



## Reproductive promiscuity in the variegated fairy-wren: an alternative reproductive strategy in the absence of helpers?

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### ARTICLE INFO

#### Article history:

Received 23 August 2017

Initial acceptance 9 October 2017

Final acceptance 26 February 2018

MS. number: A17-00679R

#### Keywords:

cooperative breeding

extrapair paternity

helping behaviour

kin selection

*Malurus*

mate choice

reproductive strategy

Cooperative breeding, in which auxiliary group members help rear related, but nondescendent young, is often explained by kin selection. Reproductive monogamy is predicted in cooperatively breeding systems, as monogamy increases intragroup relatedness and maximizes auxiliary inclusive fitness. While monogamy is observed across many systems, including eusocial insects and cooperatively breeding mammals, some cooperatively breeding birds exhibit high rates of extrapair paternity. Here we quantify paternity and examine the role of auxiliaries on extrapair paternity in the highly cooperative variegated fairy-wren, *Malurus lamberti*, a species with both male and female auxiliaries. Extrapair paternity occurred in 55.4% of nests, and 39.8% of offspring were the result of extrapair matings. The presence of both male and female auxiliaries had a positive relationship with the percentage of within-pair young sired by dominant males, however, the presence of male auxiliaries had a stronger impact than the presence of females. The number of extrapair young sired by dominant males decreased as the number of male auxiliaries increased. The total number of young sired by dominant males, however, was not predicted by group size or relatedness to their social partner, nor did group composition or relatedness to the breeding pair predict the reproductive success of subordinate males. We hypothesize that breeders use alternative reproductive strategies in the presence or absence of auxiliaries. Males and females may seek extrapair reproductive opportunities when no help is available in their group and nest survival is expected to be low. When help is available, breeders may reduce extrapair paternity, either to increase intragroup relatedness or because confidence in nest survival is high. Our data suggest that group composition is important in understanding extrapair paternity rates in cooperatively breeding birds and that variation in extrapair paternity rates may be the result of flexible breeding strategies when auxiliary presence and identity varies.

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Cooperative breeding is characterized by delayed dispersal of one or both sexes and alloparental care by auxiliary group members (Brown, 1987; Emlen, 1991). Historically, inclusive fitness theory has been used to explain the evolution of cooperative societies, both in vertebrate and nonvertebrate systems (Browning, Patrick, Rollins, Griffith, & Russell, 2012; Hamilton, 1964; Hatchwell, Gullett, & Adams, 2014; West, Griffin, & Gardner, 2007). This theory asserts that inclusive fitness gained by contributing to the raising of putative siblings can outweigh the costs of helping behaviour by auxiliaries and the benefits of independent breeding (Fitzpatrick & Bowman, 2016; Koenig, Pitelka, Carmen, Mumme, &

Stanback, 1992; Mumme, 1992; MacColl & Hatchwell, 2002). It is predicted, and generally supported, that the evolution of cooperative breeding behaviour is linked to reproductive monogamy and high intragroup relatedness (Boomsma, 2013; Cornwallis, West, Davis, & Griffin, 2010; Lukas & Clutton-Brock, 2012). In insects, the evolution of eusociality in many taxa is associated with strict monogamy (Boomsma, 2009), and in cooperatively breeding mammals a single male is responsible for most of the offspring in a social group, varying from 76% to 100% across taxa (Griffin et al., 2003; Lukas & Clutton-Brock, 2012).

Many cooperatively breeding avian taxa conform to expectations of monogamy, such as red-cockaded woodpeckers, *Picoides borealis*, or chestnut-crowned babblers, *Pomatostomus ruficeps*, in which only 0–1% of young are sired by extrapair males (Haig, Belthoff, & Allen, 1993; Haig, Walters, & Plissner, 1994; Russell, 2016). However, some cooperatively breeding avian species exhibit high rates of extrapair

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paternity, such as the superb fairy-wren, *Malurus cyaneus*, which has up to 76% of young sired by extrapair males (Mulder, Dunn, Cockburn, Lazenby-Cohen, & Howell, 1994).

Helping behaviour across avian taxa has been shown to correlate positively with auxiliary relatedness to the nestlings they are providing care to, supporting a leading role for kin selection in either the evolution or maintenance of cooperative breeding in birds (Green, Freckleton, & Hatchwell, 2016). Explaining the variation in reproductive promiscuity present in cooperatively breeding birds has been the subject of much research, as it does not conform to the expectations of a kin-selected explanation for cooperative breeding, causing auxiliaries to invest in unrelated young to themselves (Dunn, Cockburn, & Mulder, 1995). When auxiliaries are sons or daughters of the breeding pair, promiscuity can decrease the relatedness of auxiliaries to the nestlings they are rearing by 50%. Furthermore, if the mother of the auxiliaries has been replaced, and an unrelated female gains the breeding vacancy, auxiliaries may be unrelated to all offspring produced by extrapair copulations.

Fairy-wrens (Maluridae) were among the first documented cooperatively breeding birds (Boland & Cockburn, 2002), and since this discovery, every species in the genus *Malurus* that has been studied has been documented as breeding cooperatively (e.g. Brouwer, van de Pol, Atema, & Cockburn, 2011; Dunn & Cockburn, 1996; Kingma, Hall, Segelbacher, & Peters, 2009; Pruett-Jones & Tarvin, 2001; Rowley & Russell, 1995; Tidemann, 1983). While fairy-wrens serve as models for research on cooperative breeding, they are also atypical because of their extremely high rates of extrapair paternity (varying from 4% to 76%). Rather than linking helping behaviour to monogamy as expected and observed in many cooperative breeders (Green et al., 2016), the presence of auxiliaries has been correlated with increased rates of extrapair paternity in at least four fairy-wren species (Brouwer et al., 2017; Mulder et al., 1994; Webster, Tarvin, Tuttle, & Pruett-Jones, 2004). It has been suggested that the presence of auxiliaries liberates breeding females to engage in extrapair copulations by ensuring help at the nest and buffering any possible retaliatory reduction in the investment of the dominant male (Mulder et al., 1994). However, similar rates of extrapair paternity have been observed in superb fairy-wren populations with both high and low numbers of auxiliaries (Colombelli-Négrel, Schlotfeldt, & Kleindorfer, 2009), and males of the red-backed fairy-wren, *Malurus melanocephalus*, have not been found to reduce parental investment in nests with extrapair young (Varian-Ramos, Lindsay, Karubian, & Webster, 2012). These findings suggest that there are additional factors besides female liberation influencing extrapair paternity in this family, for example inbreeding avoidance, amount of help received or population density (Cockburn, Brouwer, Double, Margraf, & van de Pol, 2013; Brouwer et al., 2017).

Here we investigate rates of extrapair paternity in one of the most social of the fairy-wren species, the variegated fairy-wren, *Malurus lamberti*. In the variegated fairy-wren, auxiliaries show extreme variation in number (from 0 to 8 in some populations: D. Thrasher, personal communication), sex and contribution (Johnson, 2016). In general, delayed dispersal and helping behaviour in birds is more common in male auxiliaries (Cockburn, 1998; Cornwallis, West, & Griffin, 2009). However, in variegated fairy-wrens nearly half of all auxiliaries are female (~43% in our population). While both sexes perform helping behaviours, male auxiliaries provision nestlings at a higher rate than females (2.29 feeds/h and 0.52 feeds/h, respectively) and only 11% of male auxiliaries have been observed to not provision, whereas up to 31% of female auxiliaries do not provision (Johnson, 2016; Johnson & Pruett-Jones, 2017).

This system provides a unique opportunity to examine the role not only of group size, but also of group composition on extrapair paternity.

## METHODS

### *Study System and Field Methods*

This research was conducted at Brookfield Conservation Park (BCP) from 2012 to 2015. BCP, located in South Australia (S 34°21', E 139°29'), is a 5534 ha park characterized by mallee eucalyptus scrub forest and chenopod scrub habitat and supports populations of three species of fairy-wren, the variegated fairy-wren, the splendid fairy-wren, *Malurus splendens*, and the white-winged fairy-wren, *Malurus leucopterus* (Department for Environment and Heritage, 2005; Tibbetts & Pruett-Jones, 1999). Variegated fairy-wrens were mostly found within the mallee scrub often co-occurring with splendid fairy-wrens (Johnson, 2016; Tibbetts & Pruett-Jones, 1999).

Each year we surveyed family groups of variegated fairy-wrens from mid-September until late December. This time period encompassed the majority of breeding attempts; however, some nesting attempts were observed at the end of the field season, suggesting that some breeding likely occurs in January, as seen in the splendid fairy-wren (Van Bael & Pruett-Jones, 2000).

A colour-banded population of variegated fairy-wrens was established at this site in 2012. Adult birds were captured by targeted mist netting, a method that minimizes bicatch and the duration of time birds are left alone in the net unattended. Adults were banded with a unique combination of three colour bands and an individually numbered metal band issued by the Australian Bird and Bat Banding Scheme. We determined the age of birds when possible. Birds that were captured and banded as juveniles were of known age, while unbanded males could often be aged to 1 year if they exhibited partial plumage or if their bill colour had not yet changed from brown to black. In male variegated fairy-wrens as in some other species of fairy-wrens, the colour of the bill changes from brown to black at approximately 1 year of age, after which it remains black (Rowley & Russell, 1997; A. E. Johnson, personal observation). While some first-year males exhibit adult plumage, many exhibit either female-like plumage or partial mature plumage. Such delayed plumage maturation is also observed in other fairy-wren species (Karubian, 2002; Rathburn & Montgomerie, 2003; Rowley & Russell, 1997; Webster, Varian-Ramos, & Karubian, 2008). At the time of capture, morphological measurements were taken, and a blood sample was taken by brachial vein puncture and stored dry on Whatman® FTA cards for later DNA extraction.

Once individuals were colour banded, they could be assigned to groups that were then monitored for composition, nesting behaviour and territory size. Each year between 37 and 70 family groups were studied. Family groups contained at least one male and one female, but groups often contained auxiliary group members. Auxiliaries are often referred to as 'helpers' throughout cooperative breeding literature. In the variegated fairy-wren, auxiliary members of both sexes do help in provisioning young, among other behaviours. However, individuals and sexes vary in the degree of helping behaviour, and because we do not quantify helping behaviour of individuals here, we refer to these group members as 'auxiliaries'. The largest observed social group in our population contained seven auxiliaries (total group size of 9). Mean group size varied between years from 2.91 to 4.24, with 54.29%–75.68 % of groups containing one or more auxiliary members. As with other fairy-wren species (Margraf & Cockburn, 2013; Mulder et al., 1994;

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