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

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Published online: 25 Apr 2019.

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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 fairywrens with exclusively tropical distributions and differ from other species 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 sub-species 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.

**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. melanopechalus), suggesting a secondary Malurus recolonisation of New Guinea during a recent glacial maximum (Rowley and Russell 1997; Rowley and Russell 2007; Joseph et al. 2013). The other members of the bicoloured clade, M. melanopechalus and M. leucopterus, provide useful points of comparison with White-shouldered Fairywrens. Malurus melanopechalus and M. leucopterus both exhibit delayed
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 albescapulatus moretoni (hereafter) in the far south-east of the country, and Malurus albescapulatus 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.). 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](https://example.com/figure1.png)

**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.
more intensively than lorentzi (Figure S2), but obtained useful information from both. Monthly precipita-
tion 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 µl) 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 com-
parisons 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 mini-
mum 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 nest-
ing. 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

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 * (male – female)/(male + 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 (abs(female – average male value)) and
contrasted using a t-test. We calculated scaled cloacal
protubercane (CP) volume with the ratio of CP volume
(3.14 * (CP height/2) * (CP width/2) * 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 cate-
gories) 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 reflec-
tance 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 measure-
ments 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 labora-
tory 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 frag-
ment 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 foraying 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...
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 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

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.
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.

**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>
<thead>
<tr>
<th>Species</th>
<th>Extra-pair rate</th>
<th>Scaled CP volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amytornis textilis</td>
<td>0.063</td>
<td>2.83</td>
</tr>
<tr>
<td>Malurus coronatus</td>
<td>0.12</td>
<td>0.54</td>
</tr>
<tr>
<td>Stipiturus malachurus</td>
<td>0.48</td>
<td>0.10</td>
</tr>
<tr>
<td>Malurus alboscapulatus moretoni</td>
<td>0.33</td>
<td>0.85</td>
</tr>
<tr>
<td>Malurus alboscapulatus lorentzi</td>
<td>0.14</td>
<td>0.97</td>
</tr>
<tr>
<td>Malurus splendidens</td>
<td>0.48</td>
<td>10.26</td>
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<tr>
<td>Malurus melanocephalus</td>
<td>0.54</td>
<td>16.94</td>
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<td>Malurus lamberti</td>
<td>0.56</td>
<td>4.40</td>
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<tr>
<td>Malurus elegans</td>
<td>0.63</td>
<td>5.63</td>
</tr>
<tr>
<td>Malurus cyaneus</td>
<td>0.64</td>
<td>11.77</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Sex</th>
<th>Type</th>
<th>Measure</th>
<th>M. a. lorentzi</th>
<th>M. a. moretoni</th>
<th>Population difference (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>Morphology</td>
<td>Mass (g)</td>
<td>7.53 ± 0.45 (67)</td>
<td>8.66 ± 0.70 (156)</td>
<td>0.140***</td>
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<tr>
<td></td>
<td></td>
<td>Tarsus (mm)</td>
<td>21.38 ± 1.30 (71)</td>
<td>22.11 ± 1.02 (156)</td>
<td>0.034***</td>
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<tr>
<td></td>
<td></td>
<td>Wing (mm)</td>
<td>42.74 ± 1.39 (71)</td>
<td>44.00 ± 1.18 (156)</td>
<td>0.029***</td>
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<tr>
<td></td>
<td></td>
<td>Tail (mm)</td>
<td>48.0 ± 2.54 (94)</td>
<td>45.8 ± 2.44 (218)</td>
<td>0.470%</td>
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<tr>
<td></td>
<td></td>
<td>Bill + head (mm)</td>
<td>27.71 ± 0.57 (71)</td>
<td>29.04 ± 1.21 (156)</td>
<td>0.032***</td>
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<tr>
<td></td>
<td>Plumage</td>
<td>Chest brightness (B2)</td>
<td>32.50 ± 12.52 (29)</td>
<td>2.55 ± 0.62 (75)</td>
<td>0.170.87%</td>
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<tr>
<td></td>
<td></td>
<td>Chest R.achieved</td>
<td>0.20 ± 0.16 (29)</td>
<td>0.07 ± 0.05 (75)</td>
<td>0.915.5%</td>
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<tr>
<td></td>
<td></td>
<td>Chest dl_SP (contrast)</td>
<td>13.62 ± 4.19 (19)</td>
<td>32.21 ± 2.79 (75)</td>
<td>0.811***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shoulder brightness (B2)</td>
<td>8.00 ± 1.61 (19)</td>
<td>61.63 ± 8.63 (72)</td>
<td>1.540%</td>
</tr>
<tr>
<td>Male</td>
<td>Morphology</td>
<td>Mass (g)</td>
<td>7.88 ± 0.46 (85)</td>
<td>9.44 ± 1.70 (141)</td>
<td>0.180***</td>
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<td>Tarsus (mm)</td>
<td>21.62 ± 0.98 (86)</td>
<td>23.01 ± 1.17 (143)</td>
<td>0.062***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wing (mm)</td>
<td>44.07 ± 1.23 (86)</td>
<td>45.14 ± 1.20 (144)</td>
<td>0.024***</td>
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<tr>
<td></td>
<td></td>
<td>Tail (mm)</td>
<td>42.5 ± 2.94 (124)</td>
<td>43.0 ± 2.52 (251)</td>
<td>1.17%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bill + head (mm)</td>
<td>28.13 ± 0.52 (86)</td>
<td>29.90 ± 0.63 (143)</td>
<td>0.061***</td>
</tr>
<tr>
<td></td>
<td>Plumage</td>
<td>Scaled CP volume</td>
<td>8.97 ± 2.95 (107)</td>
<td>7.85 ± 3.66 (199)</td>
<td>0.132.3%</td>
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<tr>
<td></td>
<td></td>
<td>Chest brightness (B2)</td>
<td>1.55 ± 0.52 (28)</td>
<td>2.08 ± 0.47 (81)</td>
<td>0.293***</td>
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<tr>
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<td></td>
<td>Chest R.achieved</td>
<td>0.24 ± 0.09 (28)</td>
<td>0.23 ± 0.08 (81)</td>
<td>0.478%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chest dl_SP (contrast)</td>
<td>37.67 ± 4.36 (18)</td>
<td>35.68 ± 2.81 (76)</td>
<td>0.543%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shoulder brightness</td>
<td>59.76 ± 8.79(20)</td>
<td>65.32 ± 9.96(76)</td>
<td>0.089</td>
</tr>
</tbody>
</table>

| Average dimorphism (%) | Morphology | Population difference (%) | 0.01, ***p = 0.001. See text for details on statistical tests applied for each variable.

For each variable, statistical analyses were conducted on individual 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.
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 moulted 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.
(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 2001, 2013).

**Sexual dimorphism**

White-shouldered Fairywrens maintain adult plumage year-round. The majority of Malurus fairywrens exhibit seasonal sexual dichromatism (Friedman and Remes 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 Remes 2015; Enbody et al. 2017).

Delayed plumage maturation plays an important role in dominance and mate choice in M. melanopeplus (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 Montgomery 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 mouls 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 shouldn't Fairywren. Timing of adult mouls 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 congeners 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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