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To cite this article: Erik D. Enbody, Jordan Boersma, John Anthony Jones, Matthew W. H. Chatfield, Serena Ketaloya, Doka Nason, Daniel T. Baldassarre, Jenny Hazlehurst, Olivia Gowen, Hubert Schwabl & Jordan Karubian (2019) Social organisation and breeding biology of the White-shouldered Fairywren (*Malurus alboscapulatus*), *Emu - Austral Ornithology*, 119:3, 274-285, DOI: [10.1080/01584197.2019.1595663](https://doi.org/10.1080/01584197.2019.1595663)

To link to this article: <https://doi.org/10.1080/01584197.2019.1595663>



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Social organisation and breeding biology of the White-shouldered Fairywren (*Malurus alboscapulatus*)

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ABSTRACT

The White-shouldered Fairywren (*Malurus alboscapulatus*) is a tropical passerine bird distributed across much of New Guinea. White-shouldered Fairywrens are among few species of fairywren with exclusively tropical distributions and differ from better studied congeners in Australia because subspecies vary by female, but not male, coloration and morphology. As with many bird species in New Guinea, basic demographic, social, morphological, and breeding data are limited. From 2011 to 2018 we documented the basic biology of two subspecies representing extremes of the female ornamentation spectrum. Both subspecies form groups having an even operational sex ratio and appear to breed year-round. Extra-pair paternity occurs in the subspecies with female ornamentation; comparable data are lacking for the subspecies having unornamented females, but the greater scaled cloacal protuberance volume of males suggests similar or higher extra-pair paternity rates. Females of the ornamented subspecies are generally larger than those lacking ornamentation, but exhibit reduced tail lengths, which is thought to serve as a signal of social dominance in other fairywrens. After first achieving adult-like plumage, males and ornamented females retain ornamented plumage year-round; however, only males in the subspecies with unornamented females appear to exhibit delayed plumage maturation. Our discussion highlights similarities and differences between White-shouldered Fairywren life histories and those of better studied Australian *Malurus* species; we focus on tropical vs. temperate environments and variable female ornamentation, and we identify priorities for future research.

ARTICLE HISTORY

Received 6 December 2018
Accepted 12 March 2019

KEYWORDS

Fairywren; female ornamentation; life history; tropical birds; Maluridae; New Guinea; sexual dimorphism

Introduction

Fairywrens (Maluridae: *Malurus*) are a familiar group of Australo-Papuan passerine birds that have been the focus of considerable ornithological interest (Buchanan and Cockburn 2013). In particular, research on *Malurus* fairywrens provides textbook examples of co-operative breeding behaviour (Pruett-Jones and Lewis 1990; Mulder *et al.* 1994) and its link to male plumage coloration (Webster *et al.* 2008), as well as sexual promiscuity with social monogamy (Brooker *et al.* 1990) and its association with male colouration (Dunn and Cockburn 1999; Baldassarre and Webster 2013). However, for the malurid species of New Guinea current life history information is limited largely to observational reports (Schodde 1982; Rowley and Russell 1997). These New Guinean species are a priority for study, because the lack of information on their life histories hinders comparative studies.

White-shouldered Fairywrens (*Malurus alboscapulatus*) are grass-dwelling insectivorous birds commonly observed in community gardens and savannah throughout the island of New Guinea, ranging from sea level to 2000 m (Schodde 1982; Rowley and Russell 1997). The White-shouldered Fairywren shares a most recent common ancestor with the Australian bicoloured fairywrens (Driskell *et al.* 2011), and is sister to the Red-backed Fairywren (*M. melanocephalus*), suggesting a secondary *Malurus* recolonisation of New Guinea during a recent glacial maximum (Rowley and Russell 1997; Rowley and Russel 2007; Joseph *et al.* 2013). The other members of the bicoloured clade, *M. melanocephalus* and *M. leucopterus*, provide useful points of comparison with White-shouldered Fairywrens. *Malurus melanocephalus* and *M. leucopterus* both exhibit delayed

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 Supplemental data for this article can be accessed [here](#).

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plumage maturation in males but not females (Rowley and Russell 1995; Karubian 2002; Rathburn and Montgomerie 2003) and, as a consequence, males breed either in an ornamented or unornamented (female-like) plumage phenotype. In the non-breeding season, both these species moult to an unornamented (brown) plumage and coalesce in larger social groups containing multiple social pairs (Rowley and Russell 1995; Lantz and Karubian 2017), while during the breeding season they are facultative co-operative breeders and exhibit social monogamy with high rates of sexual promiscuity (Brouwer *et al.* 2017). The ways in which, and degree to which, White-shouldered Fairywrens differ from members of this clade and the broader genus have not been shown.

White-shouldered Fairywrens are distinctive from better studied congeners in at least two key respects. First, they have an exclusively tropical distribution, which may affect mating system and social organisation. For example, latitudinal patterns of variation in the degree of sexual dimorphism in *Malurus* (Johnson *et al.* 2013; Karubian 2013) may be related to factors such as moult strategies (Wolfe *et al.* 2010), survival rates (Wiersma *et al.* 2007) and life histories (Ricklefs 1976) that also tend to vary with latitude. Second, six White-shouldered Fairywren subspecies are recognised on the basis of variation in female ornamentation, whereas males are similar in plumage across all subspecies (Schodde 1982; Rowley and Russell 1997; Enbody *et al.* 2017; Figure 1). This female ornamentation is derived recently, as sister taxa and most other *Malurus* possess unornamented

females (Driskell *et al.* 2011; Joseph *et al.* 2013), and provides a useful context in which to study processes driving female ornament evolution – an area of growing interest among evolutionary ecologists (Amundsen 2000; Tobias *et al.* 2012).

Here, we present results of a multi-year study of the social organisation and breeding biology of the White-shouldered Fairywren of New Guinea, the first such study for a New Guinean *Malurus* species. We provide information on one White-shouldered Fairywren subspecies where females are ornamented (*M. a. moretoni*; Figure 1) and a second in which females lack ornamentation (*M. a. lorentzi*; Figure 1) and contextualise results with similar information from Australian congeners.

Methods

Study system and field methods

We studied two subspecies of White-shouldered Fairywrens in Papua New Guinea: *Malurus alboscapulatus moretoni* (*moretoni* hereafter) in the far south-east of the country, and *Malurus alboscapulatus lorentzi* (*lorentzi* hereafter) in the south-west (Figures 1 and S1). From 2011 to 2018 we studied *moretoni* in Milne Bay Province, in the village of Garuahi (150°29' E, 10°13' S, 0–10 m a.s.l.) and from 2014 to 2018 in the nearby village, Porotona (150°35' E, 10°15' S, 10–20 m a.s.l.). Based on similarities in the traits we studied, we treat them as a single population. We also monitored *lorentzi* in Obo, Western Province (141°19' E, 7°35' S, 10–20 m a.s.l.) from 2014 to 2018. We monitored

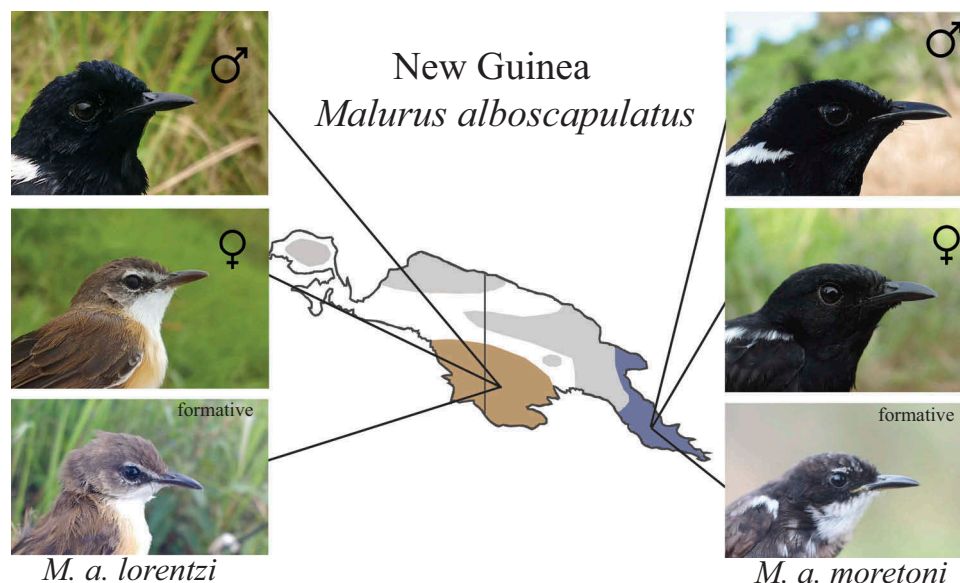


Figure 1. Approximate ranges, locations of field sites, and corresponding plumages of the two focal subspecies of White-shouldered Fairywren (*lorentzi* and *moretoni*), with ranges reproduced from (Birdlife International and NatureServe 2013). Subspecies not included in this study are in light grey. In formative plumage, males resemble females, but in *moretoni* formative plumage does not resemble adult females.

moretoni more intensively than *lorentzi* (Figure S2), but obtained useful information from both. Monthly precipitation for 2014–2018 at our field sites was obtained from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS; Funk *et al.* 2015).

We captured individuals with mist-nets using flush capture or playback and banded them with plastic coloured bands and an Australian Bird and Bat Banding Scheme Band (permit No. 2193). We collected whole blood (*ca.*30–50 μ l) in lysis buffer for genetic analyses. Feathers were collected from chest and shoulder patch (5–10 feathers per patch). We aged birds as first year (Age = 0) or adult (Age = 1+) by degree of skull ossification, gape colour, and plumage features. For analyses considering age, we make comparisons either as a binary classification between first year (Age = 0) and adult (Age = 1+), or between adults across relative age categories (i.e. based on minimum age at first capture, e.g. Age = 1+, Age = 2+, up to 5+). We observed banded individuals to determine group composition; groups were classified as having an auxiliary (helper at the nest) if adult birds other than the dominant male and female were observed consistently with the group while that group was nesting. We calculated within-group sex ratios as the ratio of adult males to females and we counted all adults and first-year individuals in calculations of group size.

We searched intensively for nests in all field seasons by following birds carrying nest material or food and by checking appropriate habitat. Active nests were monitored every third day until all individuals had fledged, or the nest failed. We calculated adult survival as the proportion of adults that survived until the following year, as recorded by both banding and re-sighting. We omitted years with prohibitively small sample sizes for analysis (*moretoni* 2011, *lorentzi* 2014, and *lorentzi* 2017).

Morphology and moult

At each capture we recorded moult intensity in head, rump, chest, belly, and tail on a scale of 0–3 (e.g. 0 = no moult, 3 = >66% feathers moulting) and recorded the presence of a brood patch (a rough approximation of nesting activity). For flight feathers, we recorded whether they were in pin, growing (and percentage growth recorded), fully grown fresh, or fully grown and worn.

We calculated sexual dimorphism for mass (g), tarsus, wing, tail, and head + bill length (cm). For recaptured individuals, we discarded obvious outliers and averaged across captures, except for tail, which can change in length over time (see below). Population-wide sexual dimorphism measures were calculated following Leitão

et al. (2018) as $(100 * (\text{male} - \text{female}) / (\text{male} + \text{female}) / 2)$. Subspecific differences were calculated by replacing sex with subspecies. We tested subspecific differences in sexual dimorphism by calculating sexual dimorphism per female as $(\text{abs}(\text{female} - \text{average male value}))$ and contrasted using a *t*-test. We calculated scaled cloacal protuberance (CP) volume with the ratio of CP volume $(3.14 * (\text{CP height}/2) * (\text{CP width}/2) * \text{CP length})$ to body mass for males (Tuttle *et al.* 1996). Scaled CP volume was averaged within years for individuals caught multiple times in one year (maximum CP produced qualitatively similar results). We accounted for changes in CP volume and tail length as individuals age (up to three age categories) by building a linear mixed model, using the interaction of subspecies and age as predictor variables and individual ID as a random effect. The residuals of both models were normally distributed. For CP volume we included a correction for variance structure between subspecies after initial model comparisons. We tested for significant predictors using a Wald chi-square type-II test as implemented in the ‘car’ package (Fox and Weisberg 2011).

We measured feather colour using a photospectrometer of chest and shoulder feathers (in the laboratory), following the methods described in Enbody *et al.* (2017). Briefly, using a USB2000+ spectrometer (R400-7-UV-VIS probe, RPH-1 probe holder) with a PX-2 pulsed xenon light source (Ocean Optics) we collected three readings for brown or black feathers and five for white feathers. We used the R package Pavo (V0.99; Maia *et al.* 2013) using reflectance values between 300 and 700 nm to generate plumage colour metrics, including brightness, chroma, and contrast between body regions, for analysis (R version 3.5.0 R core team, 2018). We used measurements of colour distances between chest and shoulder as implemented in Pavo. Only adults were included in this comparison and measurements of colour for the same individual were averaged across years.

Laboratory methods

Individuals of unknown sex were sexed using laboratory methods following Enbody *et al.* (2017). We amplified 11 microsatellite markers (developed for Red-backed Fairywrens, Brouwer *et al.*, 2017) and genotyped individuals using an Applied Biosystems 3730xl DNA Analyzer automated sequencer. We called fragment sizes with Geneious software version 8.05 (<http://www.geneious.com>).

The majority of offspring that we analysed (48 of 50) were fledged young rather than nestlings. This can weaken the inferences one can make from

paternity assignments, but we include these data here because they provide the best information available to date for this species. To assign the paternity of each juvenile found on the study site we included only families whose maternal genotypes closely matched that of the juvenile ($n = 10$ omitted, $n = 40$ retained). We assigned the most likely sire for each juvenile using the program CERVUS 3.07 (Kalinowski *et al.* 2007). In all cases we accepted the CERVUS assignment of paternity if the male chosen had 0 or 1 mismatch with the juvenile, unless a lower ranked male was the social father or known father of other offspring in the group (following Webster *et al.* 2004; Baldassarre and Webster 2013).

Results

Social organisation

In *moretoni*, adult density each season ranged from 1.02 to 2.60 individuals/ha; in *lorentzi*, adult density was 0.88–1.40 individuals/ha (Table S2). In each full field season we captured most or all adults (*moretoni*: $n = 480$ individuals over 7 years; *lorentzi*: $n = 250$ individuals over 4 years). The number of *moretoni* groups monitored per year ranged from 30 to 61 (mean = 45.5) and the number of *lorentzi* groups ranged from 21 to 38 (mean = 27). Group size ranged from 2 to 7 (*moretoni* mean = 2.5; *lorentzi* mean = 3; Table S2 and Figure S3) and within these groups the operational sex ratio in both subspecies was usually close to 1:1, with limited variation across years (Figure S4).

Pairs in both subspecies hold long-term territories. There was little variation in capture locations of adult territory holders between years (mean displacement *moretoni* = 144 ± 179 m, $n = 134$; *lorentzi* = 161 ± 111 m, $n = 33$) or at different times of year, and sexes did not differ in between-year movements (Table S3). Natal dispersal distance was greater than adult dispersal (Table S3) and first-year female dispersal distances (*moretoni* = 435 ± 476 m, $n = 3$; *lorentzi* = 236 m, $n = 1$) exceed those of males on average (*moretoni* = 270 ± 232 m, $n = 13$; *lorentzi* = 102 ± 65 m, $n = 5$).

Display behaviour

Male White-shouldered Fairywren puff the white shoulder patch and extend their neck, while simultaneously extending ear coverts and crown feathers, when singing in response to a territorial intruder (Figure S5). Notably, females in *moretoni* do not puff the shoulder patch in aggressive contexts. In contrast, females in *lorentzi* (lacking the white shoulder patch)

often extend white throat feathers while responding to territory intruders and raise wings, a behaviour not noted in *moretoni* females. Males (but not females) were observed carrying red or orange flower petals or leaves in the presence of females while foraging off territory (but not to their social mate) or in the context of playbacks of female song on their own territory (Figure S5).

Annual survival

Male survival (*moretoni*: 0.63, *lorentzi*: 0.47) was on average higher than female survival (*moretoni*: 0.50, *lorentzi*: 0.35) in both subspecies, and survival of both sexes was on average lower in *lorentzi* (Figure 2), but small sample sizes for *lorentzi* precluded interpopulation statistical comparisons. For *moretoni*, male annual survival was higher than female annual survival (paired *t*-test: $t = -3.15$, $df = 5$, $p = 0.025$).

Breeding biology and helping behaviour

Breeding occurred throughout the year. Males were in reproductive condition as indicated by enlarged cloacal protuberances and brood patches were recorded in females in all months monitored (Figure 3 and S6). In *moretoni*, a peak in breeding appears to occur between January and March, which appears to anticipate a period of high precipitation. Nests were placed low in grass or shrubs, typically within 0.5 m of the ground, and were domed and composed of dried grass

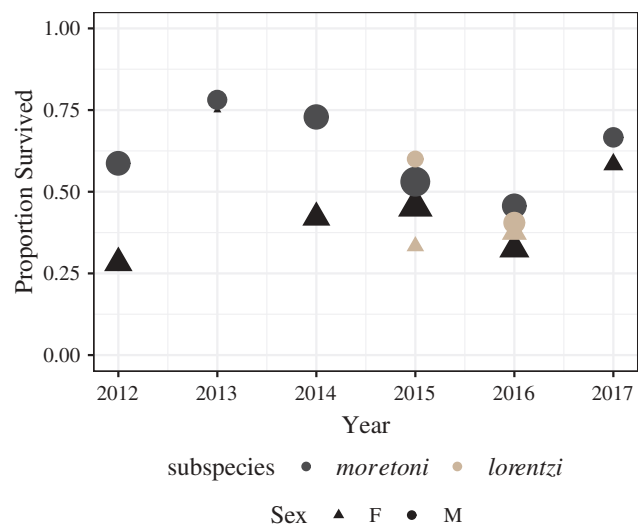


Figure 2. Proportion of all adults present in the year indicated (x-axis) that survived into the following year. Subspecies are coloured brown (M. a. *lorentzi*, light grey in print) or black (M. a. *moretoni*), shape denotes sex, and points are scaled by the number of individuals sampled that year.

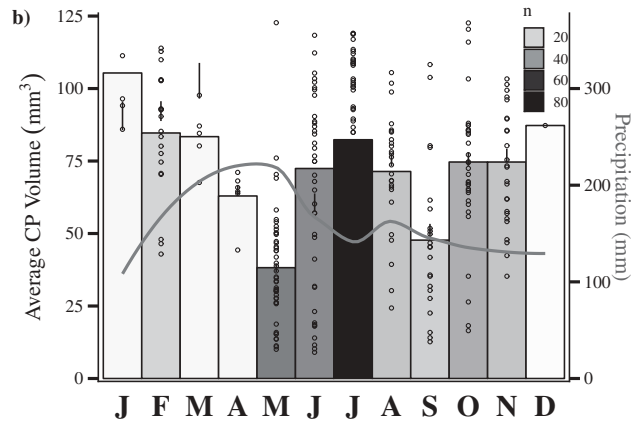
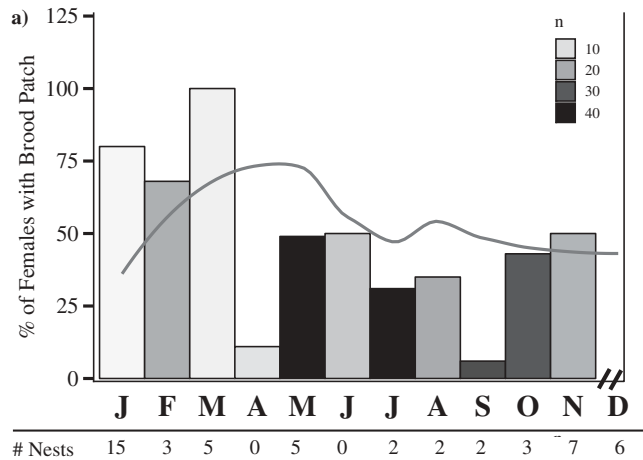
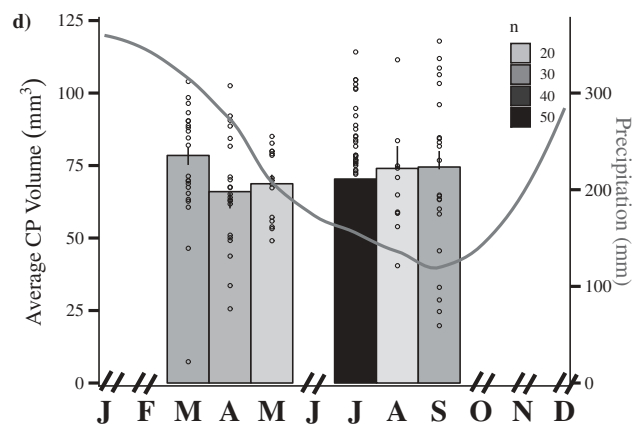
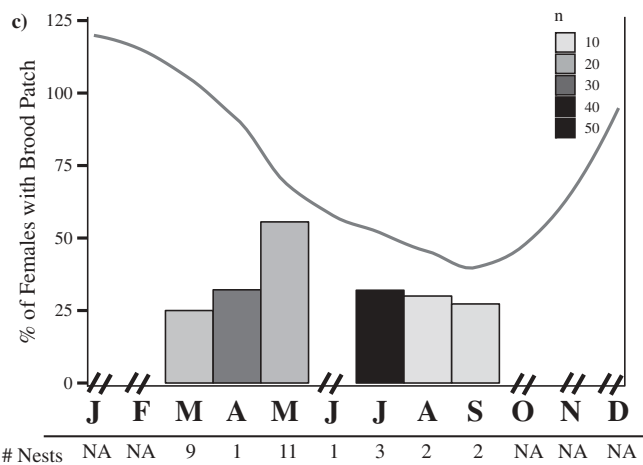
M. a. moretoni*M. a. lorentzi*

Figure 3. Bar plots of the percentage of females captured with a brood patch by month in *moretoni* (a) and *lorentzi* (c). Average cloacal protuberance volume by month (error bars are standard error) is shown for *moretoni* (b) and *lorentzi* (d). The right-hand y-axis is average monthly precipitation, represented by the blue line. Darkness of the bars represents the number of individuals captured (n). Dashes on the horizontal axis denote unsampled months. The number of active nests is tabulated below the month.

and spider webs (Figure S7), similar to the description provided by Schodde (1982). In many cases, the nest opening faced a creek bed or other opening in the habitat.

Clutch size varied from two to three eggs in both *moretoni* (mean = 2.67, $n = 33$ nests) and *lorentzi* (mean = 2.28, $n = 25$; Table S2). Eggs in *moretoni* are cream coloured with reddish speckling concentrated at one end (similar to those described in Schodde 1982; Figure S7). In the *moretoni* subspecies during July 2015–March 2016 we discovered 31 nests of which 27 failed (87% failure); most apparently were depredated by unknown animals, and one was parasitised by a Brush Cuckoo (*Cacomantis variolosus*).

We recorded 41 h of video at 16 active nests in *moretoni* in 2016 and observed 10.83 ± 4.2 feeds/h (we were unable to determine sex in most visits),

typically orthopterans or caterpillars. At least 6 of these 16 groups included auxiliary individuals other than the breeding pair (two groups had two broods). We confirmed a male auxiliary provisioning young at one *moretoni* nest and have inconclusive evidence of a female auxiliary provisioning young at a second *moretoni* nest. In one nest (with nestlings) in *lorentzi* in 2017 we observed an auxiliary male allo-feeding the female at the nest.

In *moretoni*, we estimated extra-pair parentage rates by testing the parentage of post-fledging juveniles ($n = 40$) in groups against the group's primary male and female (and $n = 2$ nestling). Twenty-seven (66%) were the offspring of the social male in the group and the remaining 13 (33% of juveniles and 31% of groups) were considered extra-pair young (Tables 1 and S4). Scaled male CP volume was larger in *lorentzi* than in

moretoni ($\chi^2 = 4.07$, $df = 1$, $p = 0.044$). Scaled CP volume on average increased up to our third age category, but this relationship was not statistically significant ($\chi^2 = 3.71$, $df = 2$, $p = 0.16$; Table S5), and varies with breeding stage in *moretoni* (Figure S8).

Sexual dimorphism

Individuals from *moretoni* were larger in all but one measurement compared to *lorentzi*; female *lorentzi* have longer tails than female *moretoni* ($\chi^2 = 7.5354$, $df = 1$,

$p < 0.01$; Table S5). Tail length decreased with age (Table S5) in both subspecies. Sexual dimorphism was pronounced for most of the morphological traits we measured (Table 2), with males being larger than females. However, the degree of sexual dimorphism was lower in *lorentzi* than in *moretoni* for tarsus and bill length, and mass (Tables 2 and S6), suggesting that the transition to female plumage ornamentation in *moretoni* corresponds with reduced sexual dimorphism in tail length, but an increase in sexual dimorphism in body size.

Adult plumage was sexually dichromatic for all plumage types in both subspecies (Table 2). In *moretoni*, white shoulder feathers and chest feathers were brighter and darker, respectively, in males than females. Consequently, achromatic contrast between the shoulder patch and the chest is higher in *moretoni* males than females. Male *moretoni* on average have higher achromatic contrast than male *lorentzi*.

Table 1. Extra-pair paternity rates (number of extra-pair offspring/total number of offspring) for *Malurus alboscapulatus* in comparison to rates from eight other Maluridae species (from Brouwer *et al.* 2017). Scaled CP volume (CP volume/mass) calculated from average values in Rowley and Russel (2007), Rowe and Pruett-Jones (2013), and Louter (2016)

| Species | Extra-pair rate | Scaled CP volume |
|--|-----------------|------------------|
| <i>Amytornis textilis</i> | 0 | 2.83 |
| <i>Malurus coronatus</i> | 0.063 | 5.04 |
| <i>Stipiturus malachurus</i> | 0.12 | 0 |
| <i>Malurus alboscapulatus moretoni</i> | 0.33 | 7.85 |
| <i>Malurus alboscapulatus lorentzi</i> | – | 8.97 |
| <i>Malurus splendens</i> | 0.48 | 10.26 |
| <i>Malurus melanocephalus</i> | 0.54 | 16.94 |
| <i>Malurus lamberti</i> | 0.56 | 4.40 |
| <i>Malurus elegans</i> | 0.63 | 5.63 |
| <i>Malurus cyaneus</i> | 0.64 | 11.77 |

Moult

Males and females of both subspecies maintained definitive adult plumage year-round but likely undergo both a pre-basic and partial pre-alternate moult. This was supported by birds undergoing body moult in the absence of flight feather moult (*moretoni*: $n = 171$, or 25%, *lorentzi*: $n = 66$,

Table 2. Morphological differences between subspecies and sexes (mean \pm SD (sample size)) for individuals averaged across captures (except for tail and CP volume; see methods). Benjamini-Hochberg corrected p-values are indicated with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. See text for details on statistical tests applied for each variable. See text for details on statistical tests applied for each variable

| Sex | Type | Measure | <i>M. a. lorentzi</i> | <i>M. a. moretoni</i> | Population difference (%) |
|------------------------|------------------------|--------------------------|------------------------|------------------------|---------------------------|
| Female | Morphology | Mass (g) | 7.53 \pm 0.45 (67) | 8.66 \pm 0.70 (156) | 0.140*** |
| | | Tarsus (mm) | 21.38 \pm 1.30 (71) | 22.11 \pm 1.02 (156) | 0.034*** |
| | | Wing (mm) | 42.74 \pm 1.39 (71) | 44.00 \pm 1.18 (156) | 0.029*** |
| | | Tail (mm) | 48.0 \pm 2.54 (94) | 45.8 \pm 2.44 (218) | –4.70% |
| | | Bill + head (mm) | 27.71 \pm 0.57 (71) | 29.04 \pm 1.21 (156) | 0.032*** |
| | Plumage | Chest brightness (B2) | 32.50 \pm 12.52 (29) | 2.55 \pm 0.62 (75) | –170.87% |
| | | Chest R.achieved | 0.20 \pm 0.16 (29) | 0.07 \pm 0.05 (75) | –91.55% |
| | | Chest dL_SP (contrast) | 13.62 \pm 4.19 (19) | 32.21 \pm 2.79 (75) | 0.811*** |
| | | Shoulder brightness (B2) | 8.00 \pm 1.61 (19) | 61.63 \pm 8.63 (72) | 1.540*** |
| | | Male | Morphology | Mass (g) | 7.88 \pm 0.46 (85) |
| Tarsus (mm) | 21.62 \pm 0.98 (86) | | | 23.01 \pm 1.17 (143) | 0.062*** |
| Wing (mm) | 44.07 \pm 1.23 (86) | | | 45.14 \pm 1.20 (144) | 0.024*** |
| Tail (mm) | 42.5 \pm 2.94 (124) | | | 43.0 \pm 2.52 (251) | 1.17% |
| Bill + head (mm) | 28.13 \pm 0.52 (86) | | | 29.90 \pm 0.63 (143) | 0.061*** |
| Plumage | Scaled CP volume | | 8.97 \pm 2.95 (107) | 7.85 \pm 3.66 (199) | –13.32% |
| | Chest brightness (B2) | | 1.55 \pm 0.52 (28) | 2.08 \pm 0.47 (81) | 0.293*** |
| | Chest R.achieved | | 0.24 \pm 0.09 (28) | 0.23 \pm 0.08 (81) | –4.78% |
| | Chest dL_SP (contrast) | | 37.67 \pm 4.36 (18) | 35.68 \pm 2.81 (76) | –5.43% |
| | Shoulder brightness | | 59.76 \pm 8.79(20) | 65.32 \pm 9.96(76) | 0.089 |
| Average dimorphism (%) | Morphology | Mass (g) | 4.54%*** | 8.62%*** | ** |
| | | Tarsus (mm) | 1.12% | 3.98%*** | ** |
| | | Wing (mm) | 3.06%*** | 2.56%*** | |
| | | Tail (mm) | 12.15%*** | 6.30%*** | ** |
| | | Bill + head (mm) | 1.50%*** | 2.92%*** | ** |
| | Plumage | Chest brightness (B2) | 181.80%*** | 20.31%*** | ** |
| | | Chest R.achieved | 18.58% | 102.15%*** | |
| | | Chest dL_SP (contrast) | 83.14%*** | 10.23%*** | ** |
| | | Shoulder brightness (B2) | 15.63%*** | 5.81%* | ** |
| | | | | | |

or 18% of adults) and a high proportion of adults moulting flight feathers in any given month (Figure 4). We also found that adults did not moult flight feathers in sequence typical of northern temperate passerine species (Pyle 1997; Rohwer 2008; primaries 1–10, secondaries 1–6, excluding tertials) but instead exhibited frequent non-sequential moults (*moretoni* $n = 103$ or 51%, *lorentzi* $n = 141$ or 59%) in which they moulted inner and outer primaries simultaneously (Figures S9 and S10).

In *moretoni*, we captured one individual at the time of fledging and 2 months post-fledging (Figure S11). The juvenile plumage at fledging was black dorsally and white ventrally. At 2 months post-fledging, flight and tail feather moult was complete and black shoulder feathers were being replaced with white (as in males and females in adult plumage), but chest and throat feathers were moulting in white (unlike adults). This supports a distinct formative plumage and moult (distinct from adult), which is replaced by an adult plumage (fully black chest) after >7 months.

In *moretoni*, we never observed males paired or breeding in any plumage other than adult male plumage. In contrast, we captured three male *lorentzi* with brown (female-like) plumage and a measurable cloacal protuberance; these males defended territories with adult females, were approximately 1 year of age, and were actively moulting brown feathers in some cases (Figure S12). In *moretoni*, adult females varied in the degree of white on the eyebrow, on the chin, or both (all *lorentzi* females have white throats and white eyebrows). The extension of the white patches on the chin or eyebrow may be more frequent in older birds, but considerable variation was recorded (Figures S13 and S14).

Discussion

Malurus fairywrens have emerged as a model system for understanding sexual selection (Cockburn *et al.* 2008), cooperative behaviour (e.g. Margraf and Cockburn 2013),

extra-pair mating (Brouwer *et al.* 2017), and ornamentation in males (e.g. Peters *et al.* 2013). Nearly all *Malurus* life history and behaviour research has focused on Australian species, and our study is the first to report results of long-term monitoring of a species from New Guinea. We expected that White-shouldered Fairywrens differ from many Australian relatives in social and life history characteristics owing to their tropical distribution and female ornamentation. Our findings suggest that White-shouldered Fairywrens are qualitatively similar in social organisation and breeding biology to close relatives, but that they also exhibit some important differences which provide promising avenues for future study.

Social organisation

In general, we might expect tropical species, such as the White-shouldered Fairywren, to exhibit year-round territoriality and breeding (Stutchbury and Morton 2001). Both subspecies of White-shouldered Fairywren exhibited year-round territoriality, which differs from most congeners for which data are available, but is similar to the two Australian species with ranges closest to the equator, the Lovely (*M. amabilis*; Leitão *et al.* 2018) and Purple-crowned (*M. coronatus*; Hall and Peters 2008) Fairywrens. This is likely associated with the occurrence of breeding in any month of the year in these exclusively tropical species (below). Group size and density were similar to Australian fairywrens. However, *lorentzi* territories tended to be larger and groups more dispersed, possibly associated with observations that *lorentzi* group composition is more fluid than in *moretoni*, and a higher rate of extra-group interactions (Boersma, Jones, Enbody pers. obs.).

Annual survival

Tropical birds are expected to have higher adult survival and a slower pace of life than temperate species

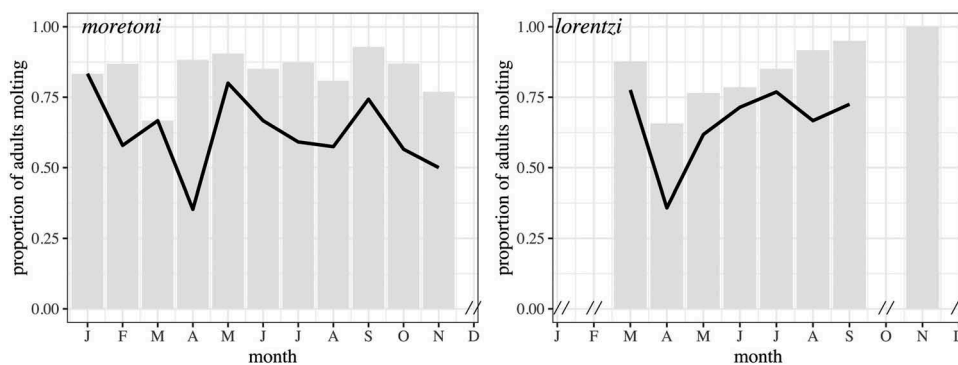


Figure 4. Proportion of adults (of both sexes combined) moulting across months. The black line shows the proportion of adults moulting primary or secondary feathers by month. The grey bars show the proportion of adults moulting body feathers by month. Left: *M. a. moretoni*; right: *M. a. lorentzi*.

(Ricklefs 1976). Annual survival varied considerably between field seasons (and was lower than other tropical *Malurus* species; Table S1). This degree of variation between years is unexpected for 'tropical' species, and may be associated with a drought caused by the El Niño climatic event in 2015 and 2016. On average, survival appeared to be lower in *lorentzi* than in *moretoni*, though differences were not significant and may have been influenced by the aforementioned drought. For this reason, continued monitoring will be necessary to obtain more reliable long-term information.

Breeding biology and helping behaviours

Similar to the tropical *M. amabilis* (Leitão *et al.* 2018) and *M. coronatus* (Rowley and Russell 1993), breeding occurred year-round, which is expected in environments with greater environmental stability. We observed possible seasonal peaks between November and March in *moretoni*; the degree of seasonality in *lorentzi* breeding is unclear because of our comparatively limited sampling efforts. During our most extensive period of monitoring, we observed nearly complete nest failure in *moretoni*, which may have been in part due to drought. Nest predation is expected to be higher in tropical than temperate species (e.g. Skutch 2018, but see discussion in Martin 1996); however, in this case, comparable rates of nest predation have been described in both tropical (Leitão *et al.* 2018) and temperate *Malurus* (Van Bael and Pruett-Jones 2000).

As in other *Malurus* species, we confirmed male helpers at the nest, suggestive of co-operative breeding, in both *moretoni* and *lorentzi* and strongly suspect a female helper provisioned nestlings in *moretoni* (present in the vicinity of the nest). White-shouldered Fairywrens may differ from 'temperate' congeners in Australia in reduced rates of sexual promiscuity (Stutchbury and Morton 2001, but see Macedo *et al.* 2008). We found moderate rates of extra-pair paternity (EPP; among already-fledged young) in *moretoni*, consistent overall with rates across fairywrens (Table 1; Brouwer *et al.* 2017), but we are lacking data from *lorentzi*. However, male *lorentzi* fairywrens had larger scaled cloacal protuberances, which in other *Malurus* species is positively associated with sperm quantity, testes size, and may be a proxy for the rate of EPP (Table 1; Tuttle *et al.* 1996; Rowe and Pruett-Jones 2011, 2013).

Sexual dimorphism

White-shouldered Fairywrens maintain adult plumage year-round. The majority of *Malurus*

fairywrens exhibit seasonal sexual dichromatism (Friedman and Remeš 2015) and sexual dimorphism in size (males > females). Notably, the year-round-breeding *M. amabilis* fairywrens also maintain adult plumage year-round (Leitão *et al.* 2018), but the year-round-breeding *M. coronatus* do not (Fan *et al.* 2017). Many *Malurus* exhibit a notable pattern of reverse sexual dimorphism in tail length (Swaddle *et al.* 2000), which may serve as a signal of social dominance (Karubian *et al.* 2009). Greater size dimorphism in *moretoni* coupled with reduced tail length dimorphism suggests that tail length is evolving independently of other morphological traits in females of this subspecies. This transition occurs in parallel with a reduction in plumage dichromatism and males are darker on the chest, whiter on the shoulder, and greater in overall contrast. Taken together, plumage contrast and tail length are consistent with differential selection pressures on males and females in *Malurus* (Johnson *et al.* 2013; Karubian 2013; Friedman and Remeš 2015; Enbody *et al.* 2017).

Delayed plumage maturation plays an important role in dominance and mate choice in *M. melanocephalus* (Karubian 2002; Karubian *et al.* 2008; Webster *et al.* 2008) and as a status signal in the clan mating system of *M. leucopterus* (Rowley and Russell 1995; Rathburn and Montgomerie 2003). The two subspecies of White-shouldered Fairywrens differ in degree of delayed plumage maturation in males, which has not been reported previously. Delayed plumage maturation occurred at very low rates ($n = 3/63$ observed mated and in breeding condition in formative plumage) in *lorentzi* males, but not *moretoni* males (150 males observed), despite considerably more sampling effort in *moretoni*. Interestingly, first-year *lorentzi* plumage is similar to that of *lorentzi* females, while first-year plumage of *moretoni* individuals of both sexes differs from that of *moretoni* adults, a trait not shared by other *Malurus* species.

Moult

The pre-formative moult we describe in *moretoni* is consistent with such a moult in other temperate and tropical species (Howell *et al.* 2003; Wolfe *et al.* 2010), but does not seem to have been characterised in *Malurus* previously. Differentiating between the pre-juvenile moult and pre-formative moults may be useful in ageing individuals, particularly in species with low seasonality in breeding. The timing of moult cycles is a predictor of male mating success in Superb Fairywrens (Dunn and Cockburn 1999), but adult moult cycles appear to take place in any month in the

White-shouldered Fairywren. Timing of adult moults may be individually linked to breeding, a consequence of reduced seasonality, as the initiation of flight feather moult generally follows the proposed peak in breeding (Figure S15).

We found that individuals of all age classes can moult flight feathers in non-sequential patterns (20% of birds). This may also occur in other fairywren species (e.g. Red-backed Fairywren; Enbody pers. obs.). Variation in moult strategies may influence survival (temperate owls; Brommer *et al.* 2003), flight performance (temperate starlings; Swaddle and Witter 1997), timing of fledging (temperate wrentits; Elrod *et al.* 2011), and timing of breeding (seabirds; Edwards 2008). More specifically, non-sequential moult could carry energetic costs associated with flight performance (Portugal *et al.* 2018), and warrants further investigation.

Female ornamentation

In *Malurus*, as in many other systems, research on females has lagged behind that on males; however, recent contributions have explored female behaviour, singing, and ornamentation (Double and Cockburn 2000; Peters 2007; Hall and Peters 2008; Varian-Ramos *et al.* 2012; Johnson *et al.* 2013; Karubian 2013; Schwabl *et al.* 2014, 2015; Lindsay *et al.* 2016; Enbody *et al.* 2017, 2018; Leitão *et al.* 2018). Female ornamentation in *Malurus* occurs in species closer to the equator (Johnson *et al.* 2013; Karubian 2013), perhaps because of associations with dense forest habitat (Medina *et al.* 2017). Both subspecies used a wide range of microhabitats, including grasslands, forest margins, and human-modified habitats (e.g. gardens), suggesting that local forest cover may not be driving patterns of variation in the female White-shouldered Fairywren.

Social structure and resulting social selection pressures may play a role in evolutionary transitions in female ornamentation (Amundsen 2000; Tobias *et al.* 2012; Karubian 2013). For example, operational sex ratios and group composition can influence female–female competition for social resources (e.g. access to mates, territories, or environmental resources) via social selection (West-Eberhard 1979, 1983; Rubenstein and Lovette 2009). We found an essentially 1:1 operational sex ratio, but most congener populations are male-biased owing to the predominance of male, rather than female, auxiliary helpers (Rathburn and Montgomerie 2005; Cockburn and Double 2008; Kingma *et al.* 2010; Varian-Ramos *et al.* 2010). Even sex ratios and year-round territoriality may lead to increased social competition among females, e.g. for access to mating opportunities or high-quality

territories. Lower extra-pair rates in *moretoni* (36%) relative to Red-backed Fairywrens (~54%; Karubian 2002; Webster *et al.* 2008), other *Malurus* (Table 1; Brouwer *et al.* 2017), and potentially *lorentzi* could also lead to greater mutual mate choice and, as a consequence, selection on female ornamentation in *moretoni*. Furthermore, standing variation in the extent of female ornamentation could be subject to sexual or social selection (e.g. via the handicap principle; Zahavi 1975). Reduced tail length in *moretoni* may support a signalling role for tail length in female *moretoni*, which are more aggressive (Enbody *et al.* 2018). Based on these findings, we conclude that the conditions are present for social selection to have played a role in female ornament evolution in the White-shouldered Fairywren.

Future directions

Variation in the degree of female ornamentation in the White-shouldered Fairywren makes them an outstanding model for studying the evolution and physiology of female ornamentation (Karubian 2013; Enbody *et al.* 2017, 2018). The degree to which group size dynamics represent fundamental differences between subspecies remains unclear, suggesting the need for more detailed quantification of social organisation and territorial behaviour in this species. Furthermore, our observation of delayed plumage maturation in *lorentzi*, but not *moretoni*, suggests a possible relationship between the timing and acquisition of male plumage and differences in female ornamentation. We also identify tail length and extent of white patches as candidates for future studies on the signalling role of female traits in *moretoni*. These future studies will improve our understanding of how variation in ecological and social environment, and resulting social selection pressures, interact to shape the complex patterns of plumage variation.

Acknowledgements

We are grateful for assistance in the field provided by M. Aliaga, B. Barkley, R. Biggoneau, P. Chaon, I. Hoppe, G. Kareba, B. Magnier, K. McDonald, M. Saiga, K. Saiga, and J. Weller. A. Lormand and H. Rust assisted with spectroscopy and monitoring nest videos. We thank N. Layman for assistance in gathering precipitation data and E. Johnson and S. Lantz for helpful discussion.

Funding

This work was supported by the National Science Foundation under Grant IOS-1354133 to J.K. and 1701781

to J.K. and E.D.E. and 1352885 to H.S. and the Disney Worldwide Conservation Fund (to J.K.); the American Ornithologist's Union (to E.D.E.); American Ornithological Society (to J.P.B. and J.A.J.); the American Museum of Natural History Chapman Memorial Fund (to E.D.E.); the National Geographic Society Young Explorers Grant (to E.D. E.); the Animal Behavior Society (to E.D.E.); the Tulane University Ecology & Evolutionary Biology Department Student Research Grant and the Gunning Fund (to E.D. E. and J.A.J.); and the Washington State University Elling Research Grant (to J.P.B.).

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References

- Amundsen, T. (2000). Why are female birds ornamented? *Trends in Ecology and Evolution* **15**, 149–155.
- Baldassarre, D. T., and Webster, M. S. (2013). Experimental evidence that extra-pair mating drives asymmetrical introgression of a sexual trait experimental evidence that extra-pair mating drives asymmetrical introgression of a sexual trait. *Proceedings of the Royal Society B* **280**, 1–7.
- Birdlife International and NatureServe (2013). 'Bird Species Distribution Maps of the World.' Available at <http://www.birdlife.org>.
- Brommer, J. E., Pihlajamäki, O., Kolunen, H., and Pietiäinen, H. (2003). Life-history consequences of partial-molt asymmetry. *Journal of Animal Ecology* **72**, 1057–1063.
- 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.
- Brouwer, L., van de Pol, M., Hidalgo Aranzamendi, N., Bain, G., Baldassarre, D. T., Brooker, L. C., Brooker, M. G., et al. (2017). Multiple hypotheses explain variation in extra-pair paternity at different levels in a single bird family. *Molecular Ecology* **26**, 6717–6729.
- Buchanan, K. L., and Cockburn, A. (2013). Fairy-wrens and their relatives (Maluridae) as model organisms in evolutionary ecology: The scientific legacy of Ian Rowley and Eleanor Russell. *Emu* **113**, i–vii.
- Cockburn, A., and Double, M. C. (2008). Cooperatively breeding superb fairy-wrens show no facultative manipulation of offspring sex ratio despite plausible benefits. *Behavioral Ecology and Sociobiology* **62**, 681–688.
- Cockburn, A., Osmond, H. L., and Double, M. C. (2008). Swingin' in the rain: Condition dependence and sexual selection in a capricious world. *Proceedings of the Royal Society B* **275**, 605–612.
- Double, M., and Cockburn, A. (2000). Pre-dawn infidelity: Females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society B* **267**, 465–470.
- Driskell, A. C., Norman, J. A., Pruett-Jones, S., Mangall, E., Sonsthagen, S., and Christidis, L. (2011). A multigene phylogeny examining evolutionary and ecological relationships in the Australo-papuan wrens of the subfamily Malurinae (Aves). *Molecular Phylogenetics and Evolution* **60**, 480–485.
- Dunn, P. O., and Cockburn, A. (1999). Extrapair mate choice and honest signaling in cooperatively breeding superb Fairy-Wrens. *Evolution* **53**, 938–946.
- Edwards, A. E. (2008). Large-scale variation in flight feather molt as a mechanism enabling biennial breeding in albatrosses. *Journal of Avian Biology* **39**, 144–151.
- Elrod, M. L., Seavy, N. E., Cormier, L., and Gardali, T. (2011). Incidence of eccentric molt in first-year Wrentits increases with fledge date. *Journal of Field Ornithology* **82**, 325–332.
- Enbody, E. D., Boersma, J., Schwabl, H., and Karubian, J. (2018). Female ornamentation is associated with elevated aggression and testosterone in a tropical songbird. *Behavioral Ecology* **29**, 1056–1066.
- Enbody, E. D., Lantz, S. M., and Karubian, J. (2017). Production of plumage ornaments among males and females of two closely related tropical passerine bird species. *Ecology and Evolution* **7**, 4024–4034.
- Fan, M., Hall, M. L., Kingma, S. A., Mandeltort, L. M., Hidalgo Aranzamendi, N., Delhey, K., and Peters, A. (2017). No fitness benefits of early molt in a fairy-wren: Relaxed sexual selection under genetic monogamy? *Behavioral Ecology* **00**, 1–13.
- Fox, J., and Weisberg, S. (2011). 'An {R} Companion to Applied Regression.' 2nd edn. (Thousand Oaks, CA: SAGE publications.)
- Friedman, N. R., and Remeš, V. (2015). Rapid evolution of elaborate male coloration is driven by visual system in Australian Fairy-wrens (Maluridae). *Journal of Evolutionary Biology* **28**, 2125–2135.
- Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., Husak, G., et al. (2015). The climate hazards infrared precipitation with stations – A new environmental record for monitoring extremes. *Scientific Data* **2**, 1–21.
- Hall, M. L., and Peters, A. (2008). Coordination between the sexes for territorial defence in a duetting fairy-wren. *Animal Behaviour* **76**, 65–73.
- Howell, S. N. G., Corben, C., Pyle, P., and Rogers, D. I. (2003). The first basic problem: A review of molt and plumage homologies. *The Condor* **105**, 635.
- Johnson, A. E., Price, J. J., and Pruett-Jones, S. (2013). Different modes of evolution in males and females generate dichromatism in fairy-wrens (Maluridae). *Ecology and Evolution* **3**, 3030–3046.
- Joseph, L., Edwards, S. V., and McLean, A. J. (2013). The Maluridae: Inferring avian biology and evolutionary history from DNA sequences. *Emu* **113**, 195–207.
- Kalinowski, S. T., Taper, M. L., and Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**, 1099–1106.
- Karubian, J. (2002). Costs and benefits of variable breeding plumage in the red-backed fairy-wren. *Evolution* **56**, 1673–1682.

- Karubian, J. (2013). Female ornamentation in *Malurus* fairy-wrens: A hidden evolutionary gem for understanding female perspectives on social and sexual selection. *Emu* **113**, 248–258.
- Karubian, J., Sillett, T. S., and Webster, M. S. (2008). The effects of delayed plumage maturation on aggression and survival in male red-backed fairy-wrens. *Behavioral Ecology* **19**, 508–516.
- Karubian, J., Swaddle, J. P., Varian-Ramos, C. W., and Webster, M. S. (2009). The relative importance of male tail length and nuptial plumage on social dominance and mate choice in the red-backed fairy-wren *Malurus melanocephalus*: Evidence for the multiple receiver hypothesis. *Journal of Avian Biology* **40**, 559–568.
- Kingma, S. A., Hall, M. L., and Peters, A. (2010). No evidence for offspring sex-ratio adjustment to social or environmental conditions in cooperatively breeding purple-crowned fairy-wrens. *Behavioral Ecology and Sociobiology* **65**, 1203–1213.
- Lantz, S. M., and Karubian, J. (2017). Environmental disturbance increases social connectivity in a passerine bird. *PLoS One* **12**, e0183144.
- Leitão, A. V., Hall, M. L., Venables, B., and Mulder, R. A. (2018). Ecology and breeding biology of a tropical bird, the Lovely Fairy-Wren (*Malurus amabilis*). *Emu - Austral Ornithology* **119**, 1–13.
- Lindsay, W. R., Barron, D. G., Webster, M. S., and Schwabl, H. (2016). Testosterone activates sexual dimorphism including male-typical carotenoid but not melanin plumage pigmentation in a female bird. *Journal of Experimental Biology* **219**, 3091–3099.
- Louter, M. (2016). The behavioural ecology of the thick-billed grasswren. Ph.d. Thesis, School of Biological Sciences. (Flinders University: Adelaide.)
- Macedo, R. H., Karubian, J., and Webster, M. S. (2008). Extrapair paternity and sexual selection in socially monogamous birds: Are tropical birds different? *The Auk* **125**, 769–777.
- Maia, R., Eliason, C. M., Bitton, -P.-P., Doucet, S. M., and Shawkey, M. D. (2013). pavo: An R package for the analysis, visualization and organization of spectral data. *Methods in Ecology and Evolution* **4**, 906–913.
- Margraf, N., and Cockburn, A. (2013). Helping behaviour and parental care in fairy-wrens (*Malurus*). *Emu* **113**, 294–301.
- Martin, T. E. (1996). Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* **27**, 263–272.
- Medina, I., Delhey, K., Peters, A., Cain, K. E., Hall, M. L., Mulder, R. A., and Langmore, N. E. (2017). Habitat structure is linked to the evolution of plumage colour in female, but not male, fairy-wrens. *BMC Evolutionary Biology* **17**, 35.
- 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 B: Biological Sciences* **255**, 223–229.
- Peters, A. (2007). Testosterone treatment of female Superb Fairy-wrens *Malurus cyaneus* induces a male-like pre-nuptial moult, but no coloured plumage. *Ibis* **149**, 121–127.
- Peters, A., Kingma, S. A., and Delhey, K. (2013). Seasonal male plumage as a multi-component sexual signal: Insights and opportunities. *Emu* **113**, 232–247.
- Portugal, S. J., White, C. R., Green, J. A., and Butler, P. J. (2018). Flight feather moult drives minimum daily heart rate in wild geese. *Biology Letters* **14**, 20180650.
- Pruett-Jones, S. G., and Lewis, M. J. (1990). Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* **348**, 541–542.
- Pyle, P. (1997). 'Identification Guide to North American Birds, Part I: Columbidae to Ploceidae.' (State Creek Press: Bolinas, CA.)
- Rathburn, M. K., and Montgomerie, R. (2003). Breeding biology and social structure of White-winged Fairy-wrens (*Malurus leucopterus*): Comparison between island and mainland subspecies having different plumage phenotypes. *Emu* **103**, 295–306.
- Rathburn, M. K., and Montgomerie, R. (2005). Offspring sex ratios correlate with pair-male condition in a cooperatively breeding fairy-wren. *Behavioral Ecology* **16**, 41–47.
- Ricklefs, R. E. (1976). Growth rates of birds in the humid new world tropics. *Ibis* **118**, 179–207.
- Rohwer, S. (2008). A primer on summarizing molt data for flight feathers. *The Condor* **110**, 799–806.
- Rowe, M., and Pruett-Jones, S. (2011). Sperm competition selects for sperm quantity and quality in the Australian Maluridae. *PLoS One* **6**, e15720.
- Rowe, M., and Pruett-Jones, S. (2013). Extra-pair paternity, sperm competition and their evolutionary consequences in the Maluridae. *Emu* **113**, 218–231.
- Rowley, I., and Russel, E. (2007). Family Maluridae (Fairywrens). In 'Handbook of the Birds of the World - Volume 12: Picathartes to Tits and Chickadees.' (Eds J. del Hoyo, A. Elliott, and D. A. Christie.) pp. 490–531. (Lynx Edicions: Barcelona, Spain.)
- Rowley, I., and Russell, E. (1993). The Purple-crowned Fairy-wren *Malurus coronatus*. II. Breeding Biology, Social organization, Demography and Management. *Emu* **93**, 235–250.
- Rowley, I., and Russell, E. (1995). The Breeding Biology of the White-winged Fairy-wren *Malurus leucopterus leucnotus* in a Western Australian Coastal Heathland. *Emu* **95**, 175–184.
- Rowley, I., and Russell, E. (1997). 'Fairy-Wrens and Grasswrens: Maluridae.' (Oxford University Press: Oxford.)
- Rubenstein, D. R., and Lovette, I. J. (2009). Reproductive skew and selection on female ornamentation in social species. *Nature* **462**, 786–789.
- Schodde, R. (1982). 'The Fairy-Wrens: A Monograph of the Maluridae.' (Landsdowne Editions: Melbourne.)
- Schwabl, H., Dowling, J., Baldassarre, D. T., Gahr, M., Lindsay, W. R., and Webster, M. S. (2015). Variation in song system anatomy and androgen levels does not correspond to song characteristics in a tropical songbird. *Animal Behaviour* **104**, 39–50.
- Schwabl, H., Lindsay, W. R., Barron, D. G., and Webster, M. S. (2014). Endocrine correlates of mate choice and promiscuity in females of a socially monogamous avian mating system with alternative male reproductive phenotypes. *Current Zoology* **60**, 804–815.
- Skutch, A. F. (2018). Clutch Size, Nesting Success, and Predation on Nests of Neotropical Birds, Reviewed Author (s): Alexander F. Skutch Source: Ornithological Monographs, No. 36, Neotropical Ornithology (1985). pp. 575–594. (American Ornithological.)

- Stutchbury, B. J. M., and Morton, E. S. (2001). 'Behavioral Ecology of Tropical Birds.' (Cambridge, Massachusetts: Academic Press.)
- Swaddle, J. P., Pruett-Jones, S., and Karubian, J. (2000). A novel evolutionary pattern of reversed sexual dimorphism in fairy-wrens: Implications for sexual selection. *Behavioral Ecology* **11**, 345–349.
- Swaddle, J. P., and Witter, M. S. (1997). The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): An experimental approach. *Canadian Journal of Zoology* **75**, 1135–1146.
- Tobias, J. A., Montgomerie, R., and Lyon, B. E. (2012). The evolution of female ornaments and weaponry: Social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 2274–2293.
- Tuttle, E. M., Pruett-Jones, S., and Webster, M. S. (1996). Cloacal protuberances and extreme sperm production in Australian fairy-wrens. *Proceedings of the Royal Society B: Biological Sciences* **263**, 1359–1364.
- Van Bael, S., and Pruett-Jones, S. (2000). Breeding biology and social behaviour of the eastern race of the Splendid Fairy-wren *Malurus splendens melanotus*. *Emu* **100**, 95–108.
- Varian-Ramos, C. W., Karubian, J., Talbott, V., Tapia, I., and Webster, M. S. (2010). Offspring sex ratios reflect lack of repayment by auxiliary males in a cooperatively breeding passerine. *Behavioral Ecology and Sociobiology* **64**, 967–977.
- Varian-Ramos, C. W., Lindsay, W. R., Karubian, J., and Webster, M. S. (2012). Female Red-backed Fairy-Wrens (*Malurus melanocephalus*) do not appear to pay a cost for high rates of promiscuity. *The Auk* **129**, 529–536.
- Webster, M. S., Tarvin, K. A., Tuttle, E. M., and Pruett-Jones, S. (2004). Reproductive promiscuity in the splendid fairy-wren: Effects of group size and auxiliary reproduction. *Behavioral Ecology* **15**, 907–915.
- Webster, M. S., Varian, C. W., and Karubian, J. (2008). Plumage color and reproduction in the red-backed fairy-wren: Why be a dull breeder? *Behavioral Ecology* **19**, 517–524.
- West-Eberhard, M. J. (1979). Sexual selection, social competition and evolution. *Proceedings of the American Philosophical Society* **123**, 222–234.
- West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *The Quarterly Review of Biology* **58**, 155–183.
- Wiersma, P., Munoz-Garcia, A., Walker, A., and Williams, J. B. (2007). Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences* **104**, 9340–9345.
- Wolfe, J. D., Ryder, T. B., and Pyle, P. (2010). Using molt cycles to categorize the age of tropical birds: An integrative new system. *Journal of Field Ornithology* **81**, 186–194.
- Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of Theoretical Biology* **53**, 205–214.