pairing when the female was off the yeller's territory ($N=7$ males). Bars show $\bar{X} \pm \text{SE}$.

the mean duration of yells was significantly positively correlated with body mass ($r_s=0.70$, $N=8$, $P=0.048$).

In the experiments in which we removed resident females in order to induce take-overs by neighbouring or settling females, males yelled at significantly higher rates when alone during the take-over period than before or after (Friedman test: $\chi^2_2=6.69$, $P=0.035$; Fig. 6), and the rate of yells given when a female was on the territory tended to be greater during the take-over period, although not significantly so ($\chi^2_2=5.03$, $P=0.081$; Fig. 6).

Did Natural Yells Attract Females?

When a female was on the territory of the yelling male but more than 20 m from him, she flew over to him in $33.5 \pm 9.3\%$ of cases. When the female was on a comate's territory, she flew to the yelling male in $42.4 \pm 15.3\%$ of cases. For nine males for which we had sufficient data, the yells to which females responded averaged longer (29.6 ± 3.7 s) than those to which females did not (18.0 ± 4.3 s), but this difference was not quite significant (Wilcoxon signed-ranks test: $Z = -1.82$, $N=9$, $P=0.069$). Females were significantly more likely to respond to bouts of yells (defined as at least three yells given within a 5-min period) than to single yells ($61.2 \pm 9.0\%$ of bouts

versus $27.3 \pm 4.7\%$ of single yells provoked the female to fly to the yeller's territory; $Z = -2.83$, $N=7$, $P=0.005$).

The rate of intrusions by females, but not males, tended to correlate positively with the yell rate of male territory owners, although not significantly so (Spearman rank correlations: females: $r_s=0.50$, $N=16$, $P=0.054$; males: $r_s=0.32$, $N=16$, $P=0.21$, excluding data from incubation/chick care stages, and excluding monogamous males that had significantly larger territories and therefore tended to have higher background rates of intrusions; see Butchart 1998; Mann-Whitney U test for intrusion rates: $Z = -1.86$, $N=5$ monogamous and 16 polyandrous males, $P=0.062$).

Did Yell Playbacks Attract Females?

Females spent significantly more time alert during the playback period than during the control periods (Friedman test: $\chi^2_2=9.0$, $P=0.011$; Fig. 7a), and they were more likely to fly from a comate's territory to the playback territory during playback than during control periods ($\chi^2_2=9.30$, $P=0.009$; Fig. 7b). The mean latency of response was 9.9 ± 2.0 min, and some females responded within 30 s of the start of the playback and flew up to 180 m to the loudspeaker. The playback male spent

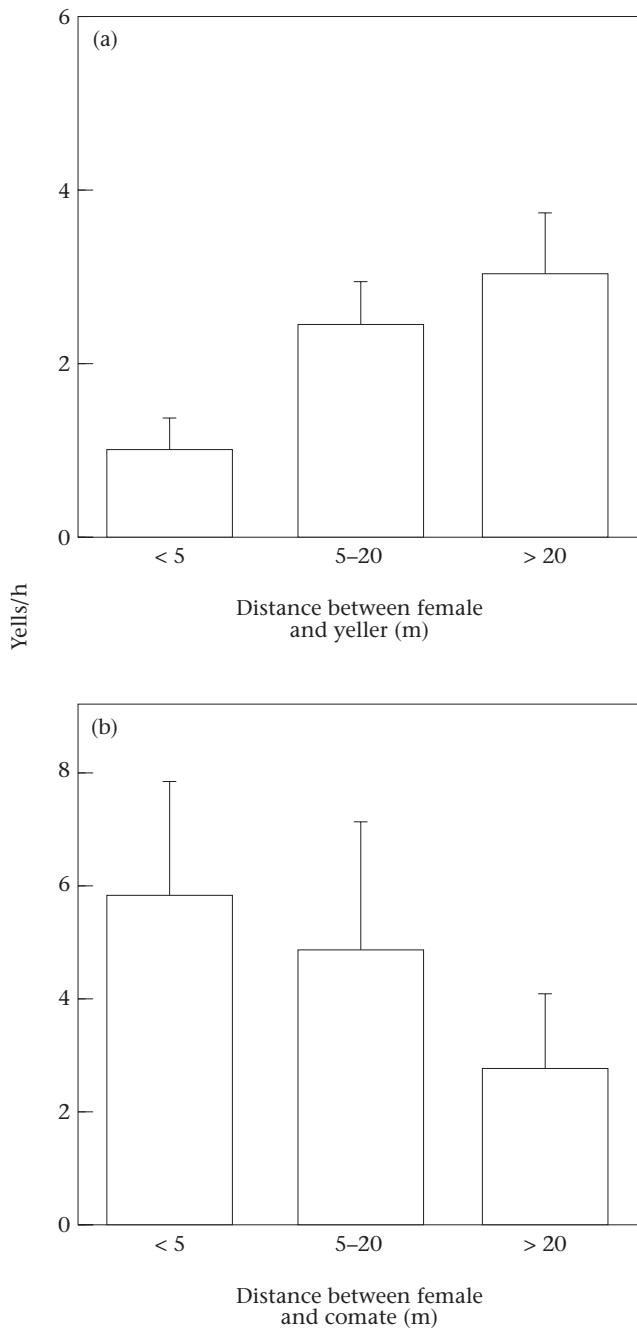


Figure 3. Rates of yells given by polyandrous males when their female mate was (a) on the yeller's territory at different distances to the yeller, and (b) on a comate's territory at different distances to the comate. Bars show $\bar{X} + SE$, $N=17$ males.

significantly more time alert during the playback than the control periods (Friedman test: $\chi^2_2=16.5$, $P=0.0003$), but he was no more likely to yell in response to playback of his own yell ($\chi^2_2=0.62$, $P=0.73$). As he remained on his territory throughout the trial, a limitation of this experiment is that the female may have responded to the male's behaviour rather than to the yell playback. However, in 86.7% of cases ($N=15$) the female flew directly to the loudspeaker rather than to the male, and in a further six cases the male was too close to the loudspeaker to

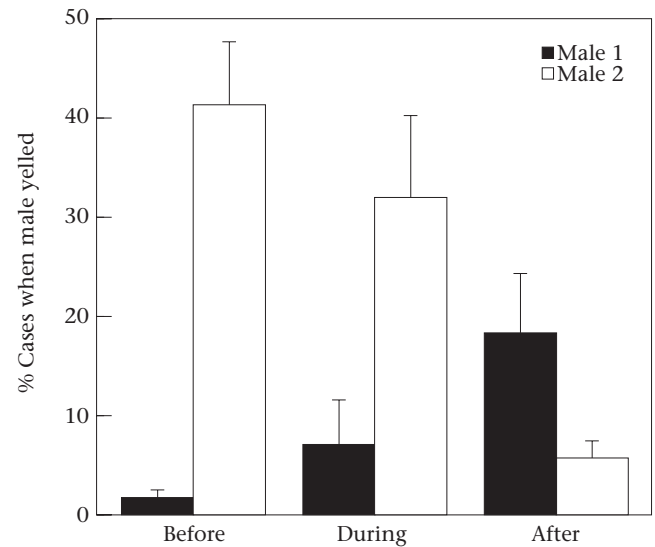


Figure 4. Percentage of cases when males yelled in the 60 s before, during and the 60 s after a polyandrous female flew from one of her males' territory ('male 1', $N=7$) to another's ('male 2', $N=7$).

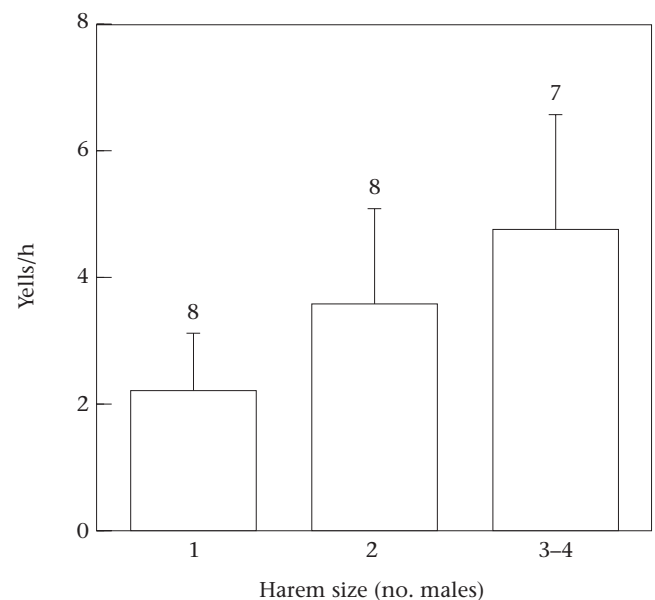


Figure 5. Rates of yells given by males in different sized harems. One randomly selected harem size and yell rate was used for each male for which there were data for more than one harem size. Data were pooled for harem sizes of three and four because there were too few data to consider these separately. Bars show $\bar{X} + SE$ yell rates when the female was off the territory; sample sizes are given above the error bars.

distinguish whether the male or the playback attracted the female. An additional trial was carried out 4 h after a male was removed as part of a series of male removal experiments (Butchart et al., in press). In this case, the female responded after 9 min of playback by flying directly to the loudspeaker. These results suggest that females flew in response to the yell playback rather than to male behaviour.

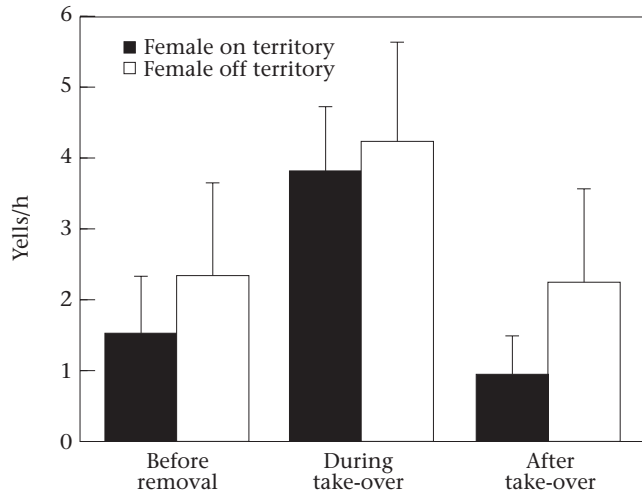


Figure 6. Rates of yells given by males before, during and after take-overs induced by experimental removals of their female mates. The data were from focal watches carried out during the week prior to the female removal ('before'), during the period after removal up to and including the first 2 days the newcomer intruded on to the territory ('during'), and 1–2 weeks after take-over by the new female ('after'). Four out of 10 males were retaken by their original mates who returned within a week of the removal. For these males the data for the 'after' category are from 1–2 weeks after their original mates retook them. Bars show $\bar{X} \pm SE$, $N=10$ males.

Comates of the playback male spent significantly more time alert during the playback period than during the control periods (Friedman test: $\chi^2_2=10.5$, $P=0.005$), but did not yell significantly more frequently during the playback ($\chi^2_2=1.59$, $P=0.45$). The rate of intrusions by males did not vary through the course of the playback experiments (Friedman test: $\chi^2_2=0.87$, $P=0.65$; Fig. 8a), but females were significantly more likely to intrude on to the playback male's territory during playback than during the control periods ($\chi^2_2=9.50$, $P=0.009$; Fig. 8b), and occasionally approached the loudspeaker to within 1.5 m.

Did Females Copulate with Yelling Males?

Although only a low percentage of all yells ($7.2 \pm 2.2\%$, $N=16$ males) were immediately followed by solicits or copulations between the yeller and the female, $45.0 \pm 4.9\%$ of sexual interactions and $38.1 \pm 4.3\%$ of copulations ($N=12$ females) were preceded by yells from the male. Considering cases where females responded to male yells by flying to them, $43.9 \pm 8.4\%$ ($N=14$ males) of such yells were then followed by sexual interactions within 10 min. Within polyandrous groups the males that yelled at the highest rates when the female was off their territory during the prelaying and laying periods received the most copulations: when males were ranked within harems for their mean yell rate and mean copulation rate, these ranks were significantly positively correlated with each other (Spearman rank correlation: $r_s=0.87$, $N=14$, $P=0.002$, using mean ranks for three males each of which occurred in two different harems in different years). In three out of four cases for which data

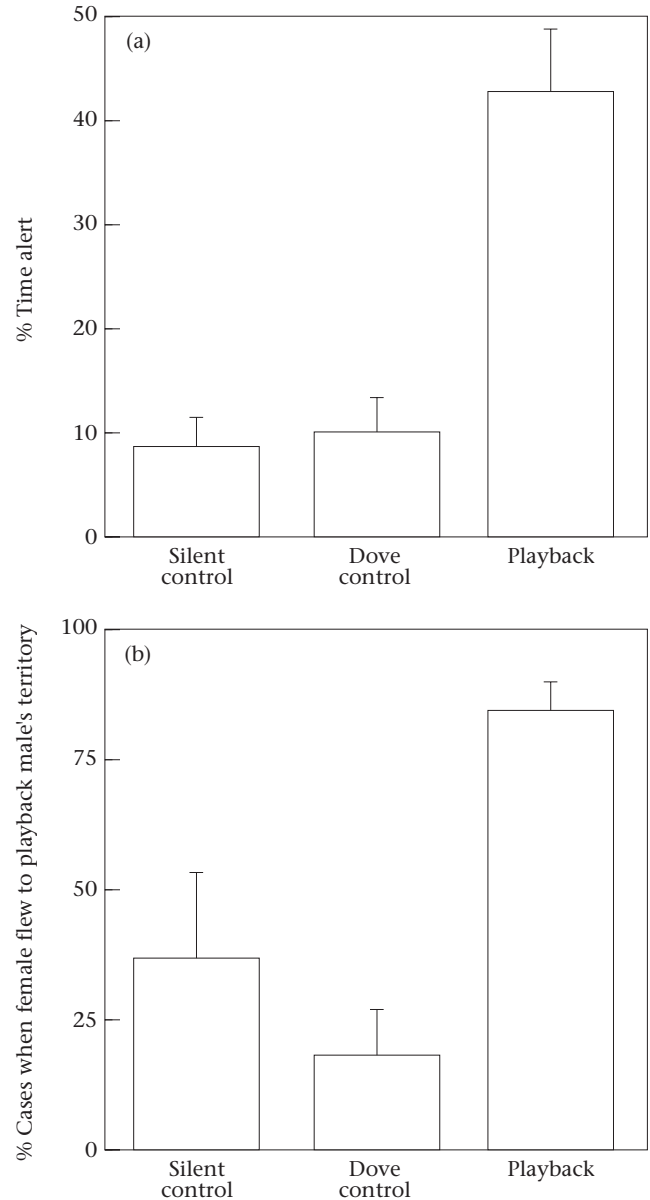


Figure 7. Responses of females to playback of the yell of one of their male mates: (a) percentage time spent alert, and (b) percentage of cases when the female flew from a comate's territory to the playback territory. Bars show $\bar{X} \pm SE$, $N=6$ females.

were available, the female laid the clutch for the male that had the highest mean yell rate and the longest mean yell duration during the prelaying period.

DISCUSSION

Female bronze-winged jacanas usually spent time and copulated with each of the males in their harem before laying a clutch for one of them. How did these males attempt to maximize their share of copulations with the female? Males were unable to monopolize access to their female mate by preventing her from visiting a comate's territory or by physically forcing her to return. Instead, observations and experiments suggested that males in

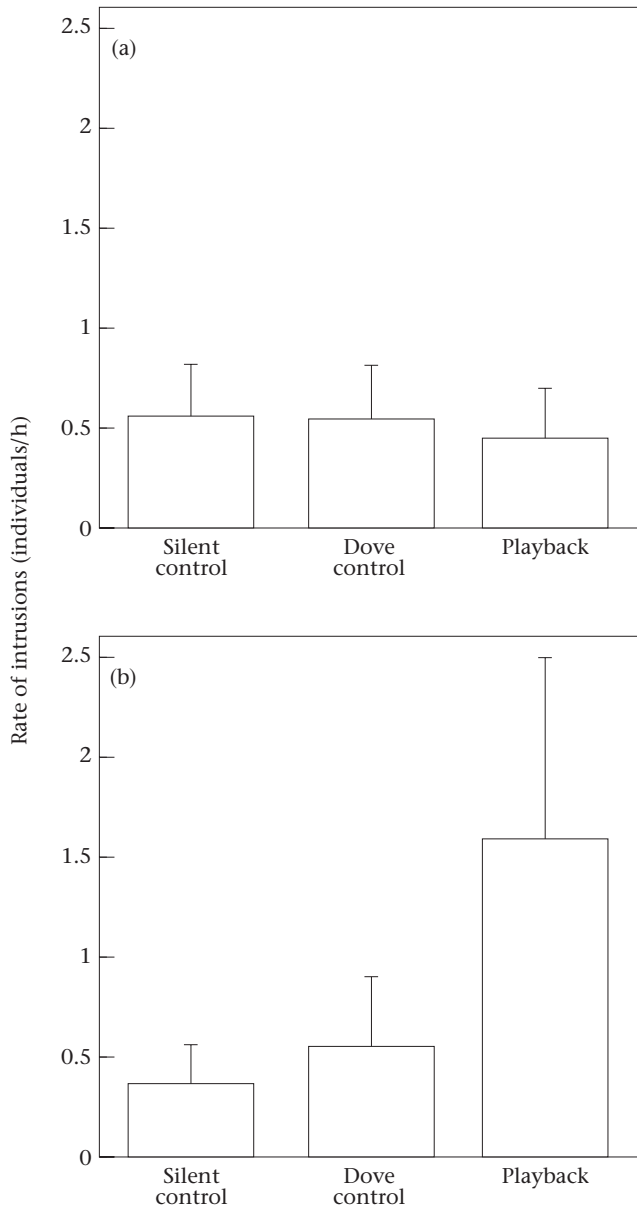


Figure 8. The rate of intrusions by (a) males, and (b) females on to the playback territory during different stages of the playback experiments. Bars show $\bar{X} \pm SE$, $N=12$ male territories.

polyandrous harems competed for sexual access to the female by giving a distinctive call (the yell) which attracted the female.

In What Contexts did Males Yell?

Males yelled at the highest rates when they did not have access to the female and when there was a risk that she might have been copulating with other males, for example, when the female was on a comate's territory, further from the yeller, or closer to the comate. Furthermore, monogamous males tended to yell at higher rates when the female foraged off the territory where she might have had access to other males. When polyandrous

females flew between territories of two comates they were more likely to fly to a yelling male than from a yelling male. Males tended to cease yelling once the female had arrived on their territory, but the male who was left alone was significantly more likely to yell after the female had left his territory. These data support the idea that polyandrous males yelled to attract the female to their territory from a comate's territory.

Males yelled at higher rates in larger harems (this was significant for both between-individual and within-individual comparisons). This would be expected if males compete for female access by yelling, because in larger harems females have to divide their time between more males. Males that received the clutch virtually ceased yelling on the day the last egg was laid (when there were no further eggs to fertilize), and yelled at significantly lower rates during the incubation and chick care periods (when they did not copulate with the female). Non-receivers continued to copulate with the female during these periods whilst she prepared to lay the next clutch, and they did not reduce their rate of yelling after the clutch was laid. These results, together with the observation that nearly half of all yells were given by males at their mating platforms (where virtually all sexual behaviour took place), strongly support the idea that males yell to gain sexual access to the female.

Settling floaters yelled at significantly higher rates before pairing than afterwards, suggesting that yells may be used by unpaired males to attract a mate. Furthermore, during female removal experiments, males yelled at higher rates when they were alone after their female had been removed and before they were taken over by a replacement female than before the removal or after take-over, as would be expected if yells function in this circumstance to attract females.

How did Females Respond to Male Yells?

Yells attracted females when they were on comates' territories or on the yeller's territory but greater than 20 m from him. Furthermore, during playback experiments females responded to recordings of a male mate's yells by flying to the loudspeaker. If the yell is a signal that attracts the female then a higher-intensity signal should be more likely to provoke a response. As predicted, females tended to be more likely to respond to longer yells, and they were significantly more likely to respond to bouts of yelling.

As predicted from the hypothesis that males yelled to attract the female in order to increase their share of sexual access, copulations often followed yelling. Within polyandrous groups the males that yelled at the highest rates received the most copulations, which supports the idea that males compete with their comates for sexual access to the female by yelling.

In polygynandrous alpine accentors, *Prunella collaris*, females sing to attract males during their fertile period, and they sing at higher rates when alone. Males approach singing females, which often solicit copulations as soon as the male arrives (Langmore et al. 1996). Congeneric

dunnoek, *P. modularis*, females in polyandrous or polygynandrous groups also compete for males by giving trill calls and occasionally complex songs when they are left alone by their mate during the prebreeding and fertile periods (Langmore & Davies 1997). In both species, females that have to compete for sexual access to males use vocalizations to attract them when they are left alone. Similarly, polyandrous male jacanas, which compete for sexual access to the female, yell to attract her when they are left alone.

Are Yells Costly to Males and Females?

Yells may be honest signals of male quality because heavier males tended to yell at higher rates and produced significantly longer yells. One potential cost of yelling is that it may attract predators. The only predation attempt we witnessed was by a female shikra hawk, *Accipiter badius*, which attacked a yelling male jacana.

Females may be forced to respond to the yells of their male mates in order to defend their territory, because yells may attract female intruders which may attempt to take over the male. These intruders might use yelling as a signal of the presence of a male whose female is not responding to his yells (males were significantly less likely to yell once their mate had flown to them) and who is available to care for a clutch (males incubating eggs or caring for chicks yelled at significantly lower rates). Female, but not male, intruders were attracted when we played back a male's yell, and males that had higher mean yell rates tended to attract more female intruders on to their territory. This was unlikely to be because males occasionally apparently responded to intruders by yelling, as only 5% of female intruders provoked yells.

Female song in bay wrens, *Thryothorus nigricapillus*, attracts males, and males sing in response to their mate to form an antiphonal duet, probably in order to guard their mates acoustically from other males (Levin 1996). In both bay wrens and jacanas, the costs of not responding to a mate's calls may be the threat of intruders, which might carry out extrapair copulations in wrens and take over the mate in jacanas.

How do Males Benefit from Yelling?

Males may gain at least two nonexclusive advantages from attracting the female on to their territory. First, if yelling increases a male's sexual access to his mate, he may gain an increased share of the paternity in the next clutch she lays. Females may allocate paternity and clutches by using the rate at which males yell in order to assess their quality. Second, males may attempt to limit the size of the harem by attracting the female to their territory for a larger proportion of time. A female has to spend time on the territory of each male in her harem in order to defend it from other females. An upper limit on harem size may be placed by a female's ability to defend multiple males' territories (Butchart et al., in press). Males might benefit from limiting harem size because male reproductive success may be lower in larger harems

(wattled jacana males have to wait significantly longer to receive a clutch in larger harems, Wrege & Emlen 1998).

Alternative Functions for Yells

There are at least four nonexclusive alternative functions for yells: they may be used in territory defence, for maintaining the pair bond, coordinating the activities of comates, or for establishing a male dominance hierarchy, but none of these possibilities seems likely.

(1) Vocalizations in many bird species have been hypothesized to function in territory defence (Catchpole 1982; Kroodsma & Byers 1991; Catchpole & Slater 1995). However, a territorial function for yells would not explain why polyandrous males yell at higher rates than monogamous males, because male territory size is constrained by both neighbouring males and comates, and males do not simply divide up female territories (Butchart et al., in press). Furthermore if yells only advertise territory ownership to other males, then this does not explain why males yelled at higher rates when the female was further away from them, and when she was closer to a comate. Finally the territoriality hypothesis does not explain why nearly half of all yells were given at mating platforms, as these are used solely for sexual interactions, they are unlikely to be a limited resource, and they do not play any part in territory ownership (Butchart 1998). Males defended their territories using hoverflights and direct aggression, and yelled at only $5.4 \pm 1.8\%$ of intruders ($N=16$ males). Females responded to 29% of these yells by helping to evict the intruder, but as only 3.6% of all yells were given in these contexts, it seems unlikely that territory defence is a major function of yelling.

(2) Yells may be a form of cooperative communication between males and females, for example, to increase female vigilance and defence of the nest. In red-winged blackbirds, *Agelaius phoeniceus*, female 'chit' calls may encourage nest defence by males (Yasukawa 1989). The benefit of this should be greatest during the incubation and chick care periods, but male jacanas yelled at the highest rates during the prelaying and laying stages, and virtually ceased yelling during incubation and whilst caring for chicks.

(3) Yelling may serve to coordinate the activities of comates nesting on the same female territory. Beletsky & Orians (1985) suggested that 'chit' calls by female red-winged blackbirds in polyandrous males' harems may help to coordinate vigilance and nest defence, or communicate information about the location of profitable foraging areas (Yasukawa et al. 1987). However, this function is unlikely to apply to male jacana yells, because males defended exclusive territories in which they fed and nested separately from their comates.

(4) Yells may be used to defend a male's status within polyandrous harems. Yasukawa & Searcy (1982) proposed that the 'teer' call of female red-winged blackbirds functioned to defend their rank in the harem (and thus to defend their priority to resources in the male's territory, or to male assistance in feeding young). However, we found no evidence for a male status hierarchy within harems, males foraged in separate territories and carried

out parental care alone, and they did not engage in bouts of counter-yelling with comates, so this hypothesized function for yelling seems implausible.

Conclusion

The pattern and contexts of yelling, and the results of removal and playback experiments, all supported the hypothesis that males compete for sexual access to the female by yelling, and that females respond to yells by approaching the yeller, and by giving most copulations to the male in the harem that yells at the highest rate. Females may respond to male yells because yells attract female intruders which might attempt to take over the territory. Females may use yells to assess male quality, and males may benefit from attracting the female by gaining an increased share of paternity, by receiving the clutch, or by limiting harem size. High levels of sperm competition in bronze-winged jacanas may have favoured acoustic competition for sexual access to females because conventional forms of mate guarding are ineffective.

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