

Polyandry and competition for territories in bronze-winged jacanas

STUART H. M. BUTCHART, NATHALIE SEDDON and JONATHAN M. M. EKSTROM*

*Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK; and *Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK*

Summary

1. We tested the hypothesis that in territorial, sex-role reversed birds the distribution of resources may determine the dispersion of males, which may, in turn, determine the dispersion of females (i.e. the converse of the classical view of breeding systems in most species).

2. Bronze-winged jacana (*Metopidius indicus*) territories were exclusive within the sexes, and female territories encompassed 1–4 male territories. The breeding density was limited by both habitat availability (floaters settled when new habitat flooded) and competition for territories (floaters filled natural and experimental vacancies).

3. Territory vacancies created by removal experiments were filled quickly either by floaters, neighbours, or male co-mates that expanded their territories. Changes in male territories had a significantly greater impact on female territories than vice versa, in terms of size and overlap before and after the experiment. Female dispersion was therefore influenced by the dispersion of males. However, males also played an active part in mate changes through occasional territory adjustments, and sexual interactions with females.

4. There was no evidence for a relationship between dispersion of resources and male territory size, but heavier males defended larger territories. Both neighbouring males and co-mates constrained the size of male territories. There was no evidence that polyandry arose through males settling on and subdividing female territories, but rather males competed for space, and female territories were superimposed on the mosaic of male territories.

5. Female territory size was positively correlated with harem size, but seemed to be unrelated to habitat quality. Females may have attempted to maximize territory size to encompass as many males as possible. Males in larger harems defended smaller territories. The degree of polyandry therefore depended on both male and female territory sizes.

Key-words: breeding system, harem size, removal experiments, sex-role reversal, territoriality.

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Introduction

The classical view of animal breeding systems is that the dispersion of females is determined by the distribution of resources (such as food and nesting sites),

and that female dispersion, in turn, determines the dispersion of males which compete to monopolize those resources or the females themselves (Emlen & Oring 1977; Davies 1991); for example, food provisioning experiments in grey-sided voles [*Clethrionomys rufocana* (Sundvall)] showed that female dispersion was dependent on resource distribution (Ims 1987), and experimental manipulation of female dispersion (using caged individuals) influ-

Correspondence: Stuart Butchart, Department of Zoology, Downing Street, Cambridge, CB2 3EJ, UK. Fax: 01223 336676, E-mail: shmb1@cus.cam.ac.uk

enced the dispersion of free-ranging males, but manipulation of male dispersion had no effect on the distribution of females (Ims 1988).

However, recent evidence that female animals may play an active role, and that the genetic quality of mates may be an important factor in mate choice, weaken the hypothesized links between resources, female dispersion and male dispersion (Reynolds 1996). Nevertheless, a modified version of the classical scheme, which incorporates the possibility of female mate choice, multiple mating, and the distinction between genetic and social partners, remains a useful framework for understanding breeding systems (Reynolds 1996).

In territorial sex-role reversed birds in which the pattern of competition for mates is reversed, the opposite of the classical scheme might be expected: female dispersion may depend on male dispersion, which may, in turn, depend on resource distribution. Jenni (1974) assumed that the territories of female northern jacanas [*Jacana spinosa* (Linnaeus)] were 'superimposed on the male territories', and Emlen, Demong & Emlen (1989) stated that territories of female wattled jacanas [*J. jacana* (Linnaeus)] 'were found to overlie the male territories', but, in contrast, Tarboton (1995) suggested that female African jacanas [*Actophilornis africana* (Gmelin)] competed for high quality territories, and then males competed 'for exclusive access to these females'. Here we present the first experimental tests of these alternatives. We also tested the idea that in sex-role reversed species that show polyandry, the number of males a female can monopolize (i.e. the degree of polyandry) may be influenced by the defendability of males, which may be related to the size and spacing of their territories. Using observations and experiments on bronze-winged jacanas [*Metopidius indicus* (Latham)] we investigated the relationship between the polyandrous breeding system and the pattern of territoriality resulting from males and females attempting to maximize individual reproductive success.

Methods

Bronze-winged jacanas inhabit floating and emergent aquatic vegetation in shallow freshwater wetlands in India and south-east Asia (Jenni 1996). They are sex-role reversed (females are larger than males which carry out all incubation and care of the precocial chicks) and polyandrous, with females simultaneously defending up to four males, and mating with and providing clutches for each of them (Mathew 1964; Butchart 1999a,b; Butchart, Seddon & Ekstrom 1999). We studied a population of 41–62 bronze-winged jacanas at Vembanur, an 18-ha freshwater lake located at 9°11'N, 77°23'E in Tamil Nadu, southern India. Between 85% (in 1995) and

98% (in 1997) of the lake was covered in floating and rooted vegetation (Butchart 1999a). Fieldwork was carried out for three breeding seasons between mid-May and mid-October 1995–97. Each year 72–90% of the population of jacanas were captured in 10-cm mesh nylon mist-nets erected above the water from canoes. Each bird was weighed and given an individual combination of 2–4 coloured plastic leg rings. Males and females were distinguished unambiguously by biometrics (Butchart 1999a). Unringed birds were sexed by estimating their size relative to ringed birds of known sex, and by noting unequivocal sex-specific calls and sexual behaviour (Butchart 1998). Each bird's status was defined as resident, floater or dependent chick. Residents foraged consistently in the same restricted area and persistently defended this territory from conspecifics of the same sex. Floaters did not show consistent territorial behaviour, and usually ranged widely over the lake to forage. A male was defined as paired to a female if the female consistently foraged with the male, defended a large proportion (usually all) of his territory, responded to his calls by approaching and persistently sexually interacted with him. A female often paired with several males who comprised her harem. In this paper we define co-mates from the perspective of a paired male to refer to additional males paired to the same female.

Territories were mapped monthly by drawing maximum convex polygons around registrations made whenever a bird moved > 5 m or every 15 min. For ten individuals with 200 or more registrations, a mean of $86.3 \pm 3.0\%$ of the final estimated territory size was achieved after 70 registrations, and $93.7 \pm 2.0\%$ after 90 registrations. In the following analyses at least 90 registrations were used for each territory map. The vegetation on the lake was mapped each month by drawing the shape and location of patches of vegetation with reference to a permanent grid of flagpoles spaced at 50 m intervals. Habitat types were defined as open water, < 50% cover of lotus (*Nelumbium speciosum*) and lily (*Limnanthemum* sp. and *Nymphaea lotus*), > 50% cover of lotus and lily, water hyacinth (*Eichhornia crassipes*), water lettuce (*Pistia stratiotes*), sedge (*Scirpus articulatus*), and grass (Graminae) (see Hooker 1872–1897 for species authorities).

FOCAL WATCHES

Territory defence behaviours and intrusion rates were recorded 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 (c. 06.45 h) until at least 09.30 h and from 15.30 h to dusk (c. 19.00 h). For polyandrous

groups two field-workers collected data simultaneously on different males, and the data for the female's behaviour on different territories were subsequently combined. The proportion of time spent on each vegetation type, and the time spent alert (characterized by the bird adopting an upright posture, not showing any foraging or sexual behaviour, and often alarm calling) was recorded using continuous observations. We recorded all flights > 5 m and 'hoverflights' (which were usually given in response to intruders, and were characterized by the bird flying up vertically 1–2 m and landing in the same spot or flying slowly 1–5 m with rapid wing-beats). We recorded the sex and status of bronze-winged jacanas that intruded into territories and noted the responses of territory owners. We compared measures of territory defence for males in different sized harems, with different sized territories, and at four stages of the breeding cycle: prebreeding, preincubation (defined as the period from 30 days before the first egg of a clutch was laid, to the day the penultimate egg was laid, as this is when most sexual activity occurred and when eggs were likely to have been fertilized), incubation and chick-care period (defined as the period until chicks were 70 days old). To avoid pseudoreplication, for all these analyses each male contributed a single data point; for males for which we had territory defence data at different stages of breeding, or in different sized harems, we used data from one randomly selected category for each male.

REMOVAL EXPERIMENTS

We carried out removal experiments on six males and six females during which an individual was captured in a mist-net and then released at a lake with similar habitat and a resident jacana population at Padmanabapuram, 13 km north-west of Vembanur. All removals were carried out on harems that did not include any males caring for eggs or chicks. We carried out focal watches on the territory and on adjacent territories before and after the experiments in order to record the responses of mates and neighbours to the vacancy, and to record the locations, behaviours and interactions of floaters. Territories were mapped during the week before and after the

experiment, and the number of registrations used in paired comparisons was matched to within 20% when fewer than 90 registrations were available (mean number of registrations used was 86 ± 7.9 , $N = 27$ individuals in male removal experiments, and 108 ± 7.1 , $N = 26$, in female removal experiments). We compared the sizes of territories before and after the experiment, and quantified shifts in territory location by calculating the area of overlap as a percentage of the mean of the area before and after the experiment. All statistical tests were two-tailed and corrected for ties where appropriate. Means are presented ± 1 SE.

Results

TERRITORY DEFENCE

Considering the whole breeding season, resident males spent a significantly larger proportion of time alert, patrolled their territories more frequently, and gave hoverflights at a higher rate than females (Table 1). Males tended to give hoverflights and flights at higher rates during the preincubation period than at other stages of the breeding cycle (Kruskal–Wallis tests, hoverflights: $H = 6.90$, $n = 23$, $P = 0.075$; flights: $H = 7.33$, $n = 23$, $P = 0.062$), and this was when male intrusions were most frequent ($H = 9.10$, $n = 23$, $P = 0.028$). There was no relationship between harem size or territory size and three measures of territory defence (% time spent alert, rate of hoverflights and rate of flights; Spearman's rank correlations: $n = 23$, P -values ranged from 0.36 to 0.92).

Resident males responded to a significantly higher proportion of male intruders than female intruders, while resident females responded to a significantly higher proportion of female intruders than male intruders (Table 2, data were pooled from throughout the breeding season and from multiple years for individuals that were resident in more than one year). Males and females were equally successful at evicting male intruders, but males were significantly less successful at excluding female intruders (Table 2). This is unsurprising given that females averaged 60% heavier than males (Butchart 1999a). Males responded to a significantly higher proportion

Table 1. Comparison of male and female residents for three measures of territory defence: the mean \pm SE proportion of time spent alert, the rate of hoverflights, and the rate of flights further than 5 m. P -values are from Mann–Whitney U -tests, $n = 26$ males, 14 females

	% time alert	Hoverflights h ⁻¹	Flights h ⁻¹
Male residents	13.4 \pm 1.8	0.57 \pm 0.08	2.94 \pm 0.45
Female residents	7.2 \pm 1.3	0.14 \pm 0.04	1.78 \pm 0.22
P	0.015	0.0002	0.046

Table 2. Comparisons of male and female residents for the mean \pm SE proportions of male and female intruders responded to, and the proportion of responses leading to successful eviction. *P*-values are from Mann-Whitney *U*-tests for comparisons between males and females, and from Wilcoxon signed-ranks tests for comparisons within the sexes ($n = 17$ male and 10 female residents)

	Male residents	Female residents	<i>P</i>
% male intruders responded to	88.1 \pm 3.0	43.4 \pm 9.1	0.0002
% female intruders responded to	49.3 \pm 8.0	84.2 \pm 5.0	0.047
<i>P</i>	0.003	0.009	
% responses to male intruders leading to successful eviction	80.1 \pm 5.9	78.9 \pm 8.4	NS
% responses to female intruders leading to successful eviction	57.6 \pm 9.2	81.6 \pm 7.1	0.030
<i>P</i>	0.008	NS	

of intrusions by resident males than floater males, but they responded to similar proportions of neighbours and co-mates (Table 3). Males tended to respond to a higher proportion of intrusions by female floaters than female neighbours, but the difference was not significant (Table 3). There were insufficient data to test for differences in responses of females to different status birds, nor for differences in the outcome of responses by males and females to individuals of different status. Females intervened in 13.0 \pm 4.5% ($n = 11$) of aggressive interactions between males in their harem. When these escalated to fights (12.3 \pm 4.0% involved males entangling their legs and wings and pecking at each other), females separated the males by vigorously pecking one or both of them until they moved apart. Males did not intervene in aggressive interactions between females.

PATTERN OF TERRITORIES

Territories were only defended on the lake, but residents occasionally left it to forage for short periods on newly sown rice fields during May–June. Territories were probably defended throughout the year because the lake did not normally dry out, suitable habitat remained all year round, new residents

settled even at the end of the season (see below), and the pattern of territories and territory owners was fairly consistent between years (Fig. 1 shows the pattern of territories in 1997; the maps for 1995 and 1996 were similar). Mean territory size over the 3 years was 7220 \pm 740 m² for males and 11970 \pm 1670 m² for females ($n = 23$ males, 16 females; territory sizes were measured in late August; mean values were used for individuals that defended territories in more than one year). Male territory size did not vary significantly between years (Kruskal–Wallis test, $H = 1.58$, d.f. = 2, $P = 0.46$; for 10 out of 23 males that defended territories in more than one year, we randomly selected one year's data for each individual; for six individuals that defended territories in each of the 3 years, there was no significant variation between years, Friedman test, $\chi^2_{22} = 3.0$, $P = 0.22$). Female territory size did not vary significantly between years either (Kruskal–Wallis test, $H = 2.85$, d.f. = 2, $P = 0.24$; for six out of 16 females that defended territories in more than one year, we randomly selected one year's data for each individual). Therefore data for males and females from all years were pooled in the following analyses. Territories were largely exclusive within sexes: mean overlap with adjacent territories of birds of the same sex was 11.4 \pm 1.9%

Table 3. Proportion of different status intruders that male residents responded to. *P*-values are from Wilcoxon signed-ranks tests, with sample sizes for the tests given in the final column

Intruder sex and status		Mean \pm SE percentage responded to	Number of matched comparisons
Male	Resident	93.1 \pm 12.8 ($n = 10$)	8
	Floater	78.5 \pm 5.9 ($n = 8$)	
	<i>P</i>	0.018	
	Neighbour	94.4 \pm 13.6 ($n = 6$)	
	Co-mate	95.8 \pm 10.2 ($n = 6$)	
	<i>P</i>	NS	5
Female	Resident	20.0 \pm 12.2 ($n = 6$)	4
	Floater	55.5 \pm 15.9 ($n = 5$)	
	<i>P</i>	NS	

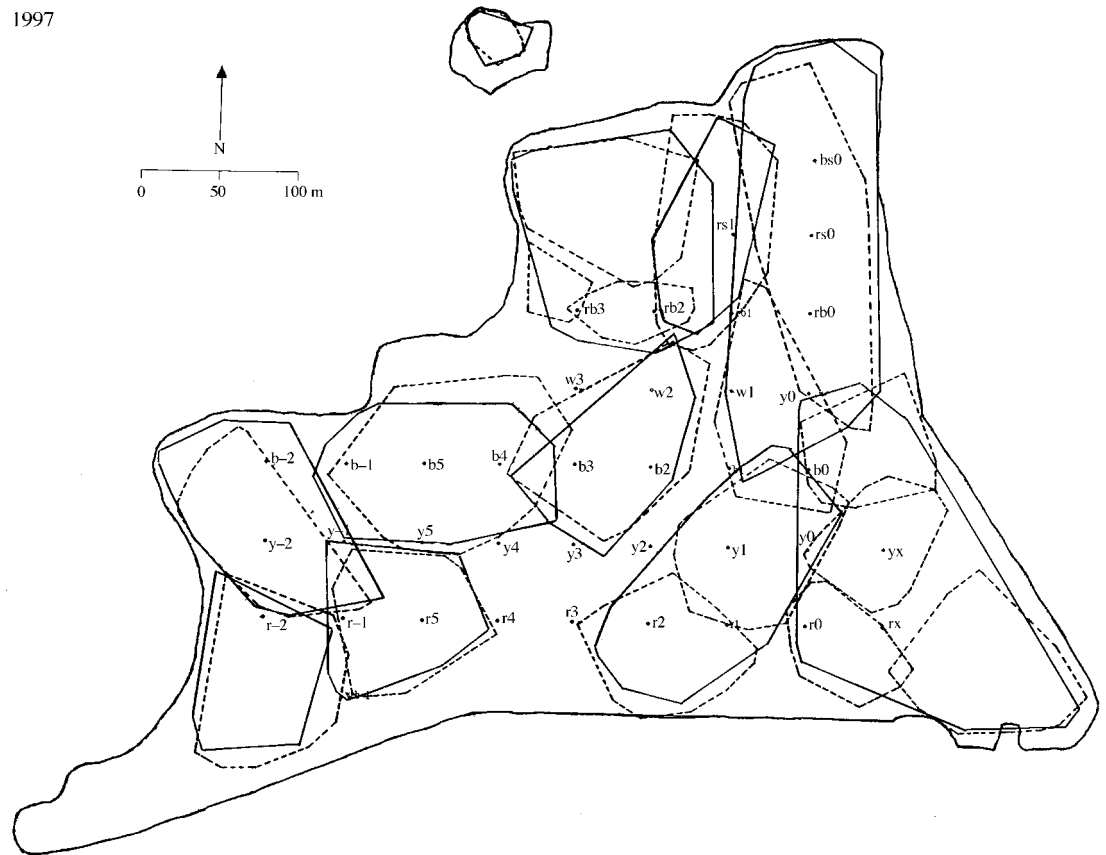


Fig. 1. Map of bronze-winged jacana territories at Vembanur lake in the middle of the breeding season (late August) in 1997. Female territories are represented by solid lines, and male territories are represented by dashed lines. The points identified by combinations of letters and numbers represent a permanent grid of flagpoles that were set up across the site to facilitate mapping. The outer solid line represents the lake shoreline (defined by a raised bank) and a small pond just north of the lake on which jacanas bred each year.

for males ($n = 23$), and $10.1 \pm 3.4\%$ for females ($n = 16$). For polyandrous males, there was no significant difference between the proportion of overlap with neighbours and with co-mates (Wilcoxon signed-ranks test, $z = -0.86$, $n = 19$, $P = 0.39$). Female territories encompassed the territories of 1–4 males (mean = 1.5 ± 0.2 males), and overlapped on average $85.8 \pm 2.0\%$ of each male's territory (Fig. 1).

Territory size was significantly positively correlated with harem size for females (Fig. 2, Spearman's rank correlation, $r_s = 2.68$, $n = 16$, $P = 0.007$), and significantly negatively correlated with harem size for males (Fig. 2, $r_s = -2.88$, $n = 22$, $P = 0.004$, using one randomly selected harem and territory size for three females and seven males that defended territories in more than one year). Four out of five males that were members of different-sized harems in different years defended smaller territories in years when their harem size was larger. All four females that had different-sized harems in different years defended larger territories in years when they had larger harems. Territory size was significantly positively correlated with body

mass for males (Spearman's rank correlation, $r_s = 0.46$, $n = 22$, $P = 0.034$), but this was not significant for females ($r_s = 0.45$, $n = 11$, $P = 0.16$). If territory size was related to habitat quality (the proportion of the territory covered in a particular vegetation type), then there should be a negative relationship between total territory size and percentage cover of that vegetation type, i.e. if a critical minimum area of a particular vegetation type was required, then territories should be larger where this vegetation was less densely distributed. However, there were no significant negative correlations between territory size and percentage cover of any vegetation type for males or females (Spearman's rank correlations, P -values ranged from 0.34 to 0.96).

Jacana territories encompassed several different vegetation types, of which lily/lotus, grass, sedge, and hyacinth covered the largest areas (Table 4). Jacanas divided their time amongst these habitats, but males spent significantly less time in grass and significantly more time in hyacinth than predicted from the proportions of the territories covered by these vegetation types (Table 4, Wilcoxon signed-

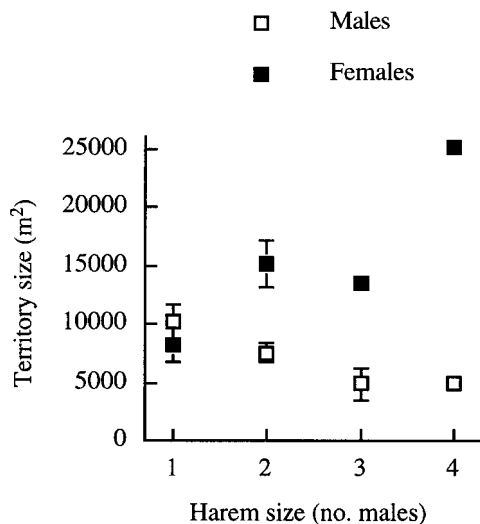


Fig. 2. The relationship between mean \pm SE territory size and harem size for males and females (sample sizes reading from left to right are 6, 8, 5, 3 males, and 8, 6, 1, 1, females; for each of seven males and three females that defended territories in more than one year; one randomly selected year's data was used).

ranks tests, grass: $z = -2.33$, $n = 15$, $P = 0.019$; hyacinth: $z = -2.10$, $n = 15$, $P = 0.036$, using one randomly selected year's territory and time-budget data for each individual that defended a territory in more than one year). There were no significant differences for females, nor were there any significant differences between males and females for the proportions of different vegetation types in their territory or for the proportion of time spent in different habitats (Mann-Whitney U -tests, $n = 15$ males, 11 females).

TERRITORY TAKEOVERS AND REPLACEMENTS

Eight cases of female takeovers were observed, when a female persistently intruded onto another female's

territory, repeatedly fought with the resident female, and ultimately took over the territory by consistently excluding the former territory owner. Two cases involved settling floaters and six involved neighbours expanding their territories. Similarly male takeovers by three settling floaters and two neighbours were observed. Territory takeovers and settlement by floaters occurred throughout the breeding season (May–October), which supports the suggestion that territories are probably defended year-round (as also found in wattled jacanas, S.T. Emlen & P.H. Wrege unpublished data). Replacements of territory holders with little change in territory boundaries occurred between seasons for six male territories (23%) and six female territories (35%). In addition, six male and three female floaters were observed to settle and defend territories when new breeding habitat became available because of rising water levels inducing growth of aquatic plants in previously shallow or dry areas.

FEMALE REMOVAL EXPERIMENTS

Six female territory vacancies were created by removal experiments (Table 5). Four were filled by neighbours expanding their territories, and two were filled by settling floaters. The four neighbours increased their territory area by $149 \pm 88\%$, whilst continuing to defend most ($73 \pm 4.3\%$) of their former territory. All were previously monogamous and by territory expansion they increased their harem sizes to two, two, three and four males, respectively. Five of the removed females returned within 2–11 days (mean = 6.2 ± 1.5 days), but the other was not resighted. Four of these returning females took over their old territories within 1–8 days, whilst the other female remained a floater for the rest of the season.

Following the removal of their female mates, five males' territories increased in size and six decreased. On average their territory sizes changed by

Table 4. Mean \pm SE percentage cover of different vegetation types on bronze-winged jacana territories, and mean \pm SE percentage time spent in different vegetation types by males and females. P -values are from Wilcoxon signed-ranks tests, $n = 15$ males, 11 females

		< 50% lily/lotus	\geq 50% lily/lotus	Sedge	Grass	Hyacinth	Pistia	Other
Males	% cover	3.7 \pm 3.2	43.3 \pm 7.1	6.5 \pm 2.1	36.0 \pm 6.6	8.1 \pm 2.4	0.5 \pm 0.5	1.9 \pm 0.6
	% time	2.6 \pm 2.1	42.7 \pm 7.2	6.0 \pm 2.3	23.2 \pm 5.1	18.1 \pm 3.7	2.9 \pm 2.7	0
	P	NS	NS	NS	0.019	0.036	NS	
Females	% cover	3.6 \pm 3.3	45.5 \pm 6.0	9.4 \pm 2.7	28.5 \pm 5.9	8.1 \pm 2.8	2.1 \pm 2.0	2.9 \pm 1.1
	% time	1.1 \pm 0.8	30.0 \pm 7.1	6.7 \pm 3.2	34.4 \pm 7.2	17.8 \pm 4.4	9.9 \pm 1.0	0
	P	NS	NS	NS	NS	NS	NS	

Table 5. Summary of female removal experiments

	Date removed	Pre-removal female status	How was vacancy filled?	Male mates territory changes	Neighbouring female territory changes	Status of replacement female	Fate of removed female
1.	26 Sep 96	Monogamous	Monogamous neighbour expanded	1. Decreased 7%	Increased 25%	Biandrous	Returned after 2 days, re-took territory immediately
2.	7 Aug 97	Triandrous	Monogamous neighbour expanded (2 males), floater settled (1 male)	1. Increased 9% 2. Increased 19% 3. Increased 30%	Increased 93%	Triandrous (neighbour), monogamous (settler)	Returned after 5 days, re-took territory 8 days later
3.	18 Aug 97	Biandrous	Floater settled	1. Decreased 6% 2. Decreased 7%	No change	Biandrous	Returned after 8 days, re-took territory 1 day later
4.	28 Aug 97	Monogamous	Floater settled	1. Increased 7%	No change	Monogamous	Returned after 11 days, remained floater
5.	5 Sep 97	Triandrous	Monogamous neighbour expanded	1. Decreased 8% 2. Increased 2% 3. Increased 23%	Increased 408%	Quadrandrous	Returned after 5 days, re-took territory immediately
6.	11 Sep 97	Monogamous	Monogamous neighbour expanded	1. Decreased 16%	Increased 70%	Biandrous	Not resighted

Table 6. Summary of male removal experiments

	Date removed	Pre-removal female status	How was vacancy filled?	Co-mate territory changes	Female territory changes	Post-removal female status	Fate of removed male
1	30 Aug 96	Biandrous	Co-mate expanded	Increased 23%	Increased 52% to takeover neighbouring male	Biandrous	Not resighted
2	29 Jun 97	Biandrous	Neighbour expanded and shifted territory	Increased 28%	Increased 12%	Biandrous	Returned after 4 days, re-took territory 11 days later
3	17 Jul 97	Biandrous	Floater settled	Decreased 7%	Decreased 64% as lost part of territory to settling female floater	Monogamous	Returned after 10 days, re-took territory 5 days later
4	1 Sep 97	Biandrous	Neighbour expanded and shifted territory	Increased 14%	Increased 14%	Biandrous	Not resighted
5	27 Sep 97	Biandrous	Co-mate expanded	Increased 239%	Decreased 19%	Monogamous	Returned after 6 days, took over vacancy 4 days later
6	3 Oct 97	Monogamous	Floater settled	No co-mate	Increased 20%	Monogamous	Not resighted

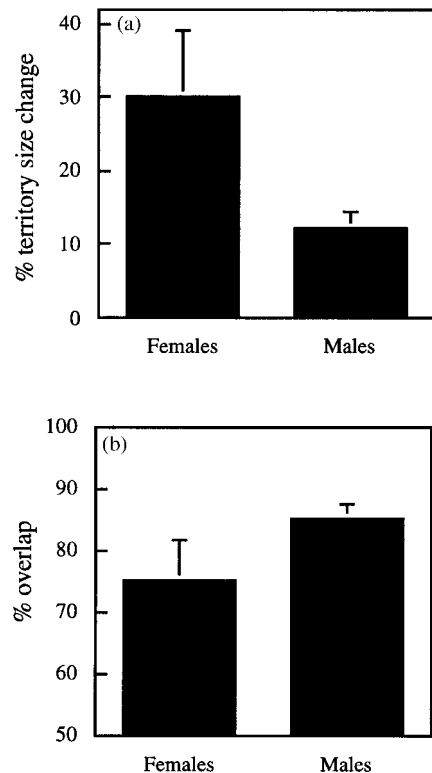


Fig. 3. Comparison of the effect of male removal experiments on female territories (lefthand histograms) with the effect of female removal experiments on male territories (righthand histograms), in terms of (a) percentage changes in territory size, and (b) percentage overlap between territories mapped before and after the experiment. Histograms show means \pm 1 SE for six females and 11 males.

$12 \pm 2.6\%$, but there was no significant overall trend (Wilcoxon signed-ranks test, $z = -0.45$, $n = 11$, $P = 0.66$), and the mean net change was an increase of only $4.3 \pm 4.5\%$. The mean percentage overlap between territories before and after removal of the mate was $85 \pm 2.3\%$. When female neighbours expanded their territories into vacancies, the territories of their male mates showed little change in size (mean change = $10 \pm 3.8\%$). Of four such male territories, two increased and two decreased after the removal, giving a mean net decrease of $4.3 \pm 6.6\%$. The mean overlap between their territories before and after the experiment was also high ($82 \pm 1.9\%$).

If females played an active role in reducing aggression between harem males, then removal of a polyandrous female might be predicted to lead to increased aggression between her males, and the expansion of some male's territories at the expense or even the exclusion of others. There were inadequate data to test whether the frequency of aggressive interactions between harem males increased following removal of the female. However, for eight male mates of three polyandrous females that were

removed, none lost their territories following the experiment, no male's territory decreased by more than 7.9%, and none increased by more than 30.4%. The three males whose territories did increase by more than 10% all expanded into peripheral areas or into neighbouring (nonharem) males' territories. These increases probably represented part of the continual adjustment of territories that occurred between competing males.

MALE REMOVAL EXPERIMENTS

Six male territory vacancies were created by removal experiments (Table 6). Two were filled by co-mates expanding their territories, two by neighbouring males moving and expanding their territories, and two by settling floaters. When vacancies were filled by neighbours or floaters, there were no changes in the harem sizes of the female mates of the removed males. When co-mates expanded to fill the vacancy, the harem size decreased from two to one male in both cases, but one of these females immediately took over a neighbouring male to become biandrous again. Three of the removed males returned within 4–10 days (mean = 6.7 ± 1.8 days), but the other three were not resighted at the release site despite searches at approximately fortnightly intervals. Two of the males that returned took over their territories again within 4–10 days, and the third took over a vacancy created by another removal experiment within 4 days of returning.

The four co-mates and neighbours increased their territory size by $155 \pm 58\%$. The mean percentage overlap between territories before and after the experiment was low ($26 \pm 11\%$) for these four males. This was because although the two co-mates continued to defend most ($73 \pm 17\%$) of their former territory, the two neighbouring males shifted their territory into the vacancy, overlapping their pre-experiment territories by only $6.6 \pm 0.5\%$. Five of the removed males were polyandrous. Their removal presented the co-mates with the opportunity to expand their territories into the vacancies. Only two out of five co-mates succeeded in doing so (Table 5). In two of the other three cases, the co-mate intruded onto the vacant territory, but was repelled by a neighbour which expanded and moved his territory into the vacancy (one case) or by a floater which settled and took over the vacancy (one case). In the final case, a neighbour expanded into the vacancy, but the co-mate of the removed male was not seen to intrude onto the vacancy.

For females whose male mates were removed, there was no significant overall trend in changes in territory size, with a mean net increase of $2.6 \pm 16\%$ (Wilcoxon signed-ranks test, $z = -0.52$, $n = 6$, $P = 0.60$). However, large territory changes occurred for three of these females: one expanded

her territory by 52% to take over a neighbouring male, another lost 64% of her territory to a female floater who settled with the replacement male, and the third shifted her territory by 31% to match the replacement male's territory. The mean change (increase or decrease) in territory size was $30 \pm 9.0\%$, and the mean overlap between territories before and after the experiment was $75 \pm 6.6\%$. Territory size changes were significantly larger, and overlap was significantly lower for female mates of removed males than male mates of removed females (Fig. 3; Mann-Whitney *U*-tests, size change: $U = 12$, $n =$ six females, 11 males, $P = 0.035$; overlap: $U = 13$, $P = 0.044$). Thus female territories changed in response to male territory dynamics significantly more than male territories changed in response to female territory dynamics.

MALE-INDUCED TERRITORY CHANGES

Wrege & Emlen (1998) proposed that mate changes in wattled jacanas may not simply result from females shifting or expanding their territories in order to take over adjacent males, but that males may play an active part in this process. Our removal experiments on bronze-winged jacanas revealed that males may occasionally relocate their territories, abandoning formerly defended areas and moving to adjacent vacant territory. In the two cases where this occurred the female mates also attempted to forage in the adjacent territory, but they were repeatedly excluded by the female owner of this territory. Both males were previously monogamous, and their movements resulted in them increasing the size of the harem they were in, but gaining larger territories. Natural observations also provided support for this idea. In one case a male's territory was increasingly encroached upon by a female neighbour for a period of 45 days before she eventually succeeded in taking over the male. The male tolerated the incoming female, and for a period of 11 days he copulated with both females, often at the same platform in quick succession. In another case a male who was paired to one female started intruding regularly into a natural vacancy in an adjacent male territory. He defended both territories for 5 days (although no sexual interactions were seen during this time) before relocating his territory and pairing to the neighbouring female. In this case the mate changes and territory dynamics seemed to result mainly from male rather than female behaviour.

Males tolerated 80% of intrusions by female neighbours into their territory (Table 3), and seven out of 19 males solicited or copulated with female neighbours. Five such males were eventually taken over by the neighbouring female: two males increased harem size, one decreased harem size, and

two experienced no change. There were insufficient data to test whether males in larger harems were more likely to tolerate intrusions by neighbouring females, thereby encouraging takeovers that reduced the harem sizes of such males. This might be expected, as Wrege & Emlen (1998) have shown that male wattled jacanas facilitate mate changes that reduce their harem size.

Discussion

HOW DO MALES AND FEMALES DIFFER IN TERRITORY DEFENCE?

Male bronze-winged jacanas defended their territory more actively than females, and males were particularly active during the period when sexual access to the female was most important (i.e. the period before the clutch was laid up to the day the penultimate egg was laid). In general, male residents responded to male intruders, and female residents responded to female intruders. Removal experiments and observations of territory dynamics showed that competition for territories within sexes was strong, so territory defence against conspecifics of the same sex would be expected. Females are likely to benefit from increased harem size, because more males are available to care for clutches in larger harems. Females might therefore be expected to be more tolerant of intruder males who represent potential new mates. Males generally tolerated female intrusions, and tended to respond to a lower proportion of intrusions by residents than floaters. This may have been because males were considerably smaller than females, particularly resident females (Butchart 1999a), and might have suffered high costs from attempting to exclude them. Alternatively, males may have benefited by tolerating those females that represented potential future mates (i.e. resident neighbours), as suggested for wattled jacanas by Wrege & Emlen (1998).

WHAT LIMITS POLYANDRY?

In larger harems male territories were smaller, and female territories were larger. For individual males and females the variation between years in territory size and harem size also fitted this pattern. This supports the hypothesis that the degree of polyandry (i.e. the degree to which females can monopolize males) is constrained by the defendability of males (i.e. the relative size and spacing of their territories) and by female territory size (larger territories encompass more males). By comparison, in wattled jacanas female territory size increases with harem size, but male territory size does not decrease (S.T. Emlen & P.H. Wrege, unpublished data).

Some evidence for polyandry being limited by male densities has been found in other studies of territorial sex-role reversed species. Osborne & Bourne (1977) recorded wattled jacanas breeding monogamously where territories were large, and polyandrously where males were more densely packed. Jenni & Collier (1972) found that small areas of optimal habitat supported a high percentage of the polyandrous groups in a population of northern jacanas, and Jenni (1974) suggested that the small size of male territories was important in facilitating polyandry. In spotted sandpipers [*Actitis macularia* (Linnaeus)] the degree of polyandry was greater at high population densities on high quality habitat both within and between populations (Hays 1972; Oring & Knudson 1972; Emlen & Oring 1977). It is important to note that it is the relative size of male territories compared to female territories rather than their absolute size that may be critical. In wattled jacanas, territories of both sexes average six times smaller, but the size distribution of harems is similar (S.T. Emlen & P.H. Wrege, unpublished data).

WHAT DETERMINES TERRITORY SIZE?

If resources determine male territory sizes and locations in sex-role reversed species, then male territory size might be expected to be smaller in areas of good quality habitat (i.e. the converse of dunlocks in which female territories are smallest in areas of highest habitat quality, Davies & Lundberg 1984). We were unable to assess habitat quality directly. However, we assumed that the most important differences between territories were the areas of different vegetation types. This is because nest sites did not appear to be limiting (jacanas built flimsy nests on floating vegetation which was widely available in all territories), and predation pressure (on real and artificial nests) seemed to be fairly constant right across the study site (Butchart 1999a). We assumed that vegetation type would be the most important factor determining the distribution of small aquatic invertebrates, seeds and plant material which jacanas gleaned from the leaves and roots of floating vegetation.

The analyses of time-budgets failed to show any strong preferences for particular vegetation types, although males seemed preferentially to spend time on hyacinth. If territory size was related to habitat quality, then there should be a negative relationship between total territory size and percentage cover of a particular vegetation type. However, we found no such relationship for hyacinth nor for any other vegetation type. Based on the data available we concluded that territory size was not related to habitat quality for either males or females. However, territory size was positively correlated with body mass for males, suggesting either that individual competi-

tive ability may be more important than habitat quality for determining territory size, or that greater body mass reflects greater access to resources on larger territories. If the former was true, then it was unclear whether an individual's absolute or relative resource holding potential (Petrie 1984) was more important for determining territory size.

TERRITORY DYNAMICS AND REMOVAL EXPERIMENTS

Observations of territory dynamics within and between seasons suggested that competition for territories was high, but that turnover of residents was fairly low and the pattern of territories was quite stable (as also found in wattled jacanas, Emlen *et al.* 1989; Wrege & Emlen 1998). Neighbours and co-mates expanded their territories when opportunities arose, and vacancies were filled quickly. Floaters became residents through defending newly formed breeding habitat which developed after vegetation grew in response to rising water levels (67% of male cases and 60% of female cases), and also by taking over territories by fighting residents. Thus the breeding density of males and females at Vembanur was limited by both habitat availability and territoriality.

Removal experiments were carried out to mimic the natural creation of territory vacancies. These showed that males adjusted their territories in response to male territory dynamics, and females adjusted their territories in response to female territory dynamics. However, changes in male territories had a significantly greater impact on female territories than vice versa, in terms of both size and degree of overlap between territories before and after the experiment. These results support the hypothesis that female dispersion is influenced by the dispersion of males. Removal experiments on wattled jacanas carried out by Emlen *et al.* (1989) also supported this idea: when three females were removed, five males remained on their territories while three neighbouring females expanded their territories to take over the males. Nevertheless, as in wattled jacanas (Wrege & Emlen 1998), male bronze-winged jacanas occasionally played an active part in mate changes, either by occasionally shifting their territory into that of a different female, or by tolerating intrusions by neighbouring females and by soliciting sexual behaviour with them, which usually led to the neighbouring female taking over the male.

If the pattern of male territories is largely independent of the pattern of female territories, then the size of male territories should be constrained by the territories of both neighbours and co-mates. Alternatively, if females defend large territories which are then subdivided by their male mates, the

size of male territories should be mainly constrained by co-mate territories. The territories of polyandrous males did not overlap neighbours' territories any more than co-mates' territories, and when bian-drous males were removed, four out of five co-mates intruded into the vacancy but only two succeeded in taking it over. These results therefore suggest that both neighbouring males and co-mates constrained the size of male territories. Males did not appear to subdivide larger female territories, but rather competition between males determined the pattern of male territories, which females then competed to monopolize. The results of the removal experiments suggested that female behaviour did not play an important part in determining territory boundaries between harem males, which further supports the idea that male territories were determined by competition between males largely independent of the pattern of female territories.

The pattern of territoriality described here for bronze-winged jacanas seems to match closely that found for northern jacanas at Turrialba, Costa Rica (Jenni & Collier 1972; Betts & Jenni 1991; Jenni 1996) and for wattled jacanas at Gamboa, Panama (Emlen *et al.* 1989; S.T. Emlen & P.H. Wrege, unpublished data). However, Tarboton's (1995) description of territories in a population of African jacanas on the Nyl river in South Africa is distinctly different. Females competed with other females for the best breeding habitat 'and males competed with males for exclusive access to these females'. Some males consistently defended exclusive territories, but others shifted position in response to female availability. This form of labile territoriality may have resulted from the ephemeral and changeable nature of the habitat in which African jacanas were studied. The area of suitable breeding habitat and the number of breeding jacanas fluctuated greatly within and between years, and the site was abandoned when it dried out (Tarboton 1995). Strategies for competition for matings may have been less constrained by territoriality in African jacanas because resources and breeding habitat were less predictably distributed through time and space. By contrast the habitat in Costa Rica, Panama and India was more stable, and jacanas probably maintained their territories throughout the year. Territoriality in bronze-winged jacanas contrasts with the pattern found in dunnocks [*Prunella modularis* (Linnaeus)], in which females set up territories in relation to resources, and males compete to monopolize female territories. The size and location of female territories is independent of male distribution, and is influenced only by competition with other females. Males move to settle on the female distribution, but not vice versa (Davies 1992). In bronze-winged jacanas the system was reversed, except that there was no evidence that

the size of male territories was determined by the distribution of resources.

MALE AND FEMALE STRATEGIES

Female reproductive success is likely to increase with the number of males they can defend (as in wattled jacanas, S.T. Emlen & P.H. Wrege, unpublished data). Female territory size was significantly positively correlated with harem size but seemed to be unrelated to habitat quality, and females adjusted their territories in response to changes in the pattern of male territories. These observations suggest that females may have attempted to maximize the size of their territory to encompass as many males as possible in order to maximize reproductive success. In wattled jacanas, males in larger harems have to wait significantly longer to receive a clutch from their female mate (Wrege & Emlen 1998), and they have a higher risk of being cuckolded (Emlen, Wrege & Webster, 1998). Male bronze-winged jacanas may also suffer costs in larger harems: they receive fewer clutches per season in larger harems (Butchart 1999a), but data on cuckoldry rates are unavailable for this species. Heavier males defended larger territories, and male territory size declined with harem size and seemed to be unrelated to habitat quality. Hence males may have attempted to maximize territory size in order to minimize the opportunity for females to exploit other males.

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