

Testing the function of petal-carrying in the Red-backed Fairy-wren (*Malurus melanocephalus*)

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Abstract. In most species of fairy-wren (*Malurus* spp.), males are known to carry brightly coloured petals and display them to conspecifics. Although petal-carrying by males is often considered an inter-sexual courtship display, anecdotal observations suggest that it may also serve an intra-sexual aggressive function. In this study, we tested hypotheses for the function of petal-carrying displays in the Red-backed Fairy-wren (*Malurus melanocephalus*) through behavioural observations and aviary-based experiments. All petal displays observed were perpetrated by males, with 90% directed toward females and 10% toward other males. Most petal displays were performed by males in nuptial plumage during intrusions into neighbouring territories, and most displays coincided with the potential fertile period of the female to whom the display was directed. Display items consisted primarily of seeds from *Gahnia* sp. and flowers from *Banksia* sp. and *Lantana* sp., all of which were red or pink and similar to the red backs of nuptial males. Aviary trials found no significant difference in the responses by adult females or adult males to stimulus males with or without petals, substantiating neither a courtship role nor an aggressive role for the display. On the basis of the context of displays in the field, we conclude that the petal-carrying display in the Red-backed Fairy-wren primarily serves an inter-sexual, courtship function, though we could not rule out an intra-sexual, aggressive function.

Introduction

Foreign objects play an important role in the displays of many Australian birds. Male bowerbirds, for example, use coloured objects such as glass, fruits, flowers, and feathers to decorate their bowers, and in at least one species (Satin Bowerbird, *Ptilonorhynchus violaceus*) the mating success of males covaries with the number and colour of decorations used (Borgia 1985). Similarly, male fairy-wrens (*Malurus*) sometimes pluck brightly coloured flower petals and display them prominently in their bill to conspecifics, a display termed petal-carrying (Rowley and Russell 1997). There are several anecdotal or descriptive accounts of petal-carrying by fairy-wrens (*sensu* Rowley and Russell 1997), but little effort has been made to test the function of this unusual and striking display.

Petal-carrying has been observed in eight of the nine species of fairy-wren found in Australia (Rowley and Russell 1997). However, careful study of petal-carrying has been limited to members of the 'blue wren' clade, specifically the Superb Fairy-wren (*Malurus cyaneus*) and the Splendid

Fairy-wren (*Malurus splendens*). Petal colour may either contrast with, or be similar to, the colour of a male's nuptial plumage. For example, Superb Fairy-wrens typically carry yellow petals, which contrast with their blue plumage (Mulder 1997), while Splendid Fairy-wrens typically carry pink or purple flower petals, which complement their blue plumage (Rowley 1991a). Although particular species consistently use the same coloured petals in their displays, use of a particular colour does not necessarily reflect the frequency of that colour in its habitat (Rowley 1991a).

It has been proposed that petal-carrying displays have a courtship function, serving as an inter-sexual signal by adult males to fertile females (Rowley and Russell 1990; Rowley 1991a). The courtship function for petal-carrying is suggested by the context in which the displays occur: most often in the presence of one or more females. A displaying male will occasionally pursue a female with a petal in his bill (Hindwood 1948; Jack 1949; Strong and Cuffe 1985; Rowley 1991a; Mulder 1997), and he may offer the petal to her (Strong and Cuffe 1985; Rowley 1991a). *Malurus* spp.

have a socially monogamous but a sexually promiscuous mating system in which a female forms a long-term social pair bond with a male but is frequently fertilised by other males (Brooker *et al.* 1990; Mulder *et al.* 1994). Although petal-carrying has been observed by male fairy-wrens in their own territories, it often occurs during intrusions into neighbouring territories (Rowley 1991a; Mulder 1997). Such intrusions and accompanied displays, including petal-carrying, have been interpreted as attempts by males to obtain extra-pair copulations (Rowley and Russell 1990).

Other observations, however, suggest that petal-carrying may also serve a non-courtship, intra-sexual function. Two lines of evidence suggest that this may be the case. First, petal-carrying sometimes occurs when females are not fertile, including months outside of the breeding season (Mulder 1997). Second, some petal-carrying displays appear to be directed to males, not females. Many accounts place petal-carrying males alone, in the presence of other males, or in mixed groups of both males and females (Hindwood 1948, 1951; Loaring 1948; Strong and Cuffe 1985; Hughes and Hughes 1988; Rowley 1991a, 1991b; Strong 1990), and it is not always clear to which bird the display is directed. In the Red-backed Fairy-wren (*Malurus melanocephalus*), for example, a significant proportion of petal-carrying displays were directed toward males, not females, as described below.

In this paper, we document petal-carrying displays in a colour-banded population of Red-backed Fairy-wrens, and we use field observations in combination with aviary-based experiments to test hypotheses for the function(s) and implications of petal-carrying in this species. Red-backed Fairy-wrens are distributed throughout northern, tropical Australia (Schodde 1982; Rowley and Russell 1997), and, to date, eight instances of petal-carrying have been documented in this species. Most of these displays have involved red objects; these included a red petal on three occasions, a red berry or seed on three occasions, an orange flower petal, and a yellow flower petal (Hindwood 1948; Jack 1949; Hughes and Hughes 1988; Strong 1990; Rowley 1991b). Red-backed Fairy-wrens maintain small territories in which an adult female and her adult male partner raise young, occasionally with the assistance of one or more adult male offspring who have delayed dispersal (Rowley and Russell 1997). Most males spend their first breeding season in female-like, brown plumage ('dull plumage') and acquire nuptial black and red plumage ('bright plumage') in subsequent breeding seasons. Both dull and bright males form pair bonds, and dull plumage is associated with reduced aggression from older males but higher levels of within-brood cuckoldry than is bright plumage (Karubian 2002).

Methods

General field methods and behavioural observation

All field research and experiments were conducted in forests surrounding the Moomin Reservoir, 5 km outside the town of Herberton, on the

Atherton Tableland in Queensland, Australia (17°23'S, 145°25'E). This study spanned three breeding seasons (October–February) from 1997 to 2000. During this time we colour-banded and monitored the population biology and behaviour of all Red-backed Fairy-wrens within an area of 2.5 × 1 km. Behaviour was quantified in focal animal samples that averaged 28.2 ± 0.12 min (range 15–45 min). In the focal samples, presence/absence on territory, distance from mate, and activity were recorded using instantaneous scan samples at 60-s intervals. Displays, departures from territory to intrude on neighbouring groups, intrusions onto territory by neighbouring males, and vocalisations were recorded on a continuous basis.

All field data presented in this paper are based on observations of banded males whose age, status and plumage were known. In addition to recording the identity of the displaying male, we also recorded the identity of the individual to whom the display appeared to be directed, and the nesting stage (i.e. pre-nest construction, nest construction, incubation, feeding nestlings, or caring for dependent fledglings) of both individuals. Nesting stage was determined by finding active nests; if a nest was found during incubation or nestling stages, dates of construction and pre-construction phases were back-calculated using average length of each stage for the population (Karubian, unpublished data). A female was considered to be potentially fertile during nest construction and pre-nest construction stages, which lasted, on average, 17 and 15 days. However, while there is good evidence that female fertility peaks in the days immediately before laying (Double and Cockburn 2000), it is not clear for how many days prior to laying a female is potentially fertilisable. Thus, the fact that we treat females in pre-nest construction phase and in the first days of nest construction phase as sexually receptive is an assumption which may or may not be true.

Aviary-based choice trials

In the year 2000, we conducted choice trials in specially constructed choice chambers (Fig. 1). All trials were conducted in January 2000, during peak breeding for the study population. Up to four trials were conducted per day, and trials took place between 0700 and 1100 or 1500 and 1700 hours. There was no difference in the outcomes of the trials in relation to time of day. All birds were banded with a single metal band and three colour bands. Colours matching the plumage of Red-backed Fairy-wrens (black, red, orange and pink) were avoided and there was no difference in outcome of the trials in relation to band colours.

Birds used in the trials were trapped off the study site and were kept as family groups in holding cages visually isolated from other holding cages. Depending upon the size of the family group, 2–6 individuals were kept in each cage. All cages were built of wood with a wire mesh front and measured 0.7 × 0.7 × 0.8 m. During captivity, birds were provided with meal worms and water *ad libitum*, as well as perches and vegetation in which to hide. Birds were weighed upon capture and during captivity to make sure they were not losing weight due to stress, and a visual examination of each bird was made before including it in the experiments. Birds used in experiments were transferred between the aviary and the choice apparatus by catching them by hand and placing them in a cloth holding bag (the choice apparatus had sliding walls (thick solid lines in Fig. 1) which could be closed to keep the 'choosing' bird in the central chamber, a small area in which capture by hand was easy). Birds used in the experiments were released at the point of capture as family groups at the end of the trials.

We conducted three types of trials, two in which females were provided with a choice between two stimulus birds, and one in which adult males were provided with a choice between two stimulus birds. In the first round of female-choice trials, a female chose between an adult male in bright plumage and a female. Eight of these 'female sexual choice' trials were conducted to determine whether females were making a sexual choice. All eight females used in these 'female sexual

choice' trials were included in subsequent 'female petal choice' trials described below. A sub-set of males used as stimulus birds in the 'female sexual choice' trials were also used as stimulus birds in subsequent trials described below ($n = 5$ males recycled), but females were never paired with the same male twice.

Following the 'female sexual choice' trials, we conducted two subsequent rounds of aviary experiments: 'female petal choice' trials and 'male petal choice' trials. In the 'female petal choice' trials, the same females from the 'female sexual choice' trials described above chose between two bright stimulus males: a control male and one with an artificial petal attached to his bill. We conducted eight of these 'female petal choice' trials, each of which used a different focal female.

Eight males were used as stimulus birds in the 'female petal choice' trials. These eight stimulus males were divided into four pairs, and each pair was used in two different trials. In one of the two trials, one male had the petal; in the second trial, the other male had the petal. Thus, each of the eight stimulus males participated in two 'female petal choice' trials, one in which he had an artificial petal attached and one in which he had no petal.

The third type of choice trial, the 'male petal choice' trials, had the same design as the 'female petal choice' trials with one difference: 'male petal choice' trials featured the response of a focal nuptial male, rather than a focal female, to two stimulus males – again, one with an artificial petal and one without. As with the other choice trials, each of

the eight 'male petal choice' trials featured a different focal male making the choice between stimulus birds.

To reduce the number of birds used in the experiments, the same stimulus males were paired together for both the 'female' and 'male' petal choice experiments. Thus, there were eight stimulus males used in all the petal choice trials. Each male was used as a stimulus male in four trials: two 'female petal choice' trials (one with and one without the petal) and two 'male petal choice' trials (one with and one without the petal). Further, each of these males was used one time as the choosing male in the 'male petal choice' trials, and a sub-set were also used as stimulus birds for the 'female sexual choice' trials. The plumage score, tarsus length, and mass of paired stimulus males were within one standard deviation of the population mean of each other. This experimental design was chosen to control for individual differences between the males and to focus on the effects of the presence or absence of the petal.

Artificial petals were created using bright pink flagging tape similar to the colour and shape of flowers of *Lantana* sp. *Lantana* sp. was a common shrub on the study site and its flowers were commonly used by free-flying males in petal-carrying displays. To standardise the petals used in the experiments, artificial petals were created by taking a hole punch of the flagging tape, which closely resembled the size and shape of flowers of *Lantana* sp. on the study site. There was no spectrophotometer available to quantify the resemblance of the artificial to the actual petals. The circular, artificial petals were temporarily affixed to the side of the top portion of the bill of stimulus males using a dab of non-toxic adhesive. At the end of each trial, the petal and glue were easily and immediately removed.

All of the choice trials were conducted in mate-choice chambers which measured $1.5 \times 0.75 \times 0.75$ m (Fig. 1). Individuals trapped within 2 km of each other were never paired in the same trial. Both males and females were allowed at least three days to acclimatise to captivity before being used in the trials. Individuals housed in the same cages were never used in the same trial. Females, but not males, went through a single 60-min acclimation period before being used in a choice trial. Only those females that visited both sides of the apparatus were used in subsequent trials.

Choice trials lasted 60 min, with a 5-min acclimation period at the onset of the trial. The choice apparatus was located in habitat in which Red-backed Fairy-wrens occur, and it was shaded from the sun. To control for side preferences associated with the habitat or stimuli from outside the apparatus, the entire apparatus was rotated 180° after the first 30 min, followed by another 5-min acclimation period. To control for side preferences associated with the apparatus itself, the side on which stimulus males were placed was randomly selected. An observer hidden in a blind 6 m from the choice apparatus recorded the behaviour of the birds in the trial, including time that the focal bird spent associating (defined as being in the side chamber of one of the two stimulus males while moving and/or vocalising at least once every 5 s) with each stimulus male and any displays or vocalisations exhibited by any of the birds. Time spent on a stimulus bird's side of the cage searching for insects, preening, or bill wiping was not recorded as associating. No food or water was provided to the birds during the trials. All individuals used in the trials were released at their point of capture at the experiment's end.

Both field- and aviary-based research were conducted with all applicable permits from the Department of Natural Resources (Queensland), the Department of Environment and Heritage (Queensland), and the Animal Care protocols of the University of Chicago (IACUC).

Statistical analyses

All tests conducted were two-tailed. Results of aviary-based choice trials were analysed using unpaired *t*-tests (i.e. each of the eight trials

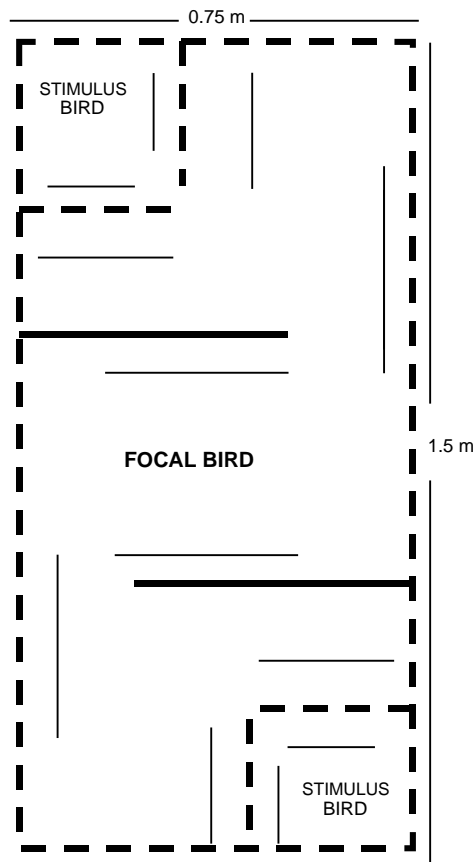


Fig. 1. Schematic of mate-choice apparatus, measuring $0.75 \text{ m} \times 0.75 \text{ m} \times 1.5 \text{ m}$. Dashed lines represent wire mesh through which birds could interact but not pass. Thin solid lines represent perches. Thick solid lines represent plywood walls through which birds could not pass or see.

was treated as a separate data point); results did not change qualitatively when pairs of stimulus males were compared using paired *t*-tests. Data are presented as means \pm standard error unless otherwise stated.

Results

Behavioural observations

We conducted 1263 focal samples (329 samples on 27 dull males and 934 samples on 70 bright males) and recorded 1214 displays. Among all displays recorded (Table 1), petal-carrying displays were relatively rare. All petal-carrying displays were conducted by breeding males (males with an enlarged cloacal protuberance who had formed a social pair with a female and who nested at least once during the course of the breeding season). Most petal-carrying displays (73 of 79 = 92%) were by males in nuptial plumage, with the remainder by males in dull plumage (6 of 79 = 8%).

Although most petal-carrying displays (71 of 79 = 90%) were directed toward adult females, about 10% (8 of 79) were directed toward breeding males or adult male helpers. Most petal-carrying displays for which information was available (50 of 68 = 74%) were directed toward females who were either in pre-nest construction or nest construction phases of breeding, when females are potentially sexually receptive. About 50% of the petal-carrying displays recorded (39 of 79) occurred when a breeding male in nuptial plumage had departed his own territory and was intruding on a neighbouring group's territory. Of the petal-carrying displays that occurred during these intrusions, 59% (23 of 39) coincided with the potential fertile period (i.e. pre-nest construction or nest construction) of that territory's female.

The most common sources of petals for displays were flowers of *Banksia* sp., red spherical seeds from the grass *Gahnia* sp. and pink flowers from *Lantana* sp. Petals and seeds used in displays were always red or pink.

Aviary-based choice trials

To test the function of petal-carrying displays, we conducted a series of aviary-based choice trials. 'Female sexual choice' trials, in which females were presented with a choice

between a bright male and a female, showed that females were making a sexual choice: focal females chose to associate more with stimulus males than with stimulus females ($t_{14} = -4.76$, $P < 0.001$) (Fig. 2). None of the eight females tested in the 'female sexual choice' trials associated more with a stimulus female than with a stimulus male. In 'female petal choice' trials, however, the presence or absence of an attached, artificial petal had no effect on the amount of time a female spent with a stimulus male ($t_{14} = -0.852$, $P = 0.41$) (Fig. 3). Similarly, in 'male petal choice' trials, there was no difference in amount of time bright males spent associating with stimulus males with or without petals ($t_{14} = -0.44$, $P = 0.66$) (Fig. 4).

During both the 'female' and 'male' petal choice trials, puffback displays (Schodde 1982; Rowley and Russell 1997) did not vary between petal and non-petal stimulus males. There was a total of eight puffbacks (three to females, five to males) given by three males with petals, as opposed to a total of four puffbacks (two to females, two to males) given by three males without petals. Central bright males directed one puffback display each to petal and non-petal stimulus males.

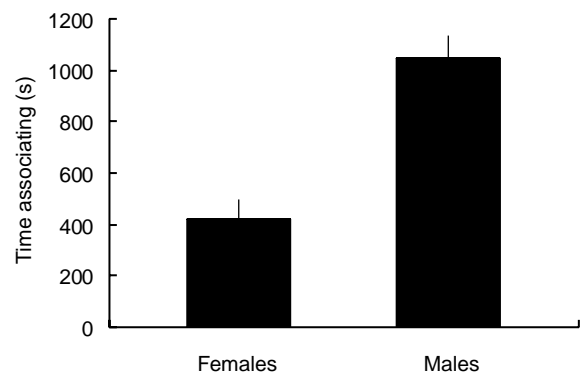


Fig. 2. Results of aviary-based 'female sexual choice' trials. Shown are means \pm standard error of time that focal females spent associating with adult males and females. Focal females spent significantly more time associating with stimulus males than with stimulus females.

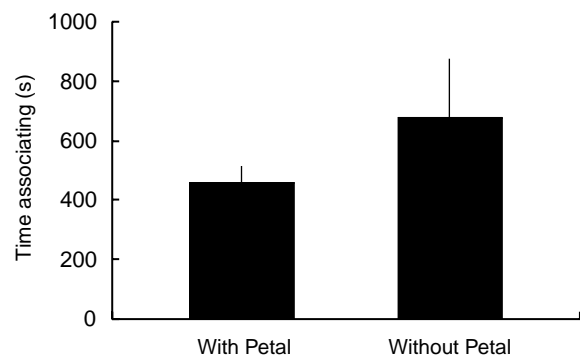


Fig. 3. Results of aviary-based 'female petal choice' trials. Shown are means \pm standard error of time that focal females spent associating with adult males with and without petals. There was no difference in the time that females spent associating with the two classes of stimulus males.

Table 1. Type and frequency of displays by adult male Red-backed Fairy-wrens

'Display recipient' refers to the sex of the individual at which the display was directed

Display	<i>n</i>	% of total	Display recipient	
			Male	Female
Puffback	325	26.8	67	258
Aggressive chase	262	21.6	252	6
Courtship chase	241	19.9	0	240
Raised crest	139	11.5	22	115
Feed mate	100	8.2	0	100
Petal-carrying	79	6.5	8	71
Wing flutter	68	5.6	3	59
Total	1214	100.0	347	854

In terms of vocalisations, there was no courtship singing, but we did record a low level of scolding [a vocalisation similar to the alarm call described in Rowley and Russell (1997), but which Red-backed Fairy-wrens also use in intraspecific, agonistic interactions]. In the trials, one non-petal male was scolded 20 times by a central female, and one petal male was scolded 50 times by a central male.

Discussion

Observation of banded individuals in the field supports the hypothesis that petal-carrying displays in Red-backed Fairy-wrens primarily serve a courtship function. Most petal-carrying displays were conducted by males in nuptial plumage and were directed toward their social mates or females upon whose territories the males had intruded. Further, nearly three-quarters of all petal-carrying displays were directed toward females who were potentially sexually receptive. Petal-carrying displays may function as a form of self-advertisement by accentuating a male's bright plumage, which females may use to assess male quality (Rowley and Russell 1997). Another possibility is that petal-carrying displays, which are conspicuous to predators as well as conspecifics, act as a handicap that could demonstrate the fitness of the displaying male (Zahavi 1977).

Nearly half the petal-carrying displays recorded in this study occurred during an intrusion by a male in nuptial plumage onto a neighbouring territory. Møller (1987) proposed three possible functions of conspecific territory invasions: prospecting for vacancies by non-territory holders, establishing territory boundaries, or seeking extra-pair copulations. Groups in the study population did not enforce strict territory boundaries (Karubian, unpublished data), and all males observed engaging in petal-carrying displays already had territories, making it likely that the intrusions and subsequent petal-carrying displays served a courtship function. This is consistent with other studies which have also demonstrated that a large proportion of petal-carrying occurs

during intrusions, i.e. 56% and 97% in the Splendid and Superb Fairy-wrens respectively (Rowley 1991a; Mulder 1997). In our study population, nuptial males (the class that most frequently engages in petal-carrying displays) have relatively low rates of cuckoldry within their own broods relative to dull males and most likely monopolise extra-pair copulations (Karubian 2002).

Although roughly 10% of the petal-carrying displays we observed appeared to be directed toward males, we found little additional evidence that the displays serve an intra-sexual, aggressive function. Further, some of the petal-carrying displays that we recorded as male–male also occurred in the presence of a female. Although these displays appeared to be directed toward the male, it is possible that they had been intended for the female. In sum, the context of petal-carrying displays observed in the field is consistent with a courtship function, but provides only limited support for an aggressive function.

Aviary-based tests of the function of petal-carrying displays were equivocal, and they failed to provide strong support for either a courtship or an aggression function for the display (Figs 3, 4). The lack of variation in the response of both adult females and adult males to the presence or absence of an artificial petal may have been related to possible stress related to captivity. However, females clearly demonstrated a strong preference for nuptial males over females in the 'female sexual choice' trials (Fig. 2), indicating that the birds used in the trials were capable of making a sexual choice. Furthermore, in comparable choice experiments based on plumage differences between adult males, both females and males showed statistically significant patterns of preference (Karubian 2002).

Alternatively, although the artificial petals used in the trials closely resembled petals of *Lantana* sp. to the human eye, they may not have been suitable replicas for the birds involved in the experiments. Neither the spectral characteristics of the artificial petals nor the flowers were quantified because a spectrophotometer was unavailable, an admitted deficiency of the experimental design. However, because Red-backed Fairy-wrens in general have been observed to use petals, berries, and seeds that span a range of colours in their displays (red, pink, orange and yellow) and because there is also large variation in colour between different *Lantana* flowers, it may be that exact matching of the spectral characteristics is not critical.

It is also possible that aviary-based experiments failed to show a pattern because Red-backed Fairy-wrens may not show an immediate response to many displays, including petal-carrying. In fairy-wrens, copulation has rarely been observed to follow a petal-carrying display (Rowley 1991a; Mulder 1997), and females in the field often show little, if any, interest in petal-carrying by males (Loaring 1948; Strong and Cuffe 1985; Rowley 1991a; Mulder 1997). In fact, most accounts do not report any female response to

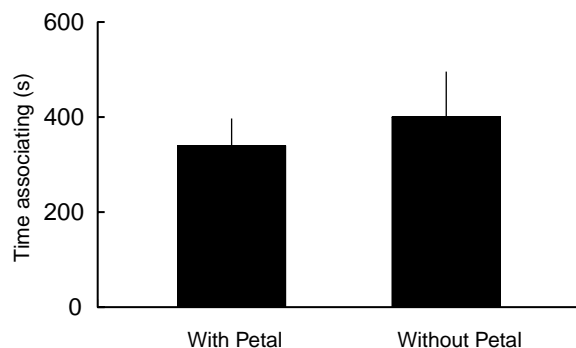


Fig. 4. Results of aviary-based 'male petal choice' trials. Shown are means \pm standard error of time that focal adult males spent associating with adult males with and without petals. There was no difference in the time that focal males spent associating with the two classes of stimulus males.

petal-carrying displays, presumably because there was none. Since many petal-carrying displays are performed by intruding males, a female's uninterested appearance could eliminate potential repercussions from her social mate such as a reduction in parental care (Burke *et al.* 1989). Alternatively, in at least one species of fairy-wren (Superb), females engage in extra-pair copulations during pre-dawn forays in which they fly to the territory of the male with whom they wish to copulate (Double and Cockburn 2000). Thus, the lack of an immediate response by females does not necessarily imply that the display was ineffective. Males in the field can also be unresponsive to petal-carrying displays; in Superb Fairy-wrens, for example, resident males frequently do not attempt to expel petal-carrying intruders from their territories (Mulder 1997).

The most commonly used display items (seeds from *Gahnia* sp. and flowers from *Lantana* sp. and *Banksia* sp.) are ubiquitous on the study site, suggesting that male Red-backed Fairy-wrens do not select display items according to their rarity value. Instead, the profusion of displays involving red and pink seeds and flowers suggests that that display items are selected to match the bright red backs of males in nuptial plumage. The Red-backed Fairy-wren is the only Australian fairy-wren that has been observed using berries and seeds, all of which have been red, in addition to flowers in these displays (see Rowley 1991a).

In sum, field evidence strongly supports a courtship role for petal-carrying displays, suggested mainly by the large proportion of petal-carrying displays directed toward fertile females. However, aviary trials neither substantiated petal-carrying as a courtship display nor indicated an aggressive function for the display. Without backing from aviary trials, the 10% of petal-carrying displays that appeared to be directed toward other males in the field are themselves insufficient to support an aggressive function.

Acknowledgments

We thank the field assistants who gathered much of the data presented in this paper through observation of banded birds in the field and of captive birds in aviary-based experiments: Team Wren 1998 (J. Mathias, B. Rodriguez and T. Wood), Team Wren 1999 (S. Bartos, R. Bright, S. Jang, J. McCormack and B. Rodriguez), and Team Wren 2000 (R. Atwater, C. Erwin, E. Rockwell and J. Swaddle). S. Lynn, R. McMorran, S. Pruett-Jones, J. Swaddle and the Rust and Risley families were especially helpful. The manuscript benefited from the comments of two anonymous reviewers. This research was supported by grants to JK from the National Science Foundation (Doctoral Dissertation Improvement Grant to S. Pruett-Jones), the American Museum of Natural History (Chapman Fund), the University of Chicago (Hinds Fund), the American Ornithologist's Union, and the Animal Behaviour Society.

References

- Borgia, G. (1985). Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behavior* **33**, 266–271.
- Brooker, M. G., Rowley, I., Adams, M., and Baverstock, P. R. (1990). Promiscuity: an inbreeding avoidance mechanism in a socially monogamous species? *Behavioral Ecology and Sociobiology* **26**, 191–199.
- Burke, T., Davies, N. B., Bruford, M. W., and Hatchwell, B. J. (1989). Parental care and mating behavior of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* **338**, 249–251.
- Double, M. C., and Cockburn, A. (2000). Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society of London (B)* **267**, 465–470.
- Hindwood, K. A. (1948). The use of flower petals in courtship display. *Emu* **47**, 389–391.
- Hindwood, K. A. (1951). Flower petals and bird display. *Emu* **50**, 208–209.
- Hughes, P., and Hughes, B. (1988). Notes on berry and petal display by Red-backed wrens at Widgee, south-east Queensland. *Sunbird* **18**, 52–53.
- Jack, N. (1949). Wren with flower, and mimicry by whistler. *Emu* **49**, 143–144.
- Karubian, J. (2002). Costs and benefits of variable breeding plumage in the Red-backed Fairy-wren. *Evolution* **56**, 1673–1682.
- Loaring, W. H. (1948). Splendid Wren with flower petal. *Emu* **48**, 163–164.
- Møller, A. P. (1987). Intruders and defenders on avian breeding territories: the effect of sperm competition. *Oikos* **48**, 47–54.
- Mulder, R. A. (1997). Extra-group courtship displays and other reproductive tactics of Superb Fairy-wrens. *Australian Journal of Zoology* **45**, 131–143.
- Mulder, R. A., Dunn, P. O., Cockburn, A., Lazenby-Cohen, K. A., and Howell, M. J. (1994). Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proceedings of the Royal Society of London (B)* **255**, 223–229.
- Rowley, I. (1991a). Petal-carrying by fairy-wrens of the genus *Malurus*. *Australian Bird Watcher* **14**, 75–81.
- Rowley, I. (1991b). Petal-carrying by the Red-backed Fairy-wren. *Sunbird* **21**, 112–113.
- Rowley, I., and Russell, E. (1990). "Philandering" – a mixed mating strategy in the Splendid Fairy-wren *Malurus splendens*. *Behavioral Ecology and Sociobiology* **27**, 431–437.
- Rowley, I., and Russell, E. (1997). 'Fairy-wrens and Grasswrens.' (Oxford University Press: Oxford.)
- Schodde, R. (1982). 'The Fairy-wrens: a monograph of the Maluridae.' (Lansdowne: Melbourne.)
- Strong, M. (1990). Furgling by the Red-backed Fairy-wren. *Sunbird* **20**, 37–38.
- Strong, M., and Cuffe, E. (1985). Petal display by the Variegated Wren. *Sunbird* **15**, 71.
- Zahavi, A. (1977). The cost of honesty. *Journal of Theoretical Biology* **67**, 603–605.

Manuscript received 23 October 2001; accepted 2 October 2002