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Behavioural differences between ornamented and unornamented male Red-backed Fairywrens (*Malurus melanocephalus*) in the nonbreeding season

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ABSTRACT

During the breeding season, male Red-backed Fairywrens (*Malurus melanocephalus*) can exhibit ornamented (red-black) or unornamented (brown, resembling females and juveniles) plumage. These distinct plumage types represent alternative reproductive tactics and are associated with behavioural differences during the breeding season. However, we lack an understanding of whether and how these plumage types may be associated with behavioural differences during non-reproductive parts of the year. To fill this knowledge gap, we carried out behavioural observations during the nonbreeding season across three years. We hypothesised that ornamented plumage remains associated with mate attraction behaviours outside of the breeding season. We examined the investment of ornamented, moulting, and unornamented males in social behaviours and found that the three plumage types were largely similar in their behaviour except ornamented males courted and, to a lesser extent, allopreened at higher rates than unornamented males. Since concurrent work in the same study population demonstrates increased extra-pair fitness for males who moult into ornamented plumage early, we speculate that ornamentation and courtship behaviour may serve a mate attraction function outside of the breeding season. We argue that future studies should consider individual-level behavioural monitoring throughout the annual cycle to better quantify the complex selection pressures that lead to the coevolution of plumage moult and alternative reproductive tactics in this system.

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Colouration; winter; allopreening; courtship; promiscuity; mate attraction

Introduction

Alternative reproductive tactics (ARTs) describe situations in which two or more distinct strategies evolve within the same sex in order to reproduce. For example, male white-faced dragonflies (*Leucorrhinia intacta*) can either defend territories to attract mates or search for mates as transients with equal reproductive success (Waltz and Wolf 1988). Historically, ARTs have provided opportunities to understand how phenotypic variation is generated (Oliveira *et al.* 2008). ARTs have been studied predominantly in the breeding season, for obvious reasons. However, a growing body of work supports the idea that events in the nonbreeding season can influence reproductive output during the subsequent breeding season (Cockburn *et al.* 2008; Reudink *et al.* 2009; Beck *et al.* 2020). However, with relatively few studies documenting nonbreeding behavioural

ecology (Marra *et al.* 2015), we are likely missing crucial social information that informs breeding outcomes. For species where nonbreeding data are scarce, comparing breeding and nonbreeding social behaviour represents an important step towards more holistic behavioural monitoring.

The Australian fairywrens exhibit ARTs and present a suitable system to compare associated behaviours in breeding and nonbreeding periods. In fairywrens, ARTs are often closely tied to different plumage types. In breeding Red-backed Fairywrens (RBFW, *Malurus melanocephalus*), ornamented males in red-black plumage are more socially dominant and invest more heavily in extra-pair courtship displays, whereas unornamented males in female-like brown plumage are less dominant and invest more in mate guarding and parental care (reviewed in Webster *et al.* 2010). These alternative

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plumage types are also present during much of the nonbreeding season due to some males moulting into breeding plumage months before the breeding season begins (Welklin *et al.* 2021), but it is unclear whether males with these plumage types also exhibit behavioural differences in the nonbreeding season consistent with the behaviours associated with ARTs during the breeding season.

In this study, we examined whether ornamented male RBFWs exhibited different behaviours than unornamented males during the nonbreeding period and, further, whether these behavioural differences were similar to those documented during the breeding season. Broadly, we hypothesised that mate attraction behaviours remain associated with ornamentation throughout the year and will be observed in the nonbreeding period, which would match similar findings from Superb Fairywrens (*Malurus cyaneus*) showing that males court females during the nonbreeding season after moulting into breeding plumage (Mulder and Magrath 1994). Specifically, we investigated the participation of ornamented, unornamented, and moulting (unornamented males transitioning into ornamented plumage) males in courtship, vocalising, chasing, allopreening, and preening (see Table S1 for definitions). These variables were chosen due to their inclusion in a previous study of RBFW ARTs in the breeding season (Karubian 2002) or their potential relevance to ARTs in a nonbreeding context. Karubian (2002) reported that ornamented males display at higher rates than unornamented males, especially to extra-pair females as part of their ART. Vocalising (specifically territorial singing) was previously investigated and was found to not differ between the ornamented and unornamented males (Karubian 2002). Chasing likely functions in both territorial disputes as well as courtship (Karubian and Alvarado 2003) but was not previously quantified in the breeding season (Karubian 2002). Allopreening has not been explicitly studied in RBFWs, but, given its functioning in pair bonding in other systems (Gill 2012; Kenny *et al.* 2017), it could serve as a nonbreeding season analogue to the mate-guarding behaviour and higher investment in parental care observed in unornamented RBFW males in the breeding season (mate guarding and parental care are difficult to quantify in the nonbreeding season since territoriality relaxes considerably; Rowley and Russell 2007; Welklin *et al.* 2022). Finally, in other species, preening is used to maintain sexually selected plumage colouration (Griggio *et al.* 2010; López-Rull *et al.* 2010) and, thus, could be associated with the early acquisition of ornamented plumage.

Methods

Study site and population

We captured RBFWs near Lake Samsonvale (27° 16' 7" S, 152° 51' 32" E) in Queensland, Australia using mist nets and banded individuals with three coloured leg bands and a numbered aluminium band provided by the Australian Bird and Bat Banding Scheme. We conducted focal observations on colour-banded fairywrens from mid-June to early August in 2016, 2017, and 2018. This period corresponds to the second half of the nonbreeding period in this population. In the nonbreeding period, RBFWs form foraging flocks of as many as 30 individuals, yet birds typically remain associated with their social mates from the preceding breeding season (Rowley and Russell 2007; Welklin *et al.* 2022). Our population included 220–240 birds per year that formed nonbreeding groups typically composed of parents and their offspring (mean group size was between 3 and 4; Welklin *et al.* 2022).

Study individuals and behavioural observations

We collected data between 0630 and 1300, six days a week, for the nonbreeding periods of three years. We scored the plumage of males by visually estimating the percentage of the body covered in red-black plumage (Karubian 2002). Observers trained as a group and regularly reviewed plumage scores assigned to moulting (intermediate) males to minimise inter-observer variation. Plumage was scored in increments of 5%, or scores were rounded to the nearest 5% value. We assigned males to one of three categories: unornamented (0–20% red-black), moulting (21–79% red-black), or ornamented (80–100% red-black). We conducted 5-minute focal observations (mean $\pm$ s.d., 5:01 mins $\pm$ 9 secs) on individual males, recording their behaviour continuously in accordance with Karubian (2002; Table S1). We followed the focal individual for approximately 5 minutes and recorded its behaviour to the nearest second using the following behaviours: allopreen, courtship, chase, vocalisation, forage, sit, fly, preen, out of sight, and other. Any observation that contained more than 180 seconds of the 'out of sight' category (see Table S1) was excluded from subsequent analysis. Behavioural observations were classified such that a focal individual could only be recorded as performing a single behaviour at a time. Observers attempted to remain more than 20 metres away from focal birds during observations. Data were collected by pairs of researchers: an observer with binoculars narrated the behaviour of a focal bird and a scribe recorded data. When possible, we randomly selected a region within the study site each day in which to focus our

sampling efforts to minimise seasonal variation in our sampling effort between groups of fairywrens and the three plumage categories (Figures S1 and S2).

The previously described focal behavioural observations were designed to quantify the investment of RBFWs in various behaviours, but they were not effective in identifying interacting pairs of RBFWs. For this reason, we supplement our primary dataset with opportunistically collected data on pairs of RBFWs from this study population engaged in allopreening, courtship, or chasing during the nonbreeding seasons of 2015–2018. These observations consisted of identifying the individuals involved (via colour bands) and their plumage scores. For courtship and chasing, we only include observations in which we were able to confidently identify a sender and receiver of the behavioural signal. For observations that included several bouts of the same behaviour between the same individuals, we only consider behaviours that are separated by at least 5 minutes. We draw on banding records to determine the sex of individuals, but we also leverage intensive monitoring efforts during the breeding season to identify if two individuals observed to be interacting during the nonbreeding period became social mates during the upcoming breeding season and if they belonged to the same breeding group (social mate, offspring, and related helpers) during the previous breeding season.

Statistical analyses

We used logistic mixed-effects models with a binomial distribution and logit link to identify which factors (i.e. the plumage category a male belongs to, age acquired from banding records, year, and day of year/Julian date) predicted whether or not a behaviour of interest (i.e. allopreening, chasing, courtship, preening, and vocalising) was observed during a focal behavioural observation. Although our primary focus was differences in plumage, age and day of year have previously been shown to affect ART-associated behaviours in this species during the breeding season (Karubian 2002; Webster *et al.* 2008; Dowling and Webster 2017), so we included them as additional fixed effects. We also include year as a fixed effect since we were interested in understanding if a major drought in 2016, which altered the proportion of plumage categories present in our study population (Figures S1, S2, and S3, Welkin *et al.* 2021), affected behaviour. Separate models were constructed for each of the five behaviours of interest, and models were run using the `glmer` function in the `lme4` package (Bates *et al.* 2015) with R version 4.2.2 (R Core Team 2022). All models included the identity of the focal male (to control for repeated measures; Figure S3) and the identity of the observer as random effects. Each model was compared to a null model including only random effects,

using a likelihood ratio test (LRT). For models identified as significant improvements over null models, we also used a LRT to compare them to models containing all fixed effects except the plumage category variable. To evaluate model fit, we calculated McFadden's pseudo R^2 (Domencich and McFadden 1975) for each model and examined residuals using the DHARMa package (Hartig 2022). Since courtship was never observed in unornamented males, the unornamented and moulting plumage categories were combined in the courtship model to provide a non-zero estimate of variance.

For the opportunistic behavioural observations, we report the proportion of interactions between two RBFWs that occurred in a particular social context (e.g. interactions between members of the same breeding group from the previous breeding season).

Results

We conducted 369 focal observations on 116 male RBFWs (194 observations on unornamented males; 42, moulting; 133, ornamented). Ornamented and moulting males exhibited courtship behaviours ($N = 26$ of 175 observations), whereas we did not record a single incidence of courtship by unornamented males. Ornamented males courted more often than the other two plumage types considered together (LRT: $\chi^2 = 36.798$, $DF = 1$, $P < 0.001$; Figure 1(a)). Variation in courtship behaviour was not associated with age, the year of study, or Julian date (Figure 1(b)). We found a similar but weaker pattern for allopreening. Ornamented males ($N = 19$ of 133 observations) were observed allopreening slightly more than unornamented males ($N = 14$ of 194 observations) (Wald Z: $Z = 2.028$, $P = 0.043$; Figure 1(c,d)). However, while the allopreening model with fixed effects outperformed the null model, the inclusion of plumage category as a fixed effect on its own did not improve model fit (LRT: $\chi^2 = 4.152$, $DF = 2$, $P = 0.125$). The remaining logistic mixed-effects models considered provided no substantial improvement over the null models (Table 1), indicating that the other behaviours we evaluated (chasing, preening, and vocalising) did not differ among the three plumage types (Figures S4 and S5). We observed considerable variation in the relative numbers of ornamented, moulting, and unornamented males across the three years of this study (Figures S1, S2, and S3), but, for courtship and allopreening, year had no effect on the probability of observing a behaviour (Figure 1(b,d)).

We opportunistically gathered information on 726 RBFW interactions. Only ornamented males engaged in courtship in these observations and directed their displays overwhelmingly towards females (80%; Figure S6). Furthermore, the recipients of courtship behaviour were

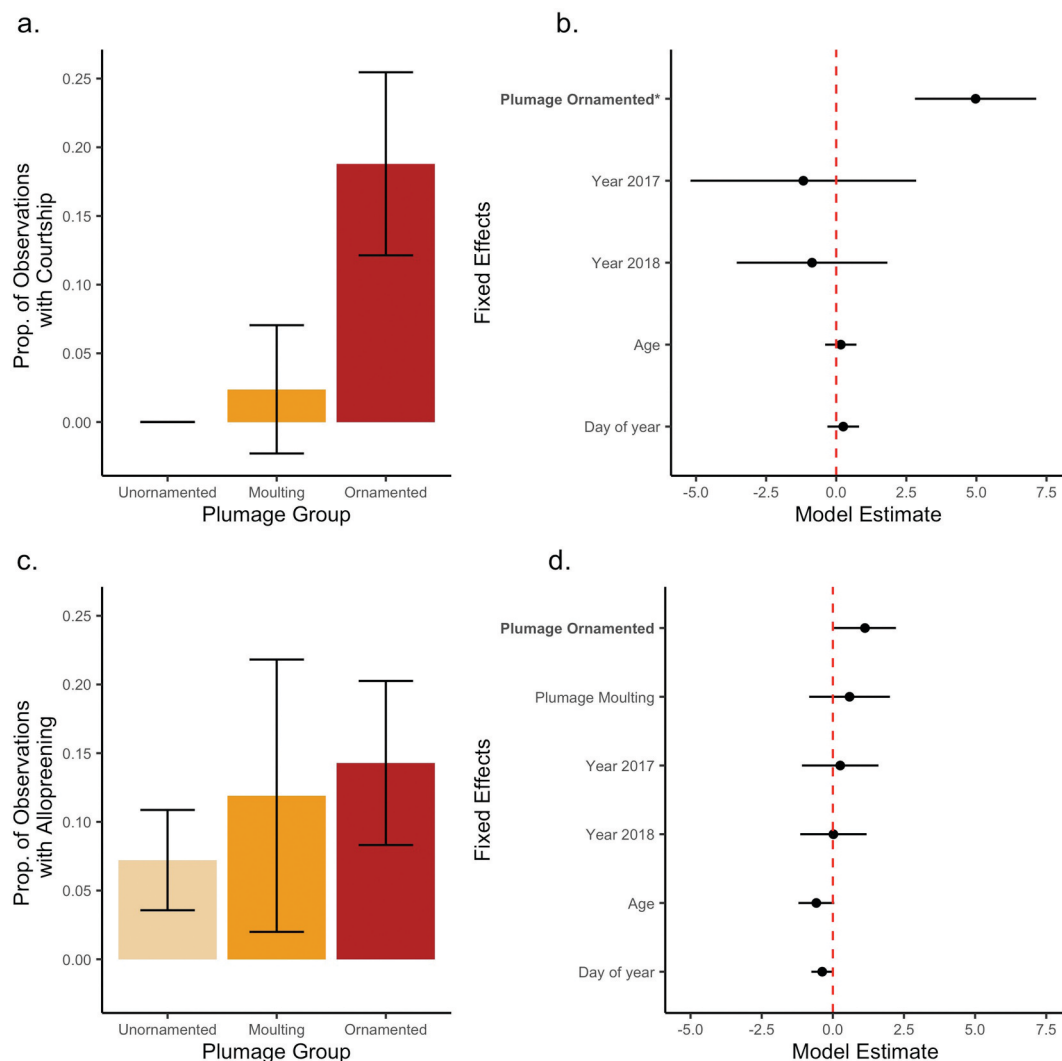


Figure 1. The average proportion of focal observations in a male Red-Backed Fairywren engaging in courtship (a) and allopreening (c). Error bars show 95% confidence intervals. b and d. Model estimates from the logistic mixed-effects models with courtship (b) and allopreening (d) as the response variables. Error bars show 95% confidence intervals. Confidence intervals that do not overlap zero are printed in bold type.

Table 1. Logistic mixed-effects models predicting the occurrence of each behaviour of interest in male Red-backed Fairywrens. Each model contained plumage category, year, age, and day of year as fixed effects and the identity of the focal male and observer as random effects.

Response variable	Likelihood ratio (χ^2)	DF	P	Pseudo R ²
Allopreening	13.233	6	0.039	0.055
Chasing	10.887	6	0.092	0.063
Courtship	49.922	5	0.000	0.312
Preening	9.888	6	0.129	0.02
Vocalising	5.451	6	0.487	0.011

mostly extra-group females (62%; Table S2). Allopreening occurred largely between social mates and members of the same breeding group (38% and 43%, respectively; Table S2). Finally, most chasing observations involved a female being chased (70%; Figure S6) and were more often a male and female from different breeding groups than social mates (43% vs. 13%; Table S2).

Discussion

Our prediction that plumage-associated behaviours in the breeding season would persist into the nonbreeding period was partially supported. Focal observations revealed differential investment in two behaviours by ornamented and unornamented males while opportunistic observations

(although non-random samples may overrepresent ornamented individuals) provided insights into the typical social contexts of these behaviours. As in the breeding season, ornamented males engaged in courtship at a higher rate and targeted potential extra-pair mates with their displays. However, the rate of courtship displays was approximately an order of magnitude lower than that observed in the breeding season (Karubian 2002). Ornamented males also appear to allopreen with kin more frequently than unornamented males contrary to our prediction that this behaviour may be a nonbreeding season analogue of the higher investment of unornamented males in parental care and mate guarding during the breeding season. The combination of these observations suggests a persistence yet flexibility of the RBFW ARTs outside of the breeding season.

A contemporaneous study in the same study population reports that males that moult into ornamented plumage earlier in the nonbreeding season have higher extra-pair reproductive success the following year (Welklin 2020), similar to previous findings in several congeners (Cockburn *et al.* 2008; Brouwer *et al.* 2011). The finding of the present study that ornamented males continue to display to potential extra-pair mates throughout the annual cycle raises the possibility that nonbreeding season ARTs play a role in driving the relationship between the timing of moult into breeding plumage and breeding season reproductive success. However, more detailed longitudinal tracking of individuals and their social behaviours throughout the year is needed to disentangle the relative contributions of breeding season and nonbreeding season social behaviours to mate choice.

We also analysed the behaviour of males with intermediate plumage (moulting males) and anticipated that their behaviour would be intermediate between that of unornamented and ornamented males. Although data visualisation shows a trend in this direction, our current sample size is too small to draw any conclusions. Previous studies investigating the breeding biology of this species have excluded moulting males from analyses due to low sample sizes (e.g. Karubian *et al.* 2008) and, despite the relatively higher proportion of moulting males present during the nonbreeding season, the quantitative conclusions we can draw from the present study are similarly limited (Figures S1, S2, and S3).

By describing RBFW behaviour in the nonbreeding season and suggesting that plumage and behaviour may covary throughout the year, this study contributes to a growing effort to fill our collective knowledge gap about behavioural ecology outside breeding periods (Marra *et al.*

2015). Although continuous behavioural monitoring is necessary to fully parse the components of mate choice in this system, the investment of ornamented males in courtship-related behaviours documented in this study is consistent with information exchange in the nonbreeding season that may affect subsequent mate choice decisions, providing insights into why certain males moult into ornamented plumage many months prior to the onset of breeding.

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Author contributions

TCH, FFD, SMT, SML, JFW, JPS, MSW, and JK conceived and designed the study. TCH, FFD, SMT, LGH, RGT, MM, SJH, MA, NC, PH, SK, CEH, SML, and JFW collected the data. TCH analysed the data. TCH and FFD wrote the manuscript. All authors provided comments and edited the paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Data availability statement

The data that support the findings of this study and the R code necessary to reproduce figures and analyses are openly available in the Figshare repository at <https://doi.org/10.6084/m9.figshare.c.5538159.v1>

Geolocation information

The data presented in the current study were gathered from a population of RBFWs near Lake Samsonvale (27° 16' 7" S 152° 51' 32" E) in Queensland, Australia.

References

- Bates, D., Mächler, M., Bolker, B. M., and Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48. doi:10.18637/jss.v067.i01
- Beck, K. B., Farine, D. R., and Kempenaers, B. (2020). Winter associations predict social and extra-pair mating patterns in a wild songbird. *Proceedings of the Royal Society B: Biological Sciences* **287**. doi:10.1098/rspb.2019.2606
- Brouwer, L., Van De Pol, M., Atema, E., and Cockburn, A. (2011). Strategic promiscuity helps avoid inbreeding at multiple levels in a cooperative breeder where both sexes are philopatric. *Molecular Ecology* **20**, 4796–4807. doi:10.1111/j.1365-294X.2011.05325.x
- 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: Biological Sciences* **275**, 605–612. doi:10.1098/rspb.2007.0916
- Domencich, T. A., and McFadden, D. (1975). 'Urban Travel Demand - A Behavioral Analysis.' (North-Holland Publishing Company Limited: Oxford.)
- Dowling, J., and Webster, M. S. (2017). Working with what you've got: Unattractive males show greater mateguarding effort in a duetting songbird. *Biology Letters* **13**, 20160682. doi:10.1098/rsbl.2016.0682
- Gill, S. A. (2012). Strategic use of allopreening in family-living wrens. *Behavioral Ecology and Sociobiology* **66**, 757–763. doi:10.1007/s00265-012-1323-6
- Griggio, M., Hoi, H., and Pilastro, A. (2010). Plumage maintenance affects ultraviolet colour and female preference in the budgerigar. *Behavioural Processes* **84**, 739–744. doi:10.1016/j.beproc.2010.05.003
- Hartig, F. (2022). 'DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models.' Available at <https://cran.r-project.org/package=DHARMA>
- Karubian, J. (2002). Costs and benefits of variable breeding plumage in the red-backed fairy-wren. *Evolution* **56**, 1673–1682. doi:10.1554/0014-3820(2002)056[1673:CABOV]2.0.CO;2
- Karubian, J., and Alvarado, A. (2003). Testing the function of petal-carrying in the Red-backed Fairy-wren (*Malurus melanocephalus*). *Emu* **103**, 87–92. doi:10.1071/MU01063
- 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. doi:10.1093/beheco/arm159
- Kenny, E., Birkhead, T. R., and Green, J. P. (2017). Allopreening in birds is associated with parental cooperation over offspring care and stable pair bonds across years. *Behavioral Ecology* **28**, 1142–1148. doi:10.1093/beheco/axx078
- López-Rull, I., Pagán, I., and Macías García, C. (2010). Cosmetic enhancement of signal coloration: Experimental evidence in the house finch. *Behavioral Ecology* **21**, 781–787. doi:10.1093/beheco/arq053
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., and Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters* **11**, 20150552. doi:10.1098/rsbl.2015.0552
- Mulder, R. A., and Magrath, M. J. L. (1994). Timing of pre-nuptial molt as a sexually selected indicator of male quality in superb fairy-wrens (*Malurus cyaneus*). *Behavioral Ecology* **5**, 393–400. doi:10.1093/beheco/5.4.393
- Oliveira, R. F., Taborsky, M., and Jane Brockmann, H. (2008). 'Alternative Reproductive Tactics: An Integrative Approach.' (Cambridge: Cambridge University Press.)
- R Core Team (2022). 'R: A language and environment for statistical computing.' Available at <https://www.r-project.org/>
- Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M., and Ratcliffe, L. M. (2009). Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences* **276**, 1619–1626. doi:10.1098/rspb.2008.1452
- Rowley, I., and Russell, E. (2007). Family Maluridae (fairy-wrens). In 'Handbook of the Birds of the World. Vol. 12. Picathartes to Tits and Chickadees'. (Eds J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana.) pp. 490–531. (Lynx Edicions: Barcelona.)
- Waltz, E. C., and Wolf, L. L. (1988). Alternative mating tactics in male white-faced dragonflies (*Leucorrhinia intacta*): Plasticity of tactical options and consequences for reproductive success. *Evolutionary Ecology* **2**, 205–231. doi:10.1007/BF02214284
- Webster, M. S., Karubian, J., and Schwabl, H. (2010). Dealing with uncertainty. Flexible reproductive strategies by a tropical passerine bird in an unstable ecological and social environment. In 'Advances in the Study of Behavior'. (Ed. R. Macedo.) pp. 123–153. (Elsevier Inc: Burlington.) doi:10.1016/S0065-3454(10)42004-5
- 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. doi:10.1093/beheco/arn015
- Welklin, J. F. (2020). Social and environmental causes and reproductive consequences of ornamented plumage in the red-backed fairywren (*Malurus melanocephalus*). Ph.D. Thesis, Cornell University, Ithaca, NY.
- Welklin, J. F., Lantz, S. M., Khalil, S., Moody, N. M., Karubian, J., and Webster, M. S. (2021). Social and abiotic factors differentially affect plumage ornamentation of young and old males in an Australian songbird. *Animal Behaviour* **182**, 173–188. doi:10.1016/j.anbehav.2021.10.007
- Welklin, J. F., Lantz, S. M., Khalil, S., Moody, N. M., Karubian, J., & Webster, M. S. (2023). Photoperiod and rainfall are associated with seasonal shifts in social structure in a songbird. *Behavioral Ecology*, **34**(1), 136–149. doi:10.1093/beheco/arac110