Coordination between the sexes for territorial defence in a duetting fairy-wren

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In territorial songbirds both sexes depend on possession of a territory, yet its defence is traditionally regarded as the domain of male birds. Studies on duetting species have examined both male and female roles in territorial defence, often focusing on potential reproductive conflict between the pair members. Surprisingly, interactions between defending partner members are rarely investigated. We combined observations on undisturbed pairs of purple-crowned fairy-wrens, *Malurus coronatus*, with experimental simulation of a strong territorial threat to quantify coordination between partners during territorial defence. Pairs formed strongly cohesive partnerships: males and females naturally spent a high proportion of time close together (75% within 5 m) in dense riparian habitat, and coordinated half their songs to form duets. Partners that spent more time close together also coordinated more of their songs to form duets. When we presented playback simulating paired intruders, females responded as aggressively as males. Intensity of approach to the playback speaker was highly correlated within pairs. Spatial coordination between partners increased dramatically when they responded to simulated intrusion so that they spent virtually all their time within 2 m of one another, and most of the songs they sang were coordinated to form duets. We conclude that the highly coordinated vocal and approach responses of male and female purple-crowned fairy-wrens to simulated intrusion in the nonbreeding season are not coincidental, or a consequence of sexual conflict over mating, but instead are likely to represent cooperative territorial defence of a valuable shared resource.
et al. 2007), although the effect of simulated intrusion on proximity between partners has not been quantified. Few studies have quantified distance between partners during playback (Marshall-Ball & Slater 2004; Marshall-Ball et al. 2006; Molles & Waas 2006), and only one study has reported these distances (Logue & Gammon 2004). We addressed this lack of information on the nature and extent of coordinated defence by quantifying both duetting and proximity between partners when they were undisturbed by intruders as well as during intrusion, and we tested three hypotheses for the coordination of vocalizations and approach. If coordination in duetting species is an incidental by-product of territorial defence against same-sex individuals (Morton 1996), then male and female responses to a territorial threat should be independent of one another. If coordination is a consequence of sexual conflict over mating (guarding patriarchy, Hall & Magrath 2000; Gill et al. 2005) then females should sing to attract males and their partners should attempt to repel rivals and guard females by joining in to form a duet and following the female closely. If coordination is a consequence of cooperative territorial defence (Wiley & Wiley 1977), then vocal and approach responses to a strong territorial threat will be highly coordinated.

We studied female and male territorial roles as well as coordination of defence in the purple-crowned fairy-wren, *Malurus coronatus*, a duetting species found only in the tropics of Australia (Rowley & Russell 1997). Since duetting may function in pair bond maintenance, mate guarding or guarding patterns in addition to territorial defence (Hall 2004), and since species in the genus *Malurus* have among the highest rates of extrapair paternity in birds (Mulder et al. 1994; Karubian 2002; Webster et al. 2004), territorial behaviour may be influenced by high levels of sexual conflict. Playback experiments on duetting species are usually conducted during the breeding season when intrusion elicits both territorial and mate-guarding responses, making it challenging to distinguish between them (Hall 2004). To allow us to investigate territorial behaviour independently of confounding effects, we minimized the potential for sexual conflict over mating by conducting the experiment late in the dry season when the birds were not breeding. To simulate an intense territorial threat and minimal threat to the pair bond or paternity, we avoided simulating unpaired intruders by using playback of duets rather than solo songs. In addition to the simulated intrusion, we monitored coordination between males and females when birds were undisturbed, since comparison against a well-established baseline allows for strong inference from experimental behaviour.

**METHODS**

**Study Species**

Purple-crowned fairy-wrens are riparian specialists of the tropical north of Australia (Rowley 1993). They belong to the family Maluridae (Corvida), and are unrelated to troglobytid wrens (Passerida) on which many duetting studies have been conducted. From July 2005 we studied a population resident on Annie Creek and the Adcock River in the Australian Wildlife Conservancy’s Mornington Wildlife Sanctuary (17°31’S, 26°6’E). Birds were captured with mist nets (under licence from the Australian Bird and Bat Banding Scheme Banding Authority and the Western Australia Department of Conservation and Land Management), and marked with a metal ABBBS band and a unique combination of coloured leg bands for individual recognition. Like other *Malurus* species, purple-crowned fairy-wrens are seasonally sexually dichromatic and live in groups: breeding pairs often share their territory with male or female subordinate ‘helpers’ (Rowley & Russell 1997). Groups occupy territories that are usually arranged linearly along creeks and riversides (Rowley & Russell 1993). We mapped territories by censusing individuals weekly. Groups maintained their territories year-round: at no time did territory boundaries break down or groups join to form flocks (personal observation). Both sexes sing and breeding partners overlap their songs to form duets (Rowley & Russell 1997). Solo songs take the form of a ‘reel’ where individuals repeat a phrase multiple times. Duets are formed when one individual overlaps its partner’s reel with its own, and elements within the phrases of the two birds overlap in both time and frequency rather than alternating (Fig. 1). Only the breeding pair duet (Rowley & Russell 1993), but dense habitat limited our ability to identify the sex of singers and determine the individual singing strategies resulting in duets. Nevertheless, we observed both males and females initiating duets and singing solo songs. Such observations could be biased by sex differences in detectability, although females did not seem harder than males to detect, and observations on the percentage of time that birds spent in cover suggested no significant difference between the sexes (unpublished data). For the current study, we focused our observations on the dominant (breeding) pair in each group, conducting baseline behavioural observations between 16 September and 25 November 2005 and playback experiments from 4 to 25 November, well before nesting started in January 2006.

**Baseline Observations**

To obtain baseline values for coordination between partners, we conducted 1 h focal observations on 26 pairs (with 0–5 subordinates, mean = 1.7) to determine the percentage of time undisturbed partners spent close together and the percentage of their songs sung in duet. All songs (duets and solos) sung by pairs during the focal observation were noted. Where possible, the sex of the initiating bird was identified to examine individual singing strategies. Since duets result from the behaviour of the ‘answering’ partner, two kinds of song rate were calculated for each sex. ‘Song initiation’ rates included all songs initiated independently of the partner (e.g. female song initiation rate = female solo songs + female-initiated duets). ‘Answering’ rates reflected responsiveness to a partner’s songs, that is, the percentage of the partner’s songs that were overlapped to form a duet (e.g. female answering rate = 100 × male-initiated duets/(male solo songs + male-initiated duets)).
For each 1 min period in the focal observation, the minimum distance between partners was estimated with the following categories: <0.5 m, 0.5–2 m, 2–5 m, 5–10 m, >10 m. Because of limited visibility in dense riparian habitat, we could not estimate the distance between partners in all 1 min intervals. We observed each pair for three to six 1 h watches and pooled the data to give a mean of 102 known intervals per pair (range 61–154), representing 33% of the total observation time (range: 18–48%). Intervals where distance apart was unknown were excluded for calculating the percentage of time that partners were close together. Estimates of time spent close together could be inflated if detectability is higher when partners are close. Consistent with this, pairs that were harder to observe (lower percentage of known intervals) had higher percentages of time close together, but the negative correlation was not statistically significant (with 2 m as threshold: Pearson correlation: $r_{24} = -0.20$, $P = 0.34$; with 5 m as threshold (non-normal distribution): Spearman correlation: $r_S = -0.29$, $N = 26$ pairs, $P = 0.15$). Single observers conducted these observations to minimize disturbance to the birds that might influence their behaviour.

**Playback Experiment**

We conducted playback trials to quantify male and female roles in defence and to assess the nature and extent of coordination between partners responding to simulated intrusion. The trials were conducted on 23 pairs (with 0–5 subordinates, mean = 1.8). Each trial comprised a 5 min preplayback period, a 1.5 min playback period, and a 5 min postplayback period. During the playback period, we broadcast a duet four times at intervals of about 20 s (mean length of stimulus duets ± SE = 5.3 ± 0.2 s). The duets used for playback stimuli were high-quality recordings selected from 22 local pairs not adjacent to the subjects. Five duets were initiated by males, four by females, and the initiator was unknown for the remainder owing to low visibility in the habitat and the fact that duets are often initiated at very low amplitude (Fig. 1). Recordings were made with a Marantz PMD 660 recorder and Sennheiser ME67 microphone. Noise was filtered out with the cursor-delimited filter in Syrinx PC (syrinxpc.com, J. Burt), songs were amplified to the same peak amplitude, and the duet pasted four times to create 90 s stimulus files. We broadcast stimulus files from a Dell Latitude D810 laptop to a Radioshack speaker 40-1441, at levels equivalent to natural amplitudes (assessed by comparing recordings from the speaker with recordings of the birds, using the recording equipment described above). The speaker was placed well within territory boundaries, 1–2 m high, and several points 10 m from the speaker were marked with flagging tape to facilitate distance estimation. We played duet songs through a single speaker because male and female notes are overlapping and in the same frequency range (Fig. 1). Natural duets therefore cannot be separated with sound analysis software into male and female parts to allow broadcasting through separate speakers (‘stereo duet playback’, Logue & Gammon 2004; Rogers et al. 2004).

We recorded vocal responses throughout the trial, and voice comments on approach responses, with a Marantz PMD 660 recorder and Sennheiser ME67 and MKH416 T

![Figure 1. Sonagrams illustrating the structure of purple-crowned fairy-wren duets. (a) Male and (b) female each repeat a phrase, (c) overlapping one another in time and frequency to form (d) a long duet.](image-url)
microphones. Because responses continued after playback ended and vocalization rates were low, response variables were quantified for playback and postplayback periods combined. We quantified three measures of individual response intensity for males and females: (1) latency = time to first entry in 10 m radius (s); (2) closest approach = closest approach to speaker (m); (3) time close = percentage of time spent within 10 m of speaker. We quantified the intensity of the pair’s vocal response as the total number of songs sung, and of each sex as their ‘song initiation rate’. The extent of coordination between partners was quantified as the percentage of time spent close together, the percentage of the pair’s songs that were duets, and the ‘answering rate’ of each sex. We quantified the time partners spent close together by dividing the playback period into three 30 s intervals and the postplayback period into five 1 min intervals, and recording the shortest distance between partners in each of these eight intervals, if known. The percentage of time spent close together was computed as the percentage of intervals with known minimum distances less than 2 m. One observer conducted the trials to minimize disturbance to the birds, and this short distance allowed the single observer to determine accurately whether partners were close together or not for most of the time (mean % intervals known ± SE = 63.7 ± 6.3, N = 20, excluding three pairs with no data on distance apart: two pairs did not approach and one approached late).

Statistical Analysis

Means are presented ± SE throughout; we used means of pair means so that each pair contributed equally. We used nonparametric methods to analyse variables that were not normalized by standard transformations. Wilcoxon signed-ranks tests were computed with the statistical software Genstat 8.1 (VSN International Ltd., Hemel Hempstead, Hertfordshire, U.K.); we report the test statistic, \( T \) (the lowest rank sum), and the corrected \( N \) (tied pairs excluded). We used JMP (SAS Institute Inc., Cary, NC, U.S.A.) for all other analyses. All statistical tests are two tailed.

RESULTS

Baseline Coordination between Males and Females

In 34 ± 2.8% of observations, purple-crowned fairy-wren partners were within 2 m of one another, and they were within 5 m of one another in 75 ± 3.4% of observations (\( N = 26 \) pairs). Pairs sang both duets and solo songs, averaging 3.25 ± 0.20 songs/h. Duets comprised 45.8 ± 4.1% of all songs sung (mean number of songs per pair = 16.8, range: 6–25). Partners that spent more time within 2 m of one another also coordinated a higher percentage of their songs to form duets (Fig. 2).

Males were more vocal than females (Fig. 3a), based on the 26 ± 2.8% of songs per pair where sex of the singer was identified (mean number of known songs per pair = 4.4, range 0–13, \( N = 26 \) pairs). Males initiated more duets than females (males: 0.22 ± 0.05 duets/h; females: 0.07 ± 0.03 duets/h; Wilcoxon signed-ranks test: \( T = 16.5, N = 16, P = 0.007 \); Fig. 3a), and also sang more solo songs than females (males: 0.41 ± 0.09 solos/h; females: 0.16 ± 0.06 solos/h; \( T = 29.0, N = 17, P = 0.02 \); Fig. 3a). Females initiated 22 ± 5.5% of all solos and duets where the initiator was known (\( N = 25 \) pairs with at least 1 known song) and ‘answered’ 40 ± 8.2% of male song initiations to form duets (\( N = 25 \) pairs with at least one male-initiated song), while males answered 32 ± 12.4% of female song initiations (\( N = 12 \) pairs with at least one female-initiated song).

Intensity of Male and Female Territorial Responses

Simulated intrusion elicited close approach and song by the dominant pair, and approach by some group members. Playback elicited approach by 21 of 23 dominant males (91%) and 20 of 23 dominant females (87%). How long birds took to approach within 10 m of the speaker was unrelated to how closely they approached (Spearman correlation: males: \( r_s = 0.25, P = 0.28 \); females: \( r_s = 0.14, P = 0.54 \), but birds that approached closest to the speaker also spent more time close to it (Spearman correlation: males: \( r_s = -0.64, P = 0.001 \); females: \( r_s = -0.57, P = 0.007 \)). Males and females responded with equally intense approach to the playback speaker, entering a 10 m radius around the speaker within about 40 s of the start of playback, approaching to about 2 m of the speaker, and remaining within a 10 m radius of the speaker for just over half of the playback and postplayback period (Table 1). Simulated intrusion caused a significant increase in pair song rate (songs per 5 min in preplayback: 0.17 ± 0.08; playback: 5.07 ± 0.62; postplayback: 1.35 ± 0.24; Friedman test: \( \chi^2 = 30.0, P < 0.001 \)). Pairs sang 2.87 ± 0.32 (range: 0–6) songs during the playback and postplayback periods combined (equivalent to a rate of 26.5 songs/h, \( N = 23 \) pairs). In 14 of 18 (78%) pairs with
To compare the response intensity of males and females, we used a Wilcoxon signed-ranks test for latency (transformation did not normalize this distribution) and paired t tests for time close together and closest approach. In a third case a subordinate approached the speaker closely alone, then left and returned with the rest of the group.

### Coordination of Male and Female Territorial Responses

The intensities of male and female responses were highly correlated within pairs in all three measures of approach behaviour (Fig. 4). Furthermore, partners closely coordinated their approach (Fig. 5) and vocal responses. Partners were within 2 m of one another in 100% of known intervals in 18 of 20 pairs (excluding two pairs that did not approach and one that approached late). This represented significantly more time close together than during baseline observations (Wilcoxon signed-ranks test: $T = 3$, $N = 20$, $P < 0.001$, pairs with data from both baseline and experiment; Fig. 6). Partners coordinated $74 \pm 6.4\%$ of their songs to form duets ($N = 21$ pairs that sang). Nine pairs sang exclusively duets, and the only pair singing no duets was the one where the female did not approach. The percentage of songs sung as duets during the playback and postplayback period was thus significantly higher than during baseline observations (Wilcoxon signed-ranks test: $Z = 22$, $N = 21$, $P < 0.001$, pairs with data from both baseline and experiment).

We examined sex differences in vocal behaviour during playback and postplayback periods using the 25 ± 6.6% songs per pair where sex of the singer was identified (Fig. 3b; mean number of known songs per pair = 0.78, range 0–3, $N = 23$ pairs). Based on this limited sample size, male-initiated duets were more common than female-initiated duets (males: 0.39 ± 0.12 duets during and after playback; females: 0.04 ± 0.04 duets; Wilcoxon signed-ranks test: $T = 4.5$, $N = 9$, $P = 0.04$), whereas male and female solo songs were equally common (males: 0.22 ± 0.13 solos; females: 0.13 ± 0.07 solos; $T = 7.5$, $N = 6$, $P = 0.81$). Females initiated 21.2 ± 12.1% of known songs ($N = 11$ pairs with at least one known song), similar to baseline observations ($T = 17.0$, $N = 8$ pairs, $P = 0.83$). Females responded to 76 ± 12.8% of male song initiations ($N = 9$ pairs with at least one male-initiated song), a non-significant trend to increase their answer rate from baseline levels ($T = 1.0$, $N = 6$ pairs, $P = 0.06$). Males responded to 17 ± 16.7% of female song initiations ($N = 3$ pairs with at least one female-initiated song; the small sample size did not allow statistical comparison with baseline observations).

Neither the proportion of time that partners spent close together nor the proportion of their songs that were duets during baseline observations was related to any measure of response to playback (all $P > 0.3$).

### DISCUSSION

Purple-crowned fairy-wrens formed strongly cohesive partnerships, and partners that spent more time close together also coordinated more of their songs to form duets. Simulated territorial intrusion elicited intense responses from both sexes and a dramatic increase in
within-pair cohesion, so that pair members spent almost all the time within 2 m of one another and coordinated most of their songs to form duets. We argue that this close coordination between partners was neither incidental nor a consequence of conflict between the sexes over mating. Rather, partners appeared to cooperate to defend their territory at a time when sexual conflict was minimal and territory value was likely to be high, although further work is needed to determine whether females guard the partnership as well.

Baseline Coordination between Males and Females

Purple-crowned fairy-wren partnerships were very cohesive, a feature that may distinguish some duetting species from their nonduetting congeners. Both sexes initiated duets and sang solo songs, males were more vocal than females (Fig. 3a), and partners coordinated almost half of their songs to form duets and spent 75% of their time within 5 m of one another. This close proximity of nonbreeding partners exceeded that seen at the peak of mate guarding in many other bird species, including a sister species: superb fairy-wren, Malurus cyaneus, partners spent around 70% of the time within 5 m of one another during the females' fertile period (Mulder 1997). Proximity estimates for nonbreeding superb fairy-wrens are not available, but in a duetting species of tropical antbird (Myrmeciza longipes) partners spent 61% of the time within 5 m of one another during the nonbreeding dry season, whereas in a nonduetting congener (M. exsul) partners spent 19% of the time within 5 m of one another (Stuchbury et al. 2005), suggesting that duetting is associated with high pair cohesion or strong pair bonds (Armstrong 1963).

Undisturbed purple-crowned fairy-wren partners that spent more time close together also coordinated more of their songs to form duets (Fig. 2). One of the earliest functions proposed for duetting was strengthening the pair bond (Armstrong 1963), yet duetting has rarely been compared with independent measures of pair bond strength. In canary-winged parakeets, Brotogeris v. versicolorus, duet rates and intrapair affiliative interactions showed no significant correlation (Arrowood 1988). However, if time spent close together serves as an index of 'pair bond

Figure 4. Within-pair Pearson correlations between male and female approach to playback: (a) latency(s) to approach within 10 m of the playback speaker ($r_{18}=0.89$, $P<0.001$); (b) percentage of time spent within 10 m of the playback speaker ($r_{13}=0.86$, $P<0.001$); and (c) closest approach (m) to the playback speaker ($r_{12}=0.90$, $P<0.001$). Several pairs approached to the same distances, so two pairs are represented by the point indicating the male at 2 m and the female at 1 m, while three pairs are represented by each of the points with both partners at 0.5, 2 and 3 m, respectively.

Figure 5. Paired purple-crowned fairy-wrens responding to playback, illustrating the close proximity maintained between partners responding to a territorial threat. The male has a purple crown, and the female a grey crown.
and responded as aggressively as males to territorial fairy-wrens, females also participated in territorial defence well as when responding to territorial threats. In superb tiated just over one-fifth of all songs when undisturbed as response to playback parallelled that of males: females ini- vocal than males, their increase in song initiation rate in closely as males (Table 1) and, although females were less intrusion. They approached the speaker as quickly and subordinate members of their group who also closely ap-

Figure 6. Increase in the percentage of time undisturbed partners spent close together (baseline) when responding to experimentally simulated intrusion.

strength’, then our data are consistent with the idea that duetting is associated with strong pair bonds. It remains to be tested whether duetting confers fitness benefits in terms of partnerships that last longer or have higher repro-
ductive success (Wickler 1980).

Alternative or additional benefits of maintaining close proximity could be the facilitation of quicker or more coordinated responses to territorial threats. However, we found no evidence that baseline proximity predicted any measure of response to playback. Close proximity increases the threat level of a joint territorial display (Hultsch & Todt 1984), and black-bellied wren, Thryotho-
rus fasciatoventris, partners that were closer together coor-
dinated more of their songs to form duets during playback than partners that stayed further apart (duetting could also reduce misdirected aggression between partners in close proximity, Logue & Gammon 2004). We were unable to assess the relation between proximity during playback and duetting in purple-crowned fairy-wrens because of a ceiling effect (all pairs spent nearly 100% of the time within 2 m of one another during playback).

Intensity of Male and Female Territorial Responses

Purple-crowned fairy-wrens responded vigorously to simulated intrusion, increasing their song rate almost 10-fold and approaching the speaker quickly and closely (Figs 3 and 4). Dominant pairs were often accompanied by subordinate members of their group who also closely ap-

Coordination of Male and Female Territorial Responses

Coordination between partners during simulated territorial intrusion was not an epiphenomenon caused by pair mates responding independently and concurrently to the playback stimulus. Both sexes approached to within a few metres of the speaker (Fig. 4c), but spent only a short amount of time at this closest distance and around half the time within a 10 m radius of the speaker (Fig. 4b), yet stayed within 2 m of one another for most of the time (often just a few centimetres apart, Figs 5 and 6), indicating deliberately coordinated rather than independent responses. In black-bellied wrens, the only other species where distance between partners during playback has been reported, average distances between partners ranged up to 15 m (Logue 2005). Vocal responses of purple-
crowned fairy-wrens were also not independent: given song lengths of about 5 s and song rates of at most 1 duet/min, the high rate of duetting was not a result of partners singing randomly with respect to one another. The percentage of songs sung as duets (74%) was also high in comparison with other duetting species: around 65% in magpie-larks, Grallina cyanoleuca, and tropical bou-
bous, Laniarius aethiopicus (Hall 2000; Grafe & Bitz 2004; Rogers et al. 2004). Therefore our findings do not support Morton's (1996) suggestion that duetting results from sex-
specific territorial defence, and we argue that in duetting species in general, independent responses to male and fe-

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specific territorial defence, and we argue that in duetting species in general, independent responses to male and fe-

male components of the stimulus are inadequate to explain highly coordinated vocal responses to territorial threats (as in Seddon & Tobias 2006).

Coordination between partners responding to simulta-

 Coordination of Male and Female Territorial Responses

Coordination between partners during simulated territorial intrusion was not an consequence of sexual conflict over mating. Playback simulating intrusion res-

results in extremely high levels of coordination between partners, but in the absence of intruders, partners that spent more time close together also coordinated more of their songs to form duets. The experiment was deliberately designed to minimize the potential for sexual conflict: it was completed more than a month before breeding started and we broadcast duets to avoid simulating solitary intruders that might be prospecting for extrapair mating opportunities (since both sister species of purple-crowned fairy-wrens have high levels of extrapair paternity, Mulder et al. 1994; Webster et al. 2004). Consistent with this,
there was no behavioural evidence of conflict between partners such as males chasing females or trying to ‘block’ their songs. Indeed, males did not guard their partner acoustically: rather, the increased coordination of songs was a consequence of female behaviour since they tended to answer more of their partners’ songs to produce duets and males showed no such trend. Similarly, ad libitum observations on flights during playback suggest that females tended to be more likely than males to follow their partner. Consistent with other studies that reject the paternity-guarding hypothesis (Hall & Magrath 2000; Gill et al. 2005), we conclude that coordination and close association between males and females responding to intrusion is not explained by sexual conflict over paternity. The coordinated response of partners to a strong territorial threat appears to represent cooperative defence of a valuable shared resource. However, in species that remain paired and territorial year-round, an individual that is usurped by a same-sex intruder loses both its partner and territory, so that defence of the territory and partnership are closely linked. Paired purple-crowned fairy-wrens are riparian specialists that defend their territories year-round, and maintaining access to resources during the dry season is likely to be particularly important for survival. We conducted the playback experiment in a relatively dry year when rivers shrank to a few isolated pools and, for example, one pair that had lost all water except for a pool on the territory boundary pushed the shared boundary back to retain access to water as the pool shrank. Paired males and females therefore probably share a common interest in territorial defence, and their highly coordinated response to intrusion may confer mutual benefits. Sex differences in response could be a consequence of males taking a leading role in this joint territorial defence, although it might be argued that females increasing their coordination with males represented an attempt to guard the partnership because they perceived the female component of the duet playback as a threat to the partnership. Females guarding the partnership (or guarding the pair bond or mate defence, Seddon & Tobias 2006) may indicate sexual conflict if they are attempting to thwart male attempts to attract replacement or additional females, but may be cooperative if, for example, a territory has sufficient resources for only a single breeding female and male reproductive success is higher with a familiar partner. Further work is needed to investigate the mating system and causes of variation in reproductive success, how social partnerships form, and whether paired males attempt to attract additional females.

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