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Cuckoldry as a cost of polyandry in the sex-role-reversed wattled jacana, *Jacana jacana*

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In this paper we provide the first molecular genetic data on extra-pair paternity in a simultaneously polyandrous, sex-role-reversed avian species, the wattled jacana (*Jacana jacana*). Female jacanas often copulated with multiple mates, provided that the mates were not actively incubating eggs or tending young chicks. Both the presence of multiple 'available' mates, and the copulation behaviour of the female near the time of nest initiation, significantly predicted the probability of extra-pair fertilizations. A male's risk of being cuckolded was 0% in monandrous pairings, rose to 41% of broods (17% of chicks) in polyandrous associations where an additional mate was 'available', and increased to 74% of broods (29% of chicks) where the female was observed to copulate with multiple mates. Unlike findings from several sequentially polyandrous bird species, few if any fertilizations resulted from sperm stored from a previous nesting. We conclude that lost paternity can constitute a very real cost of polyandry for male wattled jacanas. The source of this cost is sexually active males simultaneously paired to the same female.

Keywords: extra-pair fertilizations; jacana; polyandry; sex-role reversal; sperm competition; sperm storage

1. INTRODUCTION

Most genetic studies of parentage in birds have been conducted on socially monogamous or polygynous species (see, for example, Birkhead & Møller 1992; Westneat & Webster 1994; Westneat & Sherman 1997). Very little is known about socially polyandrous species in which females pair with more than one male in a single breeding season. Polyandry is intrinsically interesting because it is often associated with sex-role reversal, in which males perform most or all of the parental care of young. Theoretical models for the evolution of male uniparental care suggest that the parental male's confidence of paternity must be very high (Trivers 1972; Whittingham *et al.* 1992). However, males receiving a clutch in polyandrous associations (termed 'nest-males') face three possible risks to their paternity: fertilizations by males outside the female group, fertilizations by males previously mated to the female, and fertilizations by other males simultaneously paired to the same female (termed 'co-mates'). We define co-mates from the perspective of a paired male, to include males in addition to itself that are paired to the same female. Co-mate number thus equals female harem size minus one.

Studies of sex-role-reversed, sequentially polyandrous avian species have shown that females may use stored sperm from their first, or primary, mate to fertilize some of the young in subsequent broods. This suggests that cuckoldry by a previous mate can be a significant risk factor for nest-males (Oring *et al.* 1992; Owens *et al.* 1995; Birks 1997; Dale *et al.* 1999). If primary males are of higher genetic quality than subsequent mates, the use of stored sperm could be adaptive to both females and their primary male mates (Oring *et al.* 1992). Such use of stored sperm has been suggested as an important factor in the evolutionary origin of polyandry (Valle 1994).

We studied the frequency and pattern of extra-pair fertilizations (EPFs, here defined as fertilizations by any male other than the nest-male) in a sex-role-reversed, simultaneously polyandrous shorebird, the wattled jacana, *Jacana jacana*. Wattled jacanas are permanent residents at our study site in Panamá, with both sexes defending all-purpose territories on floating and emergent vegetation. Male territories were small ($1127\,\mathrm{m}^2 \pm 526$ s.d., $n=245$, or roughly 40 m in diameter assuming a circular shape), contiguous (wherever vegetation permitted), and saturated all suitable nesting habitat. Female territories encompassed the areas defended by one to four males (S. T. Emlen and P. H. Wrege, unpublished data). Female wattled jacanas are much larger than, and behaviourally dominant to, males (average mass = 135 g and 91 g, respectively). Breeding females simultaneously paired with an average of 1.6 males (range 1–4) and laid clutches of eggs sequentially for their different male mates. Fully 75% of paired males shared their female with one or more co-mates (S. T. Emlen and P. H. Wrege, unpublished data). Polyandrously mated females frequently copulated with multiple males in their harem during the production and laying of clutches of eggs (P. H. Wrege and S. T. Emlen, unpublished data). Clutch size was four eggs; males provided all incubation care and nearly all direct care to young, totalling three

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months of effort per successful brood (Osborne & Bourne 1977; S. T. Emlen and P. H. Wrege, unpublished data; see also Jenni & Collier 1972; Butchart 1999).

Here we quantify the sources and magnitude of risk of EPFs, combining molecular techniques to determine parentage with behavioural observations to characterize the mating history of each female, as well as the reproductive status of each of her male mates. After documenting the estimated population-wide frequency of EPFs, we examine the three potential sources of risk to polyandrously mated males.

2. METHODS

(a) *Field work*

We studied wattled jacanas on the Chagres River, in the Republic of Panamá, from 1990–1995. Nearly all residents within the 13 ha study site were captured and ringed for individual identification (on average, 18 females and 30 males were studied each year). All female residents, and their harems of males, were observed intensively, usually on a daily basis, for 5–6 months each year. The number of males in each female group, their identity, and their breeding status was known with certainty. Most results are based on 74 nests that successfully hatched young, and from which DNA samples were obtained. Nineteen nests were used in special analyses relating the pattern of copulations to the risk of EPF, because for these nests we had sufficiently detailed observations to estimate the apportionment of copulations between males. For each of these 19 nests, a minimum of four hours of focal observations were obtained within the six-day period beginning two days before ovulation of the first egg. This period encompasses the likely times of fertilization of the four-egg clutch. It is also the time when copulation rates are highest for both nest-males and co-mates (P. H. Wrege and S. T. Emlen, unpublished data). Fifteen of these 19 nests had more than nine hours of focal observations and/or at least ten observed copulations.

(b) *Molecular parentage analyses*

Blood samples (20–30 μl) obtained from each captured individual were stored at −20°C in TNE buffer, or at 5°C in lysis buffer until analysis. Blood samples (*ca.* 5 μl per individual) from clutches were usually obtained from chicks on the day of hatching (59 broods), or from eggs incubated to half-term (15 broods). Genetic analyses reported here are based on samples from nearly all nests that successfully hatched in 1990 and 1991 ($n = 57$), plus 17 nests from polyandrous groups specifically targeted for these analyses in later years. The 1990–1991 sample was unbiased with respect to group size in the population at large during those years, but was significantly biased compared with the distribution of group sizes over the six-year study. We therefore use the results from all 74 nests, and a correction factor to adjust for the bias in group size, when estimating the population-wide frequency of EPFs.

DNA profiles ('DNA fingerprints') were produced by following methods detailed in Westneat (1990, 1993) and Webster (1995), by means of digestion with *HaeIII* and the minisatellite probe Jeffreys 33.15 (Jeffreys *et al.* 1985*a*,*b*). The DNA profile for each offspring was compared to that of its mother, its putative father (the male that incubated and cared for it), and each of the female's other mates. In comparing a nestling to both its mother and a putative sire, a band in the nestling's profile was considered to be 'novel' if it was not found in either of the two adults. We calculated the expected rate at which novel bands would arise by mutation alone by assuming that all cases of a single novel band represented a mutation event. The per-individual probability of finding three novel bands by mutation was 0.015, and we therefore concluded that cases of three or more novel bands represented cases of misassigned parentage. The proportion of bands shared was calculated as $x = 2s/(a+b)$, where s is the number of bands found in both profiles (i.e. shared), and a and b are the total number of bands scored in each of the individual profiles. Mean band-sharing between mothers and offspring (we have no evidence to suggest intraspecific egg parasitism; see § 3) was

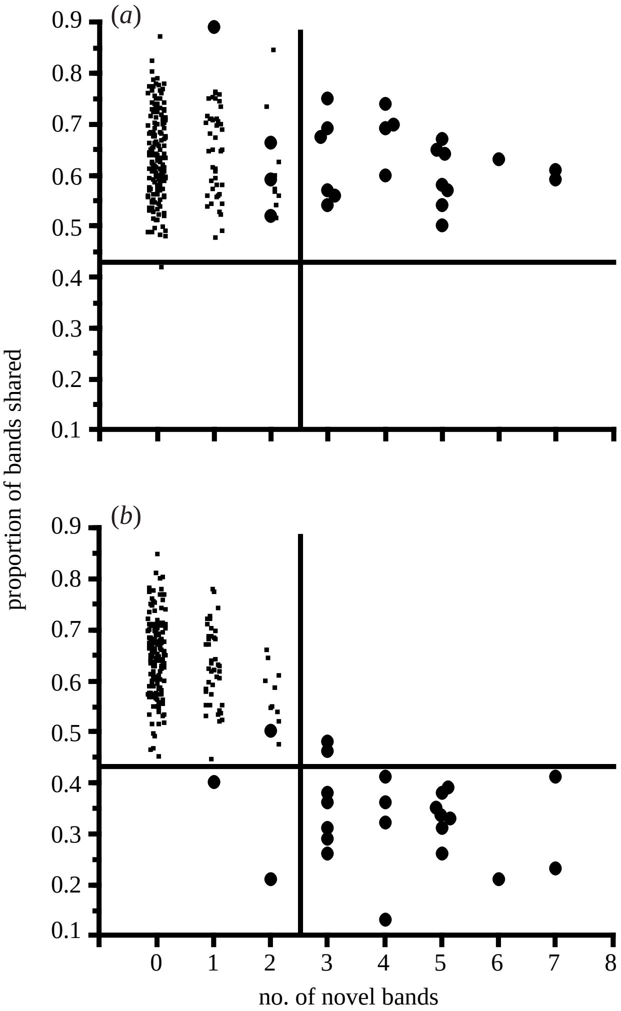

Figure 1. Band-sharing and novel band scores between 235 chicks and (*a*) their social mother and (*b*) their social father (the caretaking male). EPF chicks are indicated by large filled circles. The horizontal line represents the lower 99% confidence boundary on the distribution of band-sharing with social mothers and the vertical line represents the maximum number of novel bands (2) that might be expected to arise by mutation. Chick–social father scores that fell below and/or to the right of these lines, respectively, were considered cases of EPF. In seven cases (3% of all chicks analysed) a chick had scores that fell into the 'acceptance zone' with two different males (i.e. the social father and one co-mate). In all of these cases we assigned the chick to the male with the highest band-sharing score and fewest novel bands; six of these were assigned to the social father and one was assigned to a co-mate (this is the single filled circle in the upper left quadrant of *b*).

0.633, with an s.d. of 0.085. We used the lower 99% confidence interval on this distribution (0.43) as the cut-off for acceptable band-sharing between assigned parents and offspring. Figure 1 shows the distribution of band-sharing and novel bands between offspring and social parents for all sampled broods. Approximately 15% of the band-sharing distribution between chicks and those co-mates not assigned as sires (mean = 0.331 ± 0.095) fell above the critical cut-off of 0.43. Although this makes the single criterion of band-sharing conservative (against assigning EPFs), both band-sharing and novel band scores were available for all but 7% of chicks.

3. RESULTS

Intraspecific brood parasitism was not detected in this population. No female was rejected as the genetic mother in nests on her territory. The lack of molecular evidence for parasitism was reinforced by behavioural observations: we detected no cases of supernumerary clutches, no cases where two eggs appeared in a nest on the same day, and no cases of intruding females being tolerated within the territory of a male currently receiving a clutch.

The potential for EPFs was high in this population. Females in polyandrous groups copulated with multiple mates on the days immediately preceding and during egg laying for a particular nest-male and the copulation rate at this time was high (average 1.3 copulations per hour, or approximately 65 copulations per clutch of four eggs) (P. H. Wrege and S. T. Emlen, unpublished data). In addition, females laid clutches of eggs sequentially for their different male mates. The interval between successive clutches varied widely; the shortest was five days and 44% of intervals were ⩽15 days. This is well within the known range of viable sperm storage in birds (Birkhead & Møller 1992). Finally, males did not guard their mates, and females could potentially copulate with males paired to other females.

Despite this high potential, the overall level of extra-pair paternity in the population was low. Of 74 nests sampled, 18 contained one or more chicks that rejected the nest-male as the genetic father. Correcting for a bias towards larger groups in the sample (see § 2), the per-nest probability that any given male expended parental care raising one or more chicks fertilized by another male was 17.9%. Similarly, of 235 chicks sampled, 24 rejected the nest-male, yielding a corrected estimate of 7.5% for the population-wide frequency of extra-pair paternity.

Few EPFs were attributable to extra-group males. All positively assigned EPF sires ($n = 17$) were co-mates of the cuckolded nest-male. In four additional cases, one co-mate was either unmarked or a DNA sample was not available, and so could not be scored. In three of these cases, we observed the unsampled co-mate copulating with the female during laying (no behavioural data were collected for the fourth case), so it is likely that the co-mate sired the EPF chicks. In only three cases (from two nests) were all males in the group excluded as sires. Thus, only 3 out of 235 young (1.3%) appear to have been sired by extra-group males. Our behavioural data also indicate that female sexual activity with extra-group males is extremely rare. Copulations are visually and acoustically conspicuous in wattled jacanas, and most breeding females had extra-group males in close proximity, yet only 1 out of 1355 observed copulations close to nest initiation involved a male not already paired to the female.

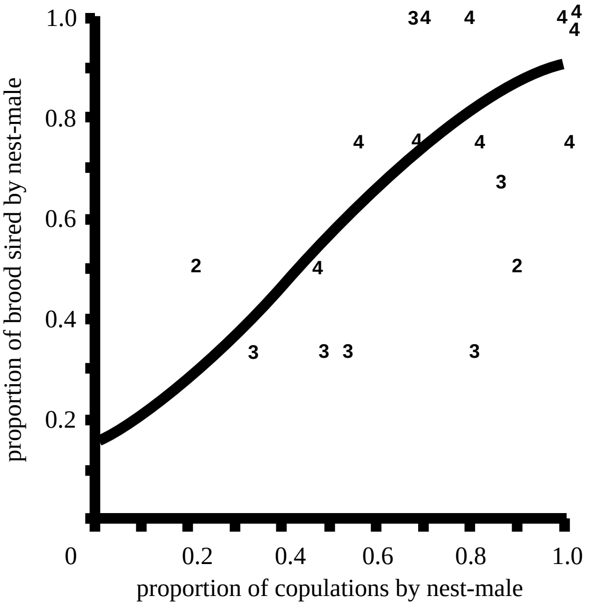

Figure 2. Siring probability as a function of the share of total copulations received. The curve is back-calculated from the regression equation estimated by a repeated-measures logistic regression analysis (62 chicks from 19 nests). Data values used in estimating the equation cannot be plotted on these axes, because each egg in a clutch (scored as 'EPF' or 'not EPF') is used in the analysis as a (repeated) measure of the likelihood of EPF for eggs in that clutch. To provide information about the range and distribution of copulations, we have simply plotted the proportion of EPFs per clutch, with the number of eggs sampled as the plot symbol.

A nest-male's risk of being cuckolded was dependent upon the pattern of sexual behaviour of its female on the days immediately before, and during, egg laying (−2 days to +3 days, first ovulation = day 0). Females that copulated with multiple mates commonly did so in rapid succession, often flying from one male to the other within minutes (P. H. Wrege and S. T. Emlen, unpublished data). The typical interval between copulations with different males was sufficiently short (median = 19 min) that complete sperm mixing is expected (Birkhead & Møller 1992). If EPFs result from copulations during this period, we would predict that the proportion of EPF young in a brood should be inversely related to the proportion of copulations received by the nest-male. We tested this prediction on data from 19 nests of polyandrous groups where we had detailed observations on female copulation behaviour. Figure 2 shows the estimated relation between a nest-male's share of copulations and his probability of siring offspring, based on a repeated-measures logistic regression analysis. The percentage of copulations received by the nest-male significantly predicted the probability of EPFs within the brood ($\chi^2 = 7.85$, $p < 0.01$). The greater the percentage of nest-male copulations, the lower the probability of an EPF.

The close association between a nest-male's probability of siring offspring and the share of copulations it receives at the time of laying suggests that females are unlikely to be using stored sperm from previous nesting cycles to fertilize eggs. Two additional lines of evidence reinforce this conclusion. First, we had behavioural observations at 13 nests where EPF sires were identified or inferred. Each of the 17 co-mate sires at these nests was observed copulating just before or during the laying of the sampled clutch. Second, nearly one-third of our sampled clutches (23 out of 74) were produced a median of ten days (range 5–25 days) after the female had laid a clutch for a co-mate. Although this interval between the last day of copulation with the co-mate (now incubating) and ovulation of the first egg in the sampled clutch was well within the range of viable sperm storage (Birkhead & Møller 1992), not a single young in the second brood was sired by the incubating male. The high copulation rate during production of a current clutch, coupled with continuous passive loss of sperm from sperm-storage tubules (affecting sperm from current as well as pervious inseminations) (Birkhead *et al*. 1995) seemingly make fertilizations by stored sperm from a former nesting a rarity.

A nest-male's risk of cuckoldry was also strongly dependent on the reproductive status of its co-mates. Not all males in a female's harem were equally likely to engage in sexual activity. It was extremely rare for the female to copulate with males that were incubating eggs or tending small chicks (less than 25 days old), whereas co-mates tending older chicks or not parentally engaged often did copulate with their females. We refer to the latter two classes of male as sexually available males.

Several lines of evidence indicate that sexually available co-mates pose a threat to the paternity of a male receiving eggs, but co-mates that are incubating eggs or tending small chicks do not. First, 15 of the 17 identified EPF sires as well as all four inferred but unsampled EPF sires were co-mates available to receive a clutch of their own (i.e. they were sexually 'available' in our terminology). The two exceptions were males tending chicks aged 15 and 19 d at the time of clutch initiation. In each of the cases for which we have behavioural data ($n=17$), the known or inferred co-mate sire was observed copulating at the time when the EPF clutch was being laid (see above).

Second, the risk of cuckoldry was strongly associated with the presence of an 'available' co-mate in the group. There were no EPF young in broods of monandrously paired males, whereas 30% of broods of polyandrously mated males contained one or more EPF young (figure 3*a*). When polyandrously mated males were partitioned according to whether or not co-mate(s) were sexually available when a clutch was being produced, a clear pattern emerged. Again, there were no EPF young in broods of polyandrously paired males when all co-mate(s) were either incubating eggs or tending small chicks. However, the frequency of broods containing EPF young rose dramatically to 38% and 50%, respectively (17% and 18% of chicks), in polyandrous associations where one, and two or more, sexually available co-mates were present (figure 3*b*). This increased risk of cuckoldry was confirmed by using a repeated-measures logistic regression, which modelled the per-chick probability of EPF ($\chi^2=14.85$, $p<0.01$). The significance is due to the presence of at least one competing co-mate; additional sexually available co-mates did not further increase risk ($\chi^2=0.74$, $p>0.3$).

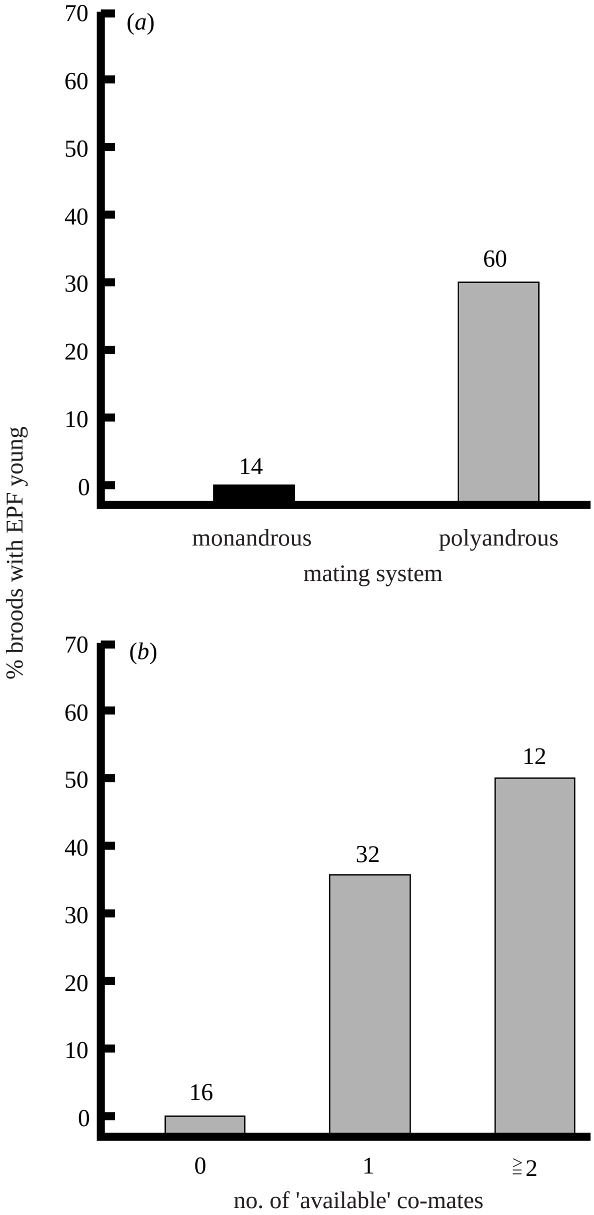

Figure 3. The risk of EPF young as a function of (*a*) mating system and (*b*) number of sexually available co-mates in polyandrous groups ('sexually available', males not incubating eggs or tending chicks of age <25 days). Sample sizes are indicated above bars. Within panels, all categories are significantly different from all others ($p<0.05$, Bonferroni-corrected), except 1 and $\geqslant 2$ in (*b*).

Finally, for broods where behavioural observations confirmed that the female had copulated with both the nest-male and a co-mate ($n=19$), 74% of broods contained EPF young (29% of chicks were of EPF origin).

4. DISCUSSION

Our finding of a relatively low population-wide frequency of EPFs (7.5% of chicks; 17.9% of broods) is similar to results obtained in studies of sex-role-reversed shorebirds that are sequentially polyandrous: 0% of chicks in Wilson's phalarope, *Phalaropus wilsonia* (Delehanty *et al*. 1998); 4.6% in the Eurasian dotterel, *Charadrius morinellus* (Owens *et al*. 1995); 6.8% in the red phalarope, *Phalaropus fulicarius* (Dale *et al*. 1999); and 8.6% in the spotted sandpiper, *Actitis macularia* (Oring *et al*. 1992). These values are considerably lower than those reported for many socially monogamous bird species (reviewed in Birkhead & Møller 1992; Westneat & Webster 1994) and are seemingly consistent with expectations of a high certainty of paternity in species where males are the primary providers of parental care.

However, our results differ from those obtained for sex-role-reversed, sequentially polyandrous species in two important ways. First, the primary source of EPFs in wattled jacanas is not sperm stored from previous matings, but rather sperm recently acquired from males simultaneously paired to the female. Such co-mates are competitors, both for receipt of the clutch (i.e. for becoming nest-males) and for copulations that may fertilize eggs within the clutch.

Second, despite a total absence of EPF young in monandrous nestings, the cuckoldry risk for male jacanas in polyandrous associations was often high. 41% of broods contained EPF young (and 17% of chicks were of EPF origin) at nests where one or more co-mates were present that were not either incubating eggs or tending young chicks. For the subsample of nests where behavioural observations confirmed that the female copulated with multiple males, the corresponding values were 74% of broods and 29% of chicks.

Paternity data are not available for other species of jacana. However, simultaneous polyandry occurs in five out of the seven additional jacana species, and in three of these (*J. spinosa* (Jenni & Collier 1972); *Actophilornis africanus* (Tarboton 1992); *Metopidius indicus* (S. H. M. Butchart, unpublished data)), the female is known to copulate with multiple mates before, and during, laying for one of them. On the basis of these similarities, we predict that polyandrous mating will entail a cuckoldry cost for males in each of these species.

This cost of polyandry would be reduced if cuckolded nest-males had a sufficient and reliable probability of siring young in broods tended by their co-mates: in essence, a system of reciprocal cuckoldry. However, over an entire breeding season, wattled jacana males in a polyandrous group differ widely in the number of nests for which they are 'available' and could potentially be cuckolders. Conversely, some males may receive clutches only during periods when all co-mates are parentally engaged and thus have minimal risk of being cuckolded. Finally, the composition of a female's harem changes over time, as new males are added or old males lost (S. T. Emlen and P. H. Wrege, unpublished data). The lack of stable harem membership, coupled with each male's selfish gain from maximizing its chances of securing EPFs in co-mate clutches while minimizing the chances of co-mates obtaining EPFs in clutches of its own, make any stable system of reciprocal cuckoldry unlikely.

The finding that a conditional class of males (those with sexually available co-mates in the same group) are at a high risk of cuckoldry seems at odds with expectations of high paternity assurance in systems with male uniparental care. This paradox is doubly surprising in our study system, where open habitat and conspicuous copulation behaviour virtually assures that nest-males can directly assess their risk of being cuckolded. Sexually active co-mates pose a potential paternity threat in all simultaneously polyandrous species, including those that do not show sex-role reversal (Burke *et al*. 1989; Jamieson *et al*. 1994; Millar *et al*. 1994; Faaborg *et al*. 1995). However, in systems with biparental or cooperative care, cuckolded males have the option of withholding some or all of their care (see, for example, Davies *et al*. 1992). This option is much more costly in sex-role-reversed systems, such as that of the wattled jacana, where females do not compensate for reduced male care. Indeed, jacanas represent an avian extreme in the development of role reversal, in that a critical component of parental behaviour, namely incubation of the clutch, is totally absent from the repertoire of females (Hoffmann 1949; Osborne & Bourne 1977; Jenni & Betts 1978; Tarboton 1992; S. T. Emlen and P. H. Wrege, unpublished data; Butchart 1999).

We suggest that, whereas a high certainty of paternity may be essential for the initial evolutionary origin of male uniparental care, it is less so for the continued maintenance of such care. This suggestion is in accord with game theoretic models, which indicate that once desertion has evolved in one sex, the other may become 'trapped' in the care-giving role (Maynard Smith 1977, 1982; Vehrencamp & Bradbury 1984).

When the risk of cuckoldry is high, sexual conflict is predicted, both between the sexes and among the males paired to the same female. Under such conditions, there should be strong selection on traits that increase the parental male's certainty of paternity. The combination of extreme sex-role reversal, simultaneous polyandry, and a high potential risk of cuckoldry, makes jacanas model systems for studying sexual conflicts between the sexes, as well as strategies of paternity protection in a species in which males are both smaller than, and behaviourally subordinate to, females.

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