

Social and abiotic factors differentially affect plumage ornamentation of young and old males in an Australian songbird

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Both abiotic environmental conditions and variation in social environment are known to impact the acquisition of sexual signals. However, the influences of abiotic environmental and social factors are rarely compared to each other. Here we test the relative importance of these factors in determining whether and when male red-backed fairy-wrens, *Malurus melanocephalus*, moult into ornamented breeding plumage, a known sexual signal. One-year-old male red-backed fairy-wrens vary in whether or not they acquire ornamentation, whereas males age 2 years and older vary in their timing of ornament acquisition. It is unclear whether these processes are determined by the same or different factors, and we examined both events using a combination of long-term breeding records and nonbreeding social networks. We found that 1-year-old males that paired prior to the start of the breeding season were more likely to acquire ornamented plumage, but rainfall did not influence whether 1-year-old males acquired ornamented plumage. Thus, for young individuals, social cues appear to play a larger role than abiotic environmental factors in determining ornament acquisition. For older males, timing of ornamented plumage acquisition was constrained by rainfall, with drier nonbreeding seasons leading to poorer physiological condition and later moult dates. Thus, sexual signal variation in older males appears to be a condition-dependent trait, driven by abiotic environmental and physiological factors rather than social cues. These findings reveal that factors influencing sexual signal expression can vary with age when age classes exhibit different forms of signal variation. Our results suggest that social environment may drive sexual signal variation in young individuals, whereas abiotic environmental variation may drive sexual signal variation in older individuals.

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Sexual ornaments are thought to convey information about the quality of a signaller when individuals vary in their ability to offset costs associated with the production and maintenance of sexual signals (Grafen, 1990; Johnstone, 1997; Zahavi, 1977). Identifying the mechanisms that link individual quality to signal quality, and thereby generate honest sexual signals, continues to be a major focus of behavioural ecology (Penn & Számadó, 2019; Webster et al., 2018). Considerable attention has been given to physiological mechanisms that are broadly categorized under the physiological cost hypothesis. This hypothesis proposes that endogenous constraints, such as energetic (Basolo & Alcaraz, 2003; Buchanan

et al., 2001), oxidative (Alonso-Alvarez et al., 2007; Pérez-Rodríguez et al., 2010) or immunosuppressive (Folstad & Karter, 1992; Saino & Møller, 1996) costs incurred during signal production or maintenance limit an individual's signalling ability. Under this hypothesis, sexual signals are thought to be condition dependent, such that individual differences in genotype, somatic states, epigenetic states and processes that influence these can determine an individual's ability to offset the physiological costs of signal production and maintenance, leading to variation in the quality of signals produced (Hill, 2011).

The physiological cost hypothesis also predicts that signals will be constrained by exogenous factors, such as abiotic environmental conditions (Cotton et al., 2004a; Rowe & Houle, 1996). This prediction can be tested by examining variation in signal quality within a population experiencing different abiotic environmental

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conditions across years (Cockburn et al., 2008; Garant et al., 2004; Mysterud et al., 2005). Variation in signal quality across different environmental contexts may manifest in many ways, including variation in ornament size (Cotton et al., 2004b; Emlen, 1997), variation in the timing or duration of a signal (Brandt, 2003; Ruiz et al., 2010), and at times, whether a signal is produced at all (Emlen, 1994). In each of these contexts, greater access to resources is predicted to be associated with higher-quality signals.

Alternatively, variation in sexual signals may be tied to the social environment (Tarvin et al., 2016), in that individuals modulate their degree of ornament expression in response to conspecific competitors and potential mates (Dey et al., 2014; Kasumovic & Brooks, 2011; Webster et al., 2018). This modulation likely occurs through the influence of social interactions on physiological state (Tibbetts, 2014; Vitousek et al., 2014), and at times, social cues can result in individuals producing no ornament at all (Hawkins et al., 2012; Lyon & Montgomerie, 1986). For example, in the African cichlid fish *Astatotilapia burtoni*, reproductive state and expression of sexually selected ornamentation are socially determined (Fernald & Maruska, 2012) and result from rapid physiological changes in response to changes in a male's social environment (Maruska et al., 2013; Maruska & Fernald, 2013).

Seasonally breeding animals typically gain and lose their sexual signals each year, providing natural experiments to test the relative importance of abiotic environmental and social cues on signal production (van de Pol et al., 2012; Vanpé et al., 2007). In birds, seasonal plumage is a widespread phenomenon that has been associated with species under strong sexual selection and high predation risk (McQueen et al., 2019). Avian species that exhibit seasonal plumage are often sexually dimorphic, with males exhibiting unornamented plumage during the nonbreeding season, then moulting into a distinct and often conspicuous (i.e. ornamented) breeding plumage prior to the beginning of the breeding season (Butcher & Rohwer, 1989). A number of bird species also show variation in whether individuals acquire ornamented breeding plumage, with some males exhibiting a plumage in their first adult breeding season that differs from that of older males, a phenomenon known as delayed plumage maturation (Cucco & Malacarne, 2000; Greene et al., 2000; Rohwer et al., 1980). Delayed plumage maturation may be driven by endogenous differences in quality between young and old males that constrain young males from producing definitive plumage (e.g. moult constraints; Rohwer & Butcher, 1988), or may be an adaptive response to avoid predation or aggression from conspecifics (Hawkins et al., 2012).

Australian fairy-wrens (genus *Malurus*) have emerged as an important system for testing the abiotic environmental and social cues associated with the production of ornamented plumage signals (Peters et al., 2013). In some of these species, the timing of seasonal pre-alternate (prebreeding) moult into ornamented plumage appears to be an important indicator of male quality (Mulder & Magrath, 1994), whereby males who acquire ornamented plumage early obtain higher rates of extrapair copulations than those who acquire ornamented plumage late (Brouwer et al., 2011; Dunn & Cockburn, 1999). In fairy-wrens, moult into ornamented plumage involves replacing all feathers but the wing feathers and is typically followed by an increase in courtship behaviour that continues throughout the breeding season (Green et al., 2000; Rowley & Russell, 1997). Combined, moult and courtship are thought to be physiologically intensive, and work on the superb fairy-wren, *Malurus cyaneus*, has shown that the acquisition of ornamented plumage is delayed in years with low rainfall when

insect food resources are less abundant (Cockburn et al., 2008). In this species, older males moult earliest within a year and at times completely skip the unornamented nonbreeding plumage, moulting straight from ornamented to ornamented plumage at the end of the breeding season (van de Pol et al., 2012).

Although most fairy-wrens exhibit complete or nearly complete ornamented plumage in their first breeding season, a few species differ in that many young males exhibit delayed plumage maturation and remain in brown unornamented plumage for their first adult breeding season (Karubian, 2002; Peters et al., 2013; Rowley & Russell, 1995). In one such species, the red-backed fairy-wren, *Malurus melanocephalus*, many 1-year-old males act as helpers at their parent's nest, but others pair and breed, either in unornamented brown plumage or in ornamented red-black plumage (Karubian, 2008; Karubian et al., 2011). Among breeders, ornamented male red-backed fairy-wrens obtain higher reproductive success than brown males, and both ornamented and brown breeders obtain higher reproductive success than helpers (Webster et al., 2008). In this species, moult into ornamented plumage can be induced by testosterone (Lindsay et al., 2011), and therefore the acquisition of ornamented plumage has been predicted to be physiologically costly (Peters, 2000, 2007). However, evidence to date gives mixed support for the physiological cost hypothesis as driven by trade-offs with testosterone in *Malurus* fairy-wrens (e.g. McQueen et al., 2020; McQueen et al., 2021), including in this species (Barron et al., 2013; Barron et al., 2015; Lindsay et al., 2009).

Here we further test the hypothesis that ornamented red-black plumage is physiologically costly to produce by examining both the likelihood of ornament acquisition by young males and the timing of seasonal ornament acquisition by older males across multiple years with varying abiotic environmental conditions. We contrast these findings with measures of social environment to understand the relative importance of abiotic environmental versus social cues in driving the likelihood and timing of ornament acquisition. Our findings provide further insight into the relative roles physiological and social costs play in generating signal variation among individuals and reveal how these factors differentially affect males of different age classes who exhibit different forms of signal variation.

METHODS

Field Methods

We studied a colour-banded population of red-backed fairy-wrens during multiple nonbreeding and breeding seasons near Lake Samsonvale in Queensland, Australia (27°16'S, 152°41'E). Breeding season data come from a long-term data set on breeding demographics collected between August and January during 2010–2018 (field seasons are named for the year in which the breeding season ends, so these years correspond to the 2011–2019 field seasons). During the breeding season, we recorded data on the composition of breeding groups, individual status (helper versus breeder), nesting attempts and male plumage types. Each male's plumage type was recorded as the highest plumage score attained during breeding, scored visually using binoculars as brown (0–32% red-black plumage), intermediate (33–66%) or red-black (>67%; Webster et al., 2008). Helper males never obtain greater than 32% red-black plumage, whereas most breeders exhibit red-black plumage and a few breeders exhibit intermediate plumage (Webster et al., 2008). For this study, we consider any male above 32% red-black plumage to be ornamented in order to separate

helper ornamentation from breeder ornamentation and determine onset of moult.

We collected nonbreeding data during five nonbreeding seasons during June–August leading up to the 2015–2019 breeding seasons. Three of these seasons (2016, 2018, 2019; hereafter: ‘wetter nonbreeding seasons’) received substantially more rainfall between January and June than the other two (2015, 2017; hereafter ‘drier nonbreeding seasons’; [Supplementary Fig. S1](#)). In each nonbreeding season, we obtained data on the timing of ornamented plumage acquisition for males by estimating with binoculars the percentage of red-black plumage for all individuals to the nearest 5% on each day that a bird was encountered. During the 2016–2019 nonbreeding seasons, we collected social network data from approximately July through mid- to late August ([Welklin, 2020](#)). Briefly, we followed flocks of fairy-wrens for 15–25 min per observation in most seasons (sometimes up to 1 h), recording the presence of individuals in flocks every 5 min using the ‘gambit of the group’ method ([Whitehead & Dufault, 1999](#)). From these observations we built yearly social networks using the simple ratio index and the R package ‘asnipe’ ([Farine, 2013](#)). To identify nonbreeding social groups, we created dendrograms of each yearly network using the UPGMA method, which organizes nodes into a tree format based on association scores ([Sneath & Sokal, 1973](#)). We identified social group membership by cutting the dendrogram at the bifurcation point associated with the highest average silhouette distance score, a clustering quality score ([Rousseeuw, 1987](#)). Nonbreeding social groups were small (mean = 3–4 individuals per group; range 2–8), with most composed of parents and their offspring from the previous breeding season, but some included new pairs that bred together in the subsequent breeding season ([Welklin, 2020](#)). We use ‘social group’ to refer to a nonbreeding season social group (i.e. not a breeding group) unless otherwise specified.

We aged most individuals using nestling banding records and considered a bird to be 1 year old in the nonbreeding and breeding season following the season it hatched. However, because the breeding season is long, males designated as 1 year old may be separated by up to 6 months in age. For individuals that were not banded as nestlings, we determined whether they were in their first year or not using a skull ossification scale previously validated for this species ([Lindsay et al., 2009](#)). Individuals of unknown age, such as those first captured as adults, were excluded from analyses involving age unless specified. To determine nonbreeding physiological condition, we visually assessed fat in the furcula cavity ([Lindsay et al., 2009](#)) and scored pectoral muscle size on a scale from 1 to 3, where 1 = little to no palpable muscle and 3 = bulging muscle on either side of the keel ([Bairlein, 1995](#)). We also calculated the residuals from a linear regression of mass on tarsus length (residual condition; [Lindsay et al., 2009](#)) for captures before 19 July. Each year of nonbreeding study eventually received appreciable rainfall prior to the beginning of the breeding season and this date marks approximately 1 month after the major rainfall events in the 2017 season. Before this date, mass scores would not likely have been affected by the increased insect abundance that presumably followed the rainfall due to the subsequent greening up of vegetation ([Welklin, 2020](#)). Comparing captures before this date allowed us to emphasize differences in condition across wetter and drier nonbreeding seasons. We used linear mixed models to test whether ecological conditions during the nonbreeding season influenced residual condition, fat and muscle scores for each age class independently. We included whether a nonbreeding season

was wet or dry as a fixed effect and individual identity as a random effect. All analyses were conducted in R v.3.5.2 ([R Core Team, 2018](#)).

Factors Influencing Ornament Acquisition

We used our long-term breeding data set to determine the factors that influenced whether or not 1- and 2-year-old males acquired ornamented plumage. For 1-year-old males, we first asked whether a male's pairing status in his first adult breeding season (helper versus breeder) influenced his likelihood of ornamented plumage acquisition. For males that paired, we then tested whether hatch date, the number of male helpers at the male's natal nest, nonbreeding residual condition score (mass/tarsus), female breeding experience (paired with an older female known to have bred previously versus paired with a young female not known to have bred previously), whether a male was a female's first mate in a breeding season and climate (see below) influenced the likelihood that a 1-year-old male acquired ornamented plumage. For 2-year-old males, we tested whether previous breeding status, previous ornamentation status and previous mating status (e.g. paired with the same female as in the first breeding season) influenced a male's likelihood of acquiring ornamented plumage in his second breeding season. We tested the importance of most of these variables using binomial logit link models and determined the significance of fixed effects using likelihood ratio tests that compared models with and without the variable of interest. When comparing proportions for categorical variables, we used Fisher's exact tests. Most variables were tested separately due to little overlap of the data sets associated with each question about ornament acquisition in young males. Details on each model can be found in the [Appendix](#).

To understand the influence of abiotic environmental factors, we used a sliding window approach with a binomial model to determine whether total rainfall, mean minimum temperature, mean maximum temperature or normalized difference vegetation index (NDVI) influenced the likelihood a 1-year-old male acquired ornamented plumage. This approach identifies which climate windows within a range of dates best improve upon a baseline model using Δ AIC scores ([van de Pol et al., 2016](#)). We used an absolute window with a reference date of 31 December and a range of 0–333 days, which corresponded to climate variation from February through to December. By February, nearly all males would have hatched, and by 31 December, any 1-year-old males that were going to moult into ornamented plumage would have done so. We required climate windows to be at least 20 days long to identify periods with extended climate differences across years, and we tested whether the top climate windows for each variable were false positives using permutation tests ([Bailey & van de Pol, 2016](#)). Very few 2-year-old males spent the breeding season in brown plumage, so we did not measure whether climate determined the likelihood a 2-year-old male acquired ornamented plumage. We tested the residual fit of all binomial models using the R package ‘DHARMa’ ([Hartig, 2018](#)).

Social Networks and Ornament Acquisition

We used nonbreeding social networks to assess the fine-scale social factors that may determine whether 1-year-old males acquire ornamented plumage. We were specifically interested in whether the timing of when a male paired with a female influenced his likelihood of acquiring ornamented plumage, however, identifying a specific date when each male paired with a female appeared

prone to arbitrary judgements (see [Appendix](#)). So instead of relying on our own assumptions of what social network measure indicated pairing, we implemented a sliding window approach to identify important differences in the timing of associations to a future mate between males who paired and acquired ornamented plumage and those who paired but remained in brown plumage. We first identified the range of weeks that we had the most complete social network data in the 4 years we collected these data. We converted calendar dates to weeks using the R package 'lubridate' ([Grolemund & Wickham, 2011](#)) and identified this period as the 28th–32nd weeks of year (8 July–11 August). We then calculated the association score for each male–female pair for each week within this period and the mean association score for all possible windows of weeks within this range. The scores from each of these windows were then added to a binomial model along with year as fixed effects to determine whether associations to a future mate during any of these windows was associated with the likelihood of ornamented plumage acquisition. We identified the window that best improved upon the baseline model using Δ AIC scores and tested whether the observed window was a false positive using a permutation test (see [Appendix](#)). Once we confirmed the top window was not a false positive, we expanded our data set to include any individual that was seen during the top window to improve our sample size and reran the model for that window only. We used a permutation test to determine the significance of the association score fixed effect. When testing positive coefficient values, as here, the *P* value for permutations represents the number of times the coefficients from the permutations were greater than the coefficient for the observed association score, divided by the number of permutations. In later permutation tests where the coefficient of interest was negative, the relationship between the observed and randomized coefficients is reversed. Reported coefficient values are the absolute difference between the observed coefficient and the mean of the randomized coefficient values ([Farine, 2017](#)). See the [Appendix](#) for full details on each permutation test.

We conducted further analyses to measure how paired 1-year-old males that eventually acquired ornamented plumage differed from those that stayed in brown plumage with regard to their social connections prior to acquiring ornamentation. We calculated each male's weighted degree (the sum of an individual's association scores) to all males, other 1-year-old males, older males and all females prior to the male acquiring ornamented plumage. We tested whether paired males that did or did not acquire ornamented plumage differed in these connections using linear mixed models with weighted degree as the response variable and future plumage and year as categorical fixed effects. We calculated the coefficient and significance of the plumage variable in each test using permutation tests.

Factors Influencing Timing of Ornamented Plumage Acquisition

Where possible, we tested hypotheses for abiotic environmental and social cues influencing the timing of ornamented plumage acquisition using males of all age classes, but in most years we did not have accurate data on timing of ornamented plumage acquisition for 3-year-old and older males. However, we were able to obtain accurate data on timing of ornamented plumage acquisition for most 2-year-old males in all years. Therefore, to measure the influence of climate variation on timing of ornamented plumage acquisition in males age 2 years and older, we first used broad analyses that compared the proportions of males in ornamented

plumage during the nonbreeding season across years. We then conducted more detailed analyses specifically on 2-year-old males to determine the fine-scale ecological and social predictors of timing of ornamented plumage acquisition.

We first used a broad sliding window analysis with an absolute window to test whether variation in rainfall led to variation in the timing of ornamented plumage acquisition across years ([van de Pol et al., 2016](#)). Each nonbreeding season we completed surveying our population by 1 July, so we assessed whether any rainfall windows occurring 0–200 days before 1 July predicted the proportion of males that acquired ornamented plumage by that date. All males in this data set eventually acquired ornamented plumage in the years they were present. Our baseline model was a generalized linear mixed model with a binomial distribution and a categorical variable of whether a male had acquired ornamented plumage by 1 July or not as our response variable, age as a fixed effect and individual identity as a random effect. For males that did not have an exact age, we used their minimum age. Measuring the influence of age on moult timing was not our main focus for this model, so we think the benefits of a larger sample size outweigh any uncertainty generated by slightly inaccurate age estimates. We required windows to be at least 20 days long to identify extended periods of rainfall variation across years and tested whether the top rainfall window was a false positive using permutation tests. We assessed the significance of the rainfall variable using a likelihood ratio test.

We tested whether climate and a male's previous experience influenced the timing of ornamented plumage acquisition on a finer scale using 2-year-old males. To build this data set, we first calculated a 'moult date' for each 2-year-old male. We found that once 2-year-old males obtained a plumage score of $\geq 33\%$ red-black plumage, the rest of moult was completed very quickly (mean = 10.9 days; [Appendix](#)). We also found that almost all males achieved 100% red-black plumage in the breeding season and very few males spent the breeding season at 90–95% red-black plumage ([Supplementary Fig. S2](#)). Therefore, we defined 'moult date' to be the first date we saw or captured a male at greater than 33% red-black plumage, and we included any male that was seen between 33% and 85% red-black in our data set because they were likely actively moulting. We removed males from our data set that were seen in brown plumage ($<33\%$ red-black) and then next seen in fully ornamented plumage ($\geq 90\%$ red-black) if the gap between these two sightings was longer than 20 days, because we could not accurately estimate moult date. We did include males that were first seen at 90% red-black or above and account for these observations using left-censoring in our survival analysis models. The only 2-year-old males that spent the breeding season at 34–90% red-black plumage appeared to obtain this plumage via adventitious moult, which took place months later than the normal pre-alternate moult. Ornamentation via adventitious moult likely represents a very different moult strategy from the normal pre-alternate moult (see [Lantz & Karubian, 2016](#)), so we did not include these males in our data set.

We tested whether a male's breeding and ornamentation status in his first year influenced the timing of ornamented plumage acquisition in his second year using semiparametric Cox proportional hazards models implemented by the R package 'icenReg' ([Anderson-Bergman, 2017](#)). We considered any male that was first seen at $\geq 90\%$ red-black plumage to be left-censored, meaning we did not observe the male's true moult date. When running these models for all years, we included year as a fixed effect to control for differences across years. We then constructed two additional

models (without year as a fixed effect) to test the influence of the same variables within relatively wetter (2016, 2018, 2019) and drier (2015 and 2017) nonbreeding seasons. We used permutation tests to test the significance of the fixed effects in each of these models and calculated *P* values and coefficients as described previously for permutation tests.

To determine in greater detail how climate influenced the timing of ornamented plumage acquisition, we performed sliding window analyses for 2-year-old males using total rainfall, mean minimum temperature anomaly, mean maximum temperature anomaly and mean NDVI climate variables. We used the 2-year-old moult date data set described above but removed individuals that were first seen in ornamented plumage because we did not know their approximate moult dates. We used Cox proportional hazards models implemented by the R package 'survival' (Therneau & Lumley, 2014), and used relative climate windows as time-dependent covariates to determine how climate influenced the likelihood of moult into ornamented plumage on a given date during the nonbreeding season. For each climate variable, we used a range of 0–300 days prior to the observation date and required windows to be at least 30 days long to identify periods of extended climate differences that influenced timing of ornamented plumage acquisition based on preliminary tests. We tested whether the climate windows were false positives using permutation tests and used likelihood ratio tests to determine the significance of the climate variables.

We used a linear mixed model to determine whether nonbreeding residual condition influenced timing of ornamented plumage acquisition in 2-year-old males. This model used restricted maximum likelihood with the number of days between capture and moult date as a response variable, residual condition as a fixed effect and year as a random effect. We assessed significance of the residual condition variable using a likelihood ratio test. We also tested whether age for males 3 years and older influenced timing of ornamented plumage acquisition by constructing a semiparametric Cox proportional hazards model with age and season as fixed effects. We tested the significance of the age variable using a permutation test.

Social Networks and Timing of Ornamented Plumage Acquisition

We used the same sliding window approach described previously for 1-year-old males to determine whether associations between 2-year-old males and their females influenced timing of ornamented plumage acquisition. We considered any windows from the 27th to the 33rd week of the year (1 July–18 August). Within the sliding window analysis, we used a Cox proportional hazards model and only included individuals for which we had observed moult dates. We also measured how social environment prior to ornamentation influenced timing of ornamented plumage acquisition for 2-year-old males by calculating weighted degree scores for 2-year-old males' connections to other 1- and 2-year-old males, older males, all females and their paired female before the males reached ornamented plumage. We tested each variable in a separate Cox proportional hazards model and used the same data set as the sliding window analyses noted above. We determined the significance of the weighted degree variables using permutation tests.

Ethical Note

All procedures involving animals were approved by the Cornell Institutional Animal Care and Use Committee (IACUC 2009-0105), Tulane University IACUC (2019-1715) and the James Cook University Animal Ethics Committee (A2100) and were performed under a

Queensland Government Department of Environment and Heritage Protection Scientific Purposes Permit (WISP15212314). We banded both adults and nestlings for identification in the field. We extracted adults from mist nets immediately after capture and held adults in cloth bags before quickly conducting standard measurements and taking a small blood sample. Red-backed fairy-wrens are highly social and rarely alone, so after processing, we released social groups together to reduce stress. Handling of nestlings was minimized by collecting a small blood sample and banding nestlings on the same day. These methods have been used previously in this species with no observable negative effect (Webster et al., 2008).

RESULTS

Acquisition of Ornamented Plumage

One quarter of 1-year-old males (24%) in our population acquired ornamented plumage in their first adult breeding season, whereas most 2-year-old males (96%) and all males 3 years and older acquired ornamented plumage (Fig. 1). Acquisition of the ornamented phenotype in 1-year-old males did not appear to be affected by climate, as all climate windows predicting moult into ornamented plumage were false positives (Supplementary Figs S3, S4, Table S1). In wetter nonbreeding seasons, 1-year-old males had higher residual condition (likelihood ratio test: $\chi^2_1 = 12.63$, $N = 169$, $P < 0.001$; Fig. 2a, Supplementary Table S2) and muscle scores (likelihood ratio test: $\chi^2_1 = 9.11$, $N = 169$, $P = 0.003$; Supplementary Table S3, Fig. S5) than in drier nonbreeding seasons, but residual condition did not influence the likelihood of ornamented plumage acquisition (likelihood ratio test: $\chi^2_1 = 0.58$, $N = 74$, $P = 0.45$; Supplementary Table S4). Fat scores did not differ across wetter and drier nonbreeding seasons for 1-year-old males (likelihood ratio test: $\chi^2_1 = 2.91$, $N = 169$, $P = 0.088$; Supplementary Table S5, Fig. S6).

In contrast, we found considerable evidence that social environment, particularly interactions with a future mate, did affect acquisition of the ornamented phenotype in 1-year-old males. First, nearly one-third of paired 1-year-old males ($N = 52$ of out of 162 paired 1-year-old males) acquired ornamented plumage, whereas no unpaired, helper 1-year-old males ($N = 52$) did so (Fisher's exact test: $N = 214$, $P < 0.001$; Fig. 3a). Among paired 1-year-old males,

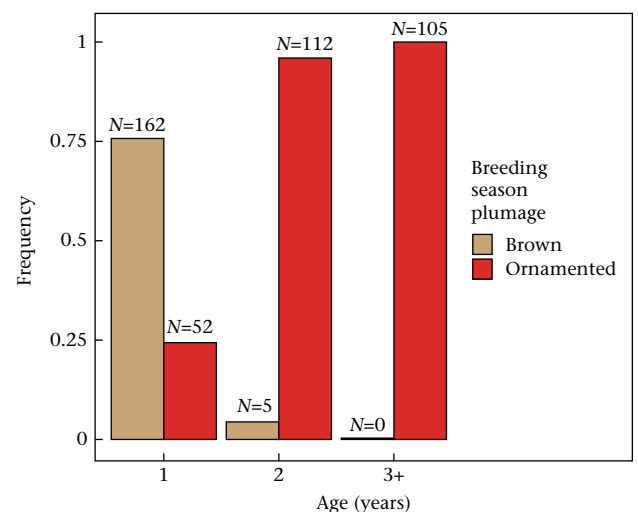


Figure 1. Proportions of males of each age class that acquired brown versus ornamented plumage.

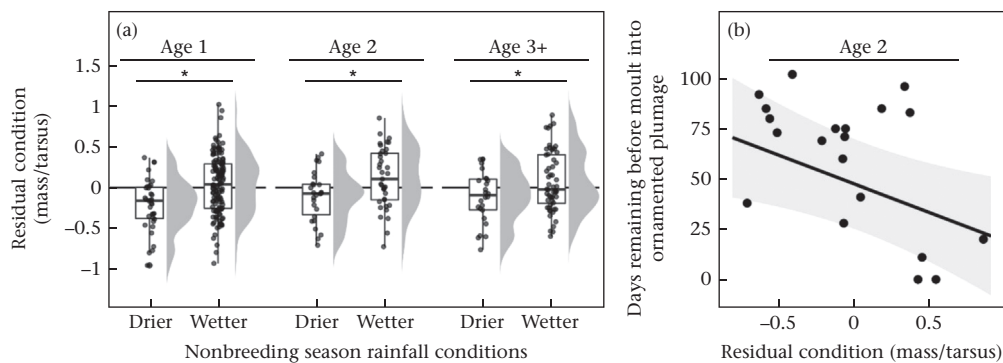


Figure 2. Relationships between residual condition and acquisition of ornamented plumage. (a) Residual condition in drier nonbreeding seasons (2015 and 2017) and in wetter nonbreeding seasons (2016, 2018, and 2019) for all age classes. * $P < 0.05$. (b) Prediction plot of the relationship between the number of days remaining before moult into ornamented plumage at capture day for a 2-year-old male and the residual condition of that individual on the capture day. Points show raw data and shaded areas show 95% confidence intervals for the model predictions.

those that hatched earlier in the previous breeding season were more likely to acquire ornamented plumage (likelihood ratio test: $\chi^2_1 = 7.87$, $N = 97$, $P = 0.005$; Fig. 3b, Supplementary Table S6), but there was no effect of hatch date on residual condition score (likelihood ratio test: $\chi^2_1 < 0.01$, $N = 36$, $P = 0.926$; Supplementary Table S7). Also, the number of male helpers at a male's natal nest was not an important predictor of whether a male acquired ornamented plumage (likelihood ratio test: $\chi^2_1 = 2.00$, $N = 97$, $P = 0.158$; Supplementary Table S6, Fig. S7), and we did not find any effect of hatch date or number of male helpers at a male's natal nest on whether a male was a helper or a breeder in his first breeding season (likelihood ratio tests: hatch date: $\chi^2_1 < 0.01$, $N = 113$, $P = 1$; helpers: $\chi^2_1 < 0.01$, $N = 113$, $P = 0.941$; Supplementary Table S8).

Second, 1-year-old males with experienced mates (i.e. had bred previously) were more likely to acquire ornamented plumage than males that paired with an inexperienced female who had not bred in previous breeding seasons (likelihood ratio test: $\chi^2_1 = 6.43$, $N = 112$, $P = 0.011$; Fig. 3c, Supplementary Table S9). Among males that paired with experienced breeders, there was a nonsignificant tendency for males who were a female's first mate in a breeding season to be more likely to acquire ornamented plumage when compared to males that filled a vacancy when the female's first mate disappeared (likelihood ratio test: $\chi^2_1 = 3.12$, $N = 62$, $P = 0.077$; Supplementary Table S10, Fig. S8).

Third, a fine-scale analysis of social interactions during the nonbreeding season revealed that 1-year-old males that paired with a female by the 30th week of the year (late July, approximately 1–4 weeks before the start of breeding) were more likely to acquire ornamented plumage than were those that paired after that date (permutation test: $\text{coef} = 7.33$, $N = 34$, $P = 0.001$; Fig. 4a, Supplementary Figs S9–S13, Table S11). The males that did acquire ornamented plumage paired with a female before moulting (Fig. 4b). Within this subset of males for which we had social network data, those that acquired ornamented plumage were not in better condition during the nonbreeding season than those that did not acquire ornamented plumage ($F_{1,26} = 2.82$, $N = 31$, $P = 0.105$; Supplementary Table S12), and condition did not influence their likelihood of acquiring ornamented plumage (likelihood ratio test: $\chi^2_1 = 0.05$, $N = 31$, $P = 0.821$; Supplementary Table S13). Not all males that were well connected (i.e. paired) to their mate by week 30 acquired ornamented plumage: of the 12 males that were well connected to their female by week 30, only half acquired ornamented plumage (Supplementary Fig. S13). All but one of these 12 males were in the same social group as the female they bred with, and those that acquired ornamented plumage ($N = 6$) were in a social group without any other male, whereas half of the males that stayed brown ($N = 3$) were in a group with another male (Fisher's exact test: $P = 0.182$). Of the males in a social group with

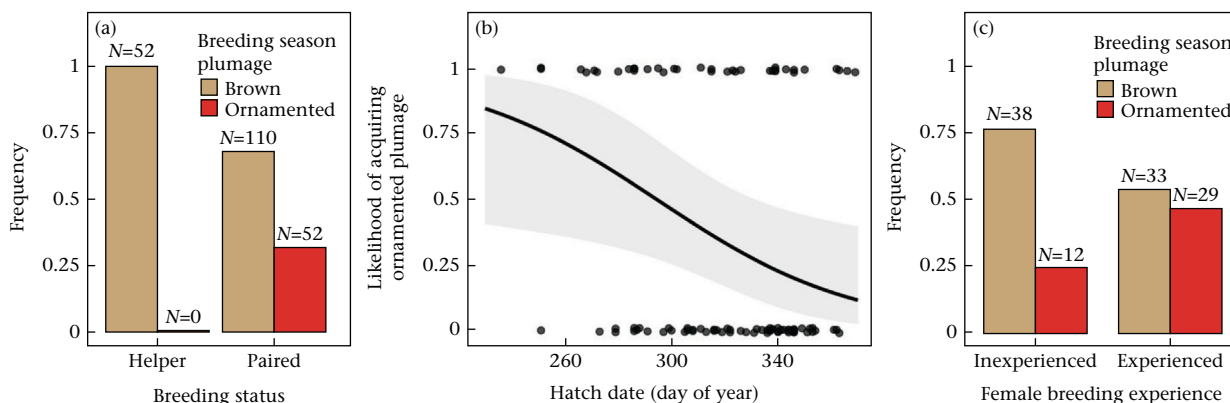


Figure 3. Predictors of whether a 1-year-old male acquired ornamented plumage. (a) Likelihood of acquiring ornamented plumage based on whether 1-year-old males were helpers or paired with a female. (b) Model prediction plot from a binomial generalized linear mixed model showing the influence of hatch date on a 1-year-old male's likelihood of acquiring ornamented plumage. Line shows the model prediction, shaded areas show 95% confidence intervals and points are the raw data jittered slightly on the Y-axis to improve visibility. (c) Likelihood of acquiring ornamented plumage based on whether 1-year-old males were paired with an experienced female who had bred previously rather or an inexperienced female who had not bred previously.

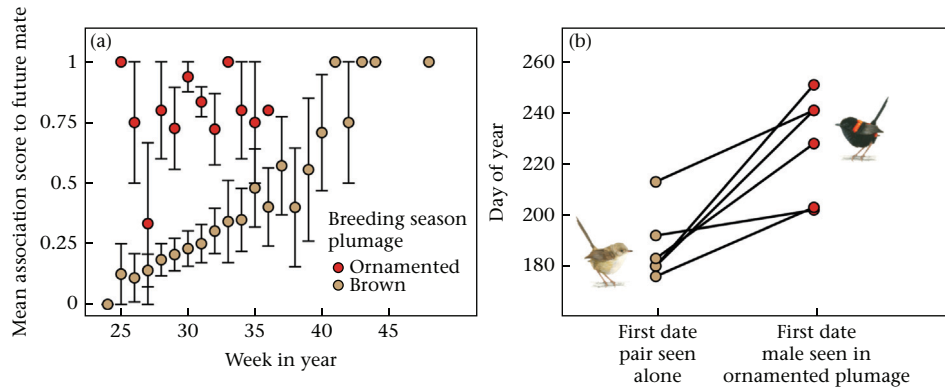


Figure 4. Associations between pairing and plumage ornamentation. (a) Differences in pairing status across time for 1-year-old males that acquired ornamented plumage and those that remained in brown plumage. Points show means for males of each breeding phenotype by week and error bars show standard errors. (b) Day of the year on which the males who acquired ornamented plumage in panel (a) were first seen alone with their mate in relation to the day of the year on which each male was first seen in ornamented plumage. Each point represents a single male and lines connect individuals across events. Fairy-wren illustrations by Allison Johnson.

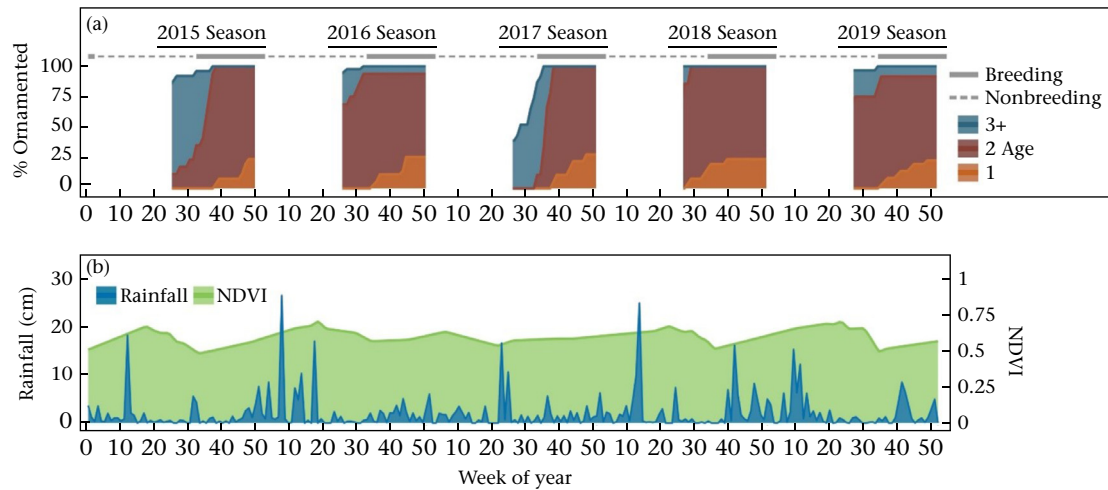


Figure 5. (a) Percentage of males in each age class in ornamented plumage by week of the year in relation to (b) total weekly rainfall and mean weekly normalized difference vegetation index (NDVI). Each plumage plot in (a) begins on 1 July and ends on 1 January, the time frame when we had sampled the entire study area. Solid grey lines show the approximate extent of peak breeding activity (mid-August to mid-January) and dashed grey lines show the primarily nonbreeding periods. Black lines show the extent of when we were present at the field site. Seasons are named for the year when they ended (i.e. most of the 2015 season took place during calendar year 2014).

their female, males that acquired ornamented plumage had lower weighted degree to individuals outside of their pair bond prior to moult into ornamented plumage than males that remained in brown plumage (permutation test: $\text{coef} = -1.38$, $N = 10$, $P = 0.019$; [Supplementary Table S14](#), [Fig. S14](#)). Together, these results indicate

that early pairing affects the likelihood of ornament acquisition by 1-year-old males, and that the presence of other males in the nonbreeding social group and in the surrounding social environment may influence ornament acquisition as well. All males that were ornamented in their first year also were ornamented in their

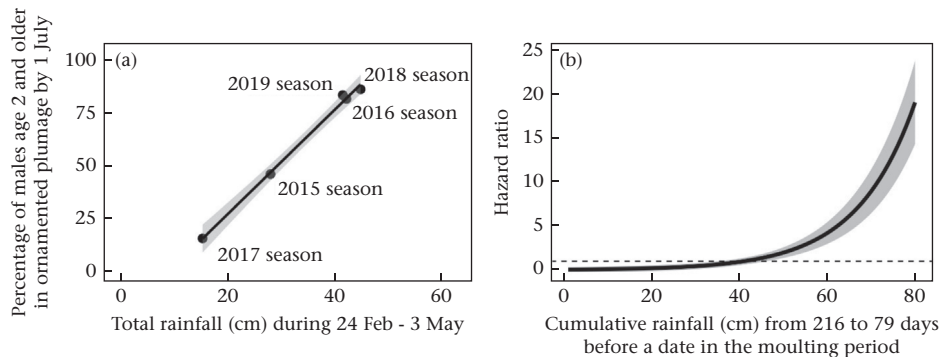


Figure 6. Relationships between acquisition of ornamented plumage and rainfall. (a) The percentage of 2-year-old and older males in ornamented plumage by 1 July in relation to total rainfall between 24 February and 3 May, a period determined by a sliding window analysis. Shaded area represents 95% confidence interval. (b) Hazard ratio plot for rainfall influencing the likelihood of acquiring ornamented plumage as determined by a sliding window analysis. The dashed line represents a hazard ratio of one.

second year, but this association could have been due to chance (Fisher's exact test: $N = 117$, $P = 0.334$).

Timing of Ornamented Plumage Acquisition

Within a given year, timing of ornamented plumage acquisition was highly dependent on age, with males 3 years old and older moulting into ornamented plumage first, followed by 2-year-old males and then some 1-year-old males (Fig. 5). Even within males ≥ 3 years old, age was an important factor determining timing of ornamented plumage acquisition, with older males moulting earlier in the nonbreeding season (permutation test: $\text{coef} = 0.54$, $N = 103$, $P = 0.006$; Supplementary Table S15, Figs S15–S16). Indeed, many of the oldest males in our study population were already in ornamented plumage (and may have moulted directly from ornamented plumage) when we arrived at our field site each year, approximately 9–12 weeks before the start of breeding (Fig. 5).

For males 2 years and older, the date they acquired ornamented plumage was affected by short-term climate variation. Across years, total rainfall between 24 February and 3 May was highly predictive of the number of males in ornamented plumage by 1 July, with wetter nonbreeding seasons leading to a greater percentage of males in ornamented plumage by that date (likelihood ratio test: $\chi^2_1 = 107.25$, $N = 281$, $P < 0.001$; Fig. 6a, Supplementary Figs S17–S18, Table S16). A more detailed analysis revealed that, for 2-year-old males, rainfall totals greater than 40 cm during a window of 216–79 days before a given date led to an increased likelihood of moult into ornamented plumage on that date (likelihood ratio test: $\chi^2_1 = 33.78$, $N = 40$, $P < 0.001$; Fig. 6b, Supplementary Tables S17–S18, Figs S19–S20). We also found that temperature and NDVI windows were important determinants of daily likelihood of moult into ornamented plumage for 2-year-old males, but these windows followed and were strongly correlated with the top rainfall window, meaning they may have been consequences of rainfall (Supplementary Tables S17–S18, Figs S19–S22). Minimum temperature was the only window that preceded the rainfall window, but when the rainfall and minimum temperature windows were added to a single model, removing minimum temperature from the model did not change model fit by more than two AIC units, so we did not include it in the final model (Supplementary Table S18).

Like young males, older males had higher residual condition scores in wetter nonbreeding seasons than in drier nonbreeding seasons (likelihood ratio tests: 2 years old: $\chi^2_1 = 5.72$, $N = 63$, $P = 0.017$; 3 years and older: $\chi^2_1 = 5.78$, $N = 82$, $P = 0.016$; Fig. 2a, Supplementary Table S2), but showed no difference in muscle (likelihood ratio tests: 2 years old: $\chi^2_1 = 1.61$, $N = 63$, $P = 0.204$; 3 years and older: $\chi^2_1 = 1.99$, $N = 82$, $P = 0.158$; Supplementary Table S3, Fig. S5) and fat scores (likelihood ratio tests: 2 years old: $\chi^2_1 = 0.38$, $N = 62$, $P = 0.537$; 3 years and older: $\chi^2_1 = 1.04$, $N = 82$, $P = 0.308$; Supplementary Table S5, Fig. S6). Within 2-year-old males, a male's residual condition score on a capture date was an important predictor of how long after the capture date the male acquired ornamented plumage, with higher condition scores leading to earlier moult dates (likelihood ratio test: $\chi^2_1 = 5.81$, $N = 20$, $P = 0.016$; Fig. 2b, Supplementary Table S19). These results suggest that differences in condition may explain the connection between climate variation and the timing of ornamented plumage acquisition.

In contrast to the effects of climate, we found little evidence that social factors affected timing of ornament acquisition for 2-year-old males. We found no effect of whether a male was paired to the

same female as in his first year on timing of ornamented plumage acquisition (Supplementary Table S20, Fig. S23), and also no effect of when a male paired with a female or any other nonbreeding social connections on timing of ornamented plumage acquisition (see Appendix, Additional Results; Supplementary Figs S26–S27, Table S23). Additionally, neither plumage phenotype nor breeding status of males in their first year were statistically significant predictors of ornamented plumage acquisition when all years were examined (plumage phenotype: permutation $\text{coef} = 0.55$, $N = 57$, $P = 0.068$; breeding status: permutation $\text{coef} = 0.56$, $N = 57$, $P = 0.093$; Supplementary Table S24, Fig. S28). However, when we ran these analyses separately for wetter versus drier nonbreeding seasons, we found that in wetter nonbreeding seasons, 2-year-old males that were ornamented in their first year moulted into ornamented plumage earlier than 2-year-old males that were not ornamented previously (permutation test: $\text{coef} = 1.26$, $N = 31$, $P = 0.014$; Supplementary Figs S29–S30, Table S25). Previous breeding status was not a predictor of timing of ornamented plumage acquisition in wetter nonbreeding seasons (permutation test: $\text{coef} = 0.62$, $N = 31$, $P = 0.151$; Supplementary Figs S29–S30, Table S25), and both previous plumage phenotype and previous breeding status were nonsignificant in drier nonbreeding seasons (plumage phenotype: $N = 26$, permutation $\text{coef} = 0.21$, $P = 0.332$; breeding status: permutation $\text{coef} = 0.32$, $N = 26$, $P = 0.304$; Supplementary Figs S29, S31, Table S26). These results indicate that climate variation, but not social environment, is a key factor in determining when older males acquire ornamented plumage within a year.

DISCUSSION

Sexual signals are thought to convey information about a signal's quality due to physiological (Hill, 2011) or social mechanisms (Rohwer, 1975; Webster et al., 2018), or a combination of these (Tibbetts, 2014; Vitousek et al., 2014) that link the production and maintenance of sexual signals to individual quality (Grafen, 1990; Johnstone, 1997; Zahavi, 1977). Identifying these mechanisms is important for understanding sources of interindividual variation in sexual signals, as well as why this variation is tied to mating success. Identifying endogenous and exogenous factors associated with ornamentation helps reveal these mechanisms (Cockburn et al., 2008; Cothran & Jeyasingh, 2010; Vergara et al., 2012). Here we tested the importance of abiotic environmental and social cues in determining variation in plumage ornamentation among male red-backed fairy-wrens. One-year-old males either do or do not obtain ornamented plumage during their first breeding season, and older males exhibit substantial variation in the timing of when they acquire ornamented plumage within a year. Both components of variation have important consequences for reproductive success (Dunn & Cockburn, 1999; Webster et al., 2008).

Acquisition of Ornamentation by Young Males

Previous work investigating variation in ornamentation in young male red-backed fairy-wrens focused on the hypothesis that the acquisition of ornamented plumage is condition dependent due to the potential costs of elevated androgens associated with ornamented plumage (Peters, 2000, 2007). This work produced mixed results: young male red-backed fairy-wrens in ornamented plumage had higher circulating androgen levels and were in better condition than brown males (Lindsay et al., 2009), but when both phenotypes were injected with GnRH, a precursor molecule to testosterone production, ornamented and brown males were able

to upregulate androgens to an equal degree (Barron et al., 2015). Furthermore, an experimental manipulation of body condition affected acquisition of ornamented plumage, but did not significantly affect androgen levels (Barron et al., 2013). These results suggested that while androgens likely play a role in ornamented plumage acquisition, physiological differences associated with androgens were not enough to explain signal variation among young males.

Here we used a combination of long-term breeding data and nonbreeding season social networks to test whether abiotic environmental or social factors are associated with acquisition of ornamented plumage in red-backed fairy-wrens. Our results show that a majority of 1-year-old males exhibit delayed plumage maturation and express unornamented brown plumage in their first breeding season, whereas nearly all older males breed in ornamented plumage, matching previous findings from a different population of this species (Karubian et al., 2011; Webster et al., 2008). We found that social cues and hatch date, but not climate variation, influenced whether 1-year-old males acquired ornamented plumage. Specifically, 1-year-old males that acquired a social mate prior to the start of the breeding season (before the end of July) and those that hatched early in the previous breeding season, were more likely to acquire ornamented plumage than those that did not pair early or that hatched late.

The importance of both hatch date and pairing suggests that both endogenous and exogenous cues are important in determining whether a 1-year-old male acquires ornamented plumage. Hatch date did not influence a male's ability to pair, but may be tied to physiological cues, as late-hatching males would theoretically have less time to acquire resources and develop prior to the oncoming breeding season. Indeed, access to resources is a common determinant of ornament expression in many taxa (Cotton et al., 2004b; Emlen, 1994). However, we found no effect of hatch date on residual condition and no effect of residual condition on the likelihood a young male acquired ornamented plumage, indicating that hatch date might influence ornament expression through different physiological constraints, such as moult constraints (Rohwer & Butcher, 1988). This finding contrasts with that of a previous experimental study in which 1-year-old males in better condition were more likely to acquire ornamented plumage, although the time frame in that study was very different from ours: Barron et al. (2013) measured condition and plumage ornamentation during breeding season captures, whereas in the present study, we measured whether nonbreeding condition influenced the likelihood of ornament acquisition later in the season. One physiological mechanism that may be influenced by hatch date is the timing of prebasic moult. Young fairy-wrens fledge their nest in a juvenile plumage, then complete a prebasic body moult during the nonbreeding season into unornamented nonbreeding plumage (Schodde, 1982). If late-hatching males complete this prebasic moult late in the nonbreeding season, it may influence when they can complete their pre-alternate moult into breeding plumage, possibly restricting their ability to produce ornamented plumage due to costs associated with overlap between moult and breeding (Echeverry-Galvis & Hau, 2012). However, males that do not moult into ornamented plumage are thought to replace their brown body and tail feathers at the beginning of the breeding season (Schodde, 1982), suggesting that moult–breeding overlap is possible. Clearly, further work is needed to determine the importance of moult constraints and moult–breeding overlap in this system.

In contrast, the mechanism behind timing of pairing seems clearer. Social interactions are widely known to influence physiological processes (Tibbetts, 2014; Vitousek et al., 2014), and because males pair before moulting into ornamented plumage, it is likely

that pairing triggers physiological changes that lead to the initiation of moult into ornamented plumage. Previous research on red-backed fairy-wrens has shown that implantation with testosterone triggers moult into ornamented plumage (Lindsay et al., 2011) and that pairing leads to increased testosterone production in red-backed fairy-wrens (Karubian et al., 2011) and other birds (reviewed in Goymann et al., 2019). Thus, in red-backed fairy-wrens, pairing may trigger increased testosterone production, which then influences gene expression in the liver, facilitating the production of metabolized carotenoids required for ornamented plumage (Khalil et al., 2020). Our findings here indicate the presence of a critical period governing this process, in which pairing may need to occur before the end of July for 1-year-old males to acquire ornamented plumage. Previous research has shown that males experimentally provided with breeding opportunities during the breeding season upregulate testosterone levels and can produce ornamented feathers to replace plucked feathers, but these males did not perform a complete moult into ornamented plumage (Karubian et al., 2011).

Interestingly, not all 1-year-old males who paired before the end of July moulted into ornamented plumage, suggesting that for some males, the benefits of pairing did not offset the costs of moult into ornamented plumage. Our results suggest that these costs of early acquisition of ornamentation by young males are likely social in origin. Competition for reproductive opportunities (Faulkes et al., 1990; Langer et al., 2004; Oi et al., 2021) and aggression from dominants towards subordinates (Tibbetts & Izzo, 2010; Young et al., 2006) are commonly observed in cooperatively breeding social groups, including fairy-wrens (e.g. Double & Cockburn, 2003; Mulder & Langmore, 1993). The costs of such competitive interactions would be reduced or avoided by males that signal that they are not competitive, such as through a lack of ornamentation. Indeed, previous work has shown that adult male fairy-wrens are more aggressive towards ornamented males than towards males in brown plumage (Karubian et al., 2008). Correspondingly, we found that young males that did pair early but did not acquire ornamented plumage had other males in their nonbreeding social group and also had more interactions with individuals other than their mate, compared to young paired males that did acquire ornamented plumage. We also found that young males who paired with experienced females were more likely to acquire ornamented plumage compared to those who paired with inexperienced females. Males that pair with an inexperienced female may have to carve out a new territory in a potentially crowded social environment, whereas males that pair with an experienced female may face less opposition from other social groups by filling a vacancy on an established territory.

Together these results support the importance of social cues as a mechanism underlying variation in delayed plumage maturation (Hawkins et al., 2012) and suggest that 1-year-old male red-backed fairy-wrens modulate their plumage phenotype for the breeding season based on their social role and their social environment by the end of July. Breeding typically begins in August or September (Welklin, 2020), and males that obtained a mate prior to the start of breeding in an area with few neighbouring groups were likely to acquire ornamented plumage. In contrast, males with many neighbouring groups and those that entered August still unpaired remained in brown plumage. This indicates that the benefits of ornamented plumage – namely increased reproductive success (Webster et al., 2008) – may outweigh the costs only when males are likely to obtain a breeding role in an uncrowded environment, or that males are constrained from obtaining ornamented plumage after the start of breeding.

Timing of Ornamented Plumage Acquisition

We measured the timing of ornamented plumage acquisition over five nonbreeding seasons to determine whether moult into ornamented plumage is constrained by environmental conditions, as predicted by the physiological cost hypothesis (Cotton et al., 2004a; Rowe & Houle, 1996). Previous research has shown that early-moulting males obtain higher reproductive success than late-moulting males in two other species of fairy-wren (Brouwer et al., 2011; Dunn & Cockburn, 1999), suggesting that timing of ornamented plumage acquisition may be an indicator of male quality (Mulder & Magrath, 1994). For males 2-years and older, we found that nonbreeding rainfall, specifically between February and May, was an important predictor of variation in the timing of ornamented plumage acquisition across years. Further detailed analyses on 2-year-old males indicated that rainfall 31–11 weeks before a given date during the nonbreeding season was predictive of whether males acquired ornamented plumage on that date, matching similar findings for superb fairy-wrens showing that rainfall in the preceding 25 weeks influenced timing of ornamented plumage acquisition (van de Pol et al., 2012).

We also found that males exhibited lower condition scores in drier nonbreeding seasons than in wetter nonbreeding seasons and that residual condition was an important predictor of when a male acquired ornamented plumage. As insectivores, physiological condition in red-backed fairy-wrens is likely highly dependent on the availability of insects, and earlier analyses using these same climate data found rainfall was an important predictor of NDVI (Welklin, 2020), which is often positively correlated with insect abundance (Recher et al., 1996). Although minimum temperature was not the main determinant of timing of ornamented plumage acquisition, we did find that higher-than-average minimum temperatures were correlated with higher rainfall (Supplementary Table S16). Together, these findings indicate that warmer periods during the early nonbreeding season led to increased rainfall, higher NDVI scores, and likely increased insect abundance, leading to earlier moult into ornamented plumage for 2-year-old and older males.

In contrast to the determinants of whether a young male moulted into ornamented plumage, we found no evidence that social cues drive timing of ornamented plumage acquisition for older males. This result may not be surprising, as older males may be expected to be more socially stable than younger males, and previous research has shown that moult into ornamented plumage by older males may not be dependent on circulating androgens (Lantz et al., 2017). Many older males remained paired to the same female across seasons, and breeding groups tend to stay together throughout the nonbreeding season in an area that encompasses their breeding season territory (Welklin, 2020). However, it should also be noted that the only year we had enough data to measure the influence of social connections on the timing of ornamented plumage acquisition was our 2017 season, which was by far the driest nonbreeding season we observed, resulting in nearly all males moulting very late (Figs 5, 6a). If we had started our nonbreeding field seasons earlier, and in less extreme years, it is possible that we would have found evidence that social environment affects the timing of ornamented plumage acquisition in older males.

Conclusion

Combined, these findings indicate that for red-backed fairy-wrens, the different forms of signal variation among age classes are affected by different processes. For 1-year-old males, signal variation is primarily determined by whether or not males acquire ornamented plumage. We found that hatch date and social cues,

especially whether a male paired with a female prior to the beginning of the breeding season, were important in determining whether a 1-year-old male acquired ornamented plumage. In contrast, for older males, signal variation is determined by the timing of ornamented plumage acquisition. In older males, we found that abiotic environmental cues such as rainfall were associated with the timing of ornamented plumage acquisition across years, likely through effects on physiological condition. These results provide support for the hypothesis that social cues determine the acquisition of sexual signals by younger males, but that physiological condition affects the timing of ornament acquisition in older males. The latter result may be due to the physiological costs of ornament acquisition, such as trade-offs between moult and immunity (Ellis et al., 2012) or to males in poorer condition being less able to tolerate social costs of early ornament acquisition. We have shown that both social and physiological processes can lead to signal variation within the same species through their influence on males of different age classes. We propose this difference among age classes occurs because older males are nearly always territory holders, and thus are established in their social environment, whereas young males can exhibit flexible social roles in their first breeding season depending on whether they pair with a female or not. For young males, a mismatch in ornamentation and social status (i.e. ornamented helper male) may elicit aggression from other males (Rohwer, 1977; Tibbetts & Dale, 2004). However, ornamentation in older, established males who are territory holders may simply be a signal of their status as a dominant breeding male. Ultimately, further experimental work is required to fully resolve the hypotheses presented here, but these results reveal the importance of considering both social and abiotic environmental factors when investigating the causes of sexual signal variation.

Data Accessibility

All data are available from the Dryad database (<https://doi.org/10.5061/dryad.59zw3r27w>).

Author Contributions

Joseph F. Welklin: Project administration; Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Software; Visualization; Writing – original draft. **Samantha M. Lantz:** Project administration; Conceptualization; Investigation; Methodology; Writing – review & editing. **Sarah Khalil:** Project administration; Conceptualization; Investigation; Methodology; Writing – review & editing. **Nicole M. Moody:** Conceptualization; Investigation; Methodology; Writing – review & editing. **Jordan Karubian:** Funding acquisition, Project administration; Conceptualization; Supervision; Writing – review & editing. **Michael S. Webster:** Funding acquisition, Project administration; Conceptualization; Supervision; Writing – review & editing.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2021.10.007>.

References

- Alonso-Alvarez, C., Bertrand, S., Faivre, B., Chastel, O., & Sorci, G. (2007). Testosterone and oxidative stress: The oxidation handicap hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611), 819–825. <https://doi.org/10.1098/rspb.2006.3764>
- Anderson-Bergman, C. (2017). icenReg: Regression models for interval censored data in R. *Journal of Statistical Software*, 81, 12. <https://doi.org/10.18637/jss.v081.i12>
- Bailey, L. D., & van de Pol, M. (2016). Climwin: An R toolbox for climate window analysis. *PLoS One*, 11(12), 1–27. <https://doi.org/10.1371/journal.pone.0167980>
- Bairlein, F. (1995). *Manual of field methods: European–African songbird migration network*. Wilhelmshaven: Institut für Vogelforschung.
- Barron, D. G., Webster, M. S., & Schwabl, H. (2013). Body condition influences sexual signal expression independent of circulating androgens in male red-backed fairy-wrens. *General and Comparative Endocrinology*, 183, 38–43. <https://doi.org/10.1016/j.ygcen.2012.12.005>
- Barron, D. G., Webster, M. S., & Schwabl, H. (2015). Do androgens link morphology and behaviour to produce phenotype-specific behavioural strategies? *Animal Behaviour*, 100, 116–124. <https://doi.org/10.1016/j.anbehav.2014.11.016>
- Basolo, A. L., & Alcaraz, G. (2003). The turn of the sword: Length increases male swimming costs in swordtails. *Proceedings of the Royal Society B: Biological Sciences*, 270(1524), 1631–1636. <https://doi.org/10.1098/rspb.2003.2388>
- Brandt, Y. (2003). Lizard threat display handicaps endurance. *Proceedings of the Royal Society B: Biological Sciences*, 270(1519), 1061–1068. <https://doi.org/10.1098/rspb.2003.2343>
- Brouwer, L., van de Pol, M., Atema, E., & Cockburn, A. (2011). Strategic promiscuity helps avoid inbreeding at multiple levels in a cooperative breeder where both sexes are philopatric. *Molecular Ecology*, 20(22), 4796–4807. <https://doi.org/10.1111/j.1365-294X.2011.05325.x>
- Buchanan, K. L., Evans, M. R., Goldsmith, A. R., Bryant, D. M., & Rowe, L. V. (2001). Testosterone influences basal metabolic rate in male house sparrows: A new cost of dominance signalling? *Proceedings of the Royal Society B: Biological Sciences*, 268(1474), 1337–1344. <https://doi.org/10.1098/rspb.2001.1669>
- Butcher, G. S., & Rohwer, S. (1989). The evolution of conspicuous and distinctive coloration for communication in birds. In D. M. Powell (Ed.), *Current ornithology* (pp. 51–108). Boston: Springer.
- Cockburn, A., Osmond, H. L., & 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(1635), 605–612. <https://doi.org/10.1098/rspb.2007.0916>
- Cotthran, R. D., & Jeyasingh, P. D. (2010). Condition dependence of a sexually selected trait in a crustacean species complex: Importance of the ecological context. *Evolution*, 64(9), 2535–2546. <https://doi.org/10.1111/j.1558-5646.2010.00998.x>
- Cotton, S., Fowler, K., & Pomiankowski, A. (2004a). Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? *Proceedings of the Royal Society B: Biological Sciences*, 271(1541), 771–783. <https://doi.org/10.1098/rspb.2004.2688>
- Cotton, S., Fowler, K., & Pomiankowski, A. (2004b). Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Evolution*, 58(5), 1038–1046. <https://doi.org/10.1111/j.0014-3820.2004.tb00437.x>
- Cucco, M., & Malacarne, G. (2000). Delayed maturation in passerine birds: An examination of plumage effects and some indications of a related effect in song. *Ethology Ecology & Evolution*, 12(3), 291–308. <https://doi.org/10.1080/08927014.2000.9522802>
- Dey, C. J., Dale, J., & Quinn, J. S. (2014). Manipulating the appearance of a badge of status causes changes in true badge expression. *Proceedings of the Royal Society B: Biological Sciences*, 281(1775), 20132680. <https://doi.org/10.1098/rspb.2013.2680>
- Double, M. C., & Cockburn, A. (2003). Subordinate superb fairy-wrens (*Malurus cyaneus*) parasitize the reproductive success of attractive dominant males. *Proceedings of the Royal Society B: Biological Sciences*, 270(1513), 379–384. <https://doi.org/10.1098/rspb.2002.2261>
- Dunn, P. O., & Cockburn, A. (1999). Extrapair mate choice and honest signaling in cooperatively breeding superb fairy-wrens. *Evolution*, 53(3), 938–946. <https://doi.org/10.2307/2640733>
- Echeverry-Galvis, M. A., & Hau, M. (2012). Molt–breeding overlap alters molt dynamics and behavior in zebra finches, *Taeniopygia guttata castanotis*. *Journal of Experimental Biology*, 215(11), 1957–1964. <https://doi.org/10.1242/jeb.065474>
- Ellis, V. A., Merrill, L., Wingfield, J. C., O'Loughlin, A. L., & Rothstein, S. I. (2012). Changes in immunocompetence and other physiological measures during molt in brown-headed cowbirds (*Molothrus ater*). *Auk*, 129(2), 231–238. <https://doi.org/10.1525/auk.2012.11215>
- Emlen, D. J. (1994). Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proceedings of the Royal Society B: Biological Sciences*, 256(1346), 131–136. <https://doi.org/10.1098/rspb.1994.0060>
- Emlen, D. J. (1997). Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proceedings of the Royal Society B: Biological Sciences*, 264(1381), 567–574. <https://doi.org/10.1098/rspb.1997.0081>
- Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asinpe. *Methods in Ecology and Evolution*, 4(12), 1187–1194. <https://doi.org/10.1111/2041-210X.12121>
- Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, 8(10), 1309–1320. <https://doi.org/10.1111/2041-210X.12772>
- Faulkes, C. G., Abbott, D. H., & Jarvis, J. U. M. (1990). Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber*. *Journal of Reproduction and Fertility*, 88(2), 559–568. <https://doi.org/10.1530/jrf.0.0880559>
- Fernald, R. D., & Maruska, K. P. (2012). Social information changes the brain. *Proceedings of the National Academy of Sciences of the United States of America*, 109(Suppl. 2), 17194–17199. <https://doi.org/10.1073/pnas.1202552109>
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, 139(3), 603–622. <https://doi.org/10.1086/285346>
- Garant, D., Sheldon, B. C., & Gustafsson, L. (2004). Climatic and temporal effects on the expression of secondary sexual characters: Genetic and environmental components. *Evolution*, 58(3), 634–644. <https://doi.org/10.1111/j.0014-3820.2004.tb01685.x>
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, 202, 18–27.
- Goymann, W., Moore, I. T., & Oliveira, R. F. (2019). Challenge hypothesis 2.0: A fresh look at an established idea. *BioScience*, 69(6), 432–442. <https://doi.org/10.1093/biosci/biz041>
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, 144(4), 517–546. [https://doi.org/10.1016/S0022-5193\(05\)80088-8](https://doi.org/10.1016/S0022-5193(05)80088-8)
- Green, D. J., Osmond, H. L., Double, M. C., & Cockburn, A. (2000). Display rate by male fairy-wrens (*Malurus cyaneus*) during the fertile period of females has little influence on extra-pair mate choice. *Behavioral Ecology and Sociobiology*, 48(6), 438–446. [https://doi.org/10.1016/S0022-5193\(05\)80088-8](https://doi.org/10.1016/S0022-5193(05)80088-8)
- Greene, E., Lyon, B. E., Muehter, V. R., Ratcliffe, L., Oliver, S. J., & Boag, P. T. (2000). Disruptive sexual selection for plumage coloration in a passerine bird. *Nature*, 407(6807), 1000–1003. <https://doi.org/10.1007/s002650000258>
- Grolemund, G., & Wickham, H. (2011). Dates and times made easy with lubridate. *Journal of Statistical Software*, 40(3), 1–25. <https://doi.org/10.18637/jss.v040.i03>
- Hartig, F. (2018). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models (R package Version 0.2.0) <https://cran.r-project.org/web/packages/DHARMA/index.html>
- Hawkins, G. L., Hill, G. E., & Mercadante, A. (2012). Delayed plumage maturation and delayed reproductive investment in birds. *Biological Reviews*, 87(2), 257–274. <https://doi.org/10.1111/j.1469-185X.2011.00193.x>
- Hill, G. E. (2011). Condition-dependent traits as signals of the functionality of vital cellular processes. *Ecology Letters*, 14(7), 625–634. <https://doi.org/10.1111/j.1461-0248.2011.01622.x>
- Johnstone, R. A. (1997). The evolution of animal signals. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 155–178). Oxford: Blackwell Science.
- Karubian, J. (2002). Costs and benefits of variable breeding plumage in the red-backed fairy-wren. *Evolution*, 56(8), 1673–1682. <https://doi.org/10.1111/j.0014-3820.2002.tb01479.x>
- Karubian, J. (2008). Changes in breeding status are associated with rapid bill darkening in male red-backed fairy-wrens *Malurus melanocephalus*. *Journal of Avian Biology*, 39(1), 81–86. <https://doi.org/10.1111/j.0908-8857.2008.04161.x>
- Karubian, J., Lindsay, W. R., Schwabl, H., & Webster, M. S. (2011). Bill coloration, a flexible signal in a tropical passerine bird, is regulated by social environment and androgens. *Animal Behaviour*, 81(4), 795–800. <https://doi.org/10.1016/j.anbehav.2011.01.012>
- Karubian, J., Sillett, T. S., & Webster, M. S. (2008). The effects of delayed plumage maturation on aggression and survival in male red-backed fairy-wrens. *Behavioral Ecology*, 19(3), 508–516. <https://doi.org/10.1093/beheco/arm159>
- Kasumovic, M. M., & Brooks, R. C. (2011). It's all who you know: The evolution of socially cued anticipatory plasticity as a mating strategy. *Quarterly Review of Biology*, 86(3), 181–197. <https://doi.org/10.1086/661119>

- Khalil, S., Welklin, J. F., McGraw, K. J., Boersma, J., Schwabl, H., Webster, M. S., & Karubian, J. (2020). Testosterone regulates CYP2J19-linked carotenoid signal expression in male red-backed fairywrens (*Malurus melanocephalus*). *Proceedings of the Royal Society B: Biological Sciences*, 287(1935), 20201687. <https://doi.org/10.1098/rspb.2020.1687>
- Langer, P., Hogendoorn, K., & Keller, L. (2004). Tug-of-war over reproduction in a social bee. *Nature*, 428(6985), 844–847. <https://doi.org/10.1038/nature02431>
- Lantz, S. M., Boersma, J., Schwabl, H., & Karubian, J. (2017). Early-moulting red-backed fairywren males acquire ornamented plumage in the absence of elevated androgens. *Emu*, 117(2), 170–180. <https://doi.org/10.1080/01584197.2017.1297206>
- Lantz, S. M., & Karubian, J. (2016). Male red-backed fairywrens appear to enhance a plumage-based signal via adventitious molt. *Auk*, 133(3), 338–346. <https://doi.org/10.1642/AUK-15-185.1>
- Lindsay, W. R., Webster, M. S., & Schwabl, H. (2011). Sexually selected male plumage color is testosterone dependent in a tropical passerine bird, the red-backed fairy-wren (*Malurus melanocephalus*). *PLoS One*, 6(10), Article e26067. <https://doi.org/10.1371/journal.pone.0026067>
- Lindsay, W. R., Webster, M. S., Varian, C. W., & Schwabl, H. (2009). Plumage colour acquisition and behaviour are associated with androgens in a phenotypically plastic tropical bird. *Animal Behaviour*, 77(6), 1525–1532. <https://doi.org/10.1016/j.anbehav.2009.02.027>
- Lyon, B. E., & Montgomerie, R. D. (1986). Delayed plumage maturation in passerine birds: Reliable signaling by subordinate males? *Evolution*, 40(3), 605–615. <https://doi.org/10.2307/2408581>
- Maruska, K. P., & Fernald, R. D. (2013). Social regulation of male reproductive plasticity in an African cichlid fish. *Integrative and Comparative Biology*, 53(6), 938–950. <https://doi.org/10.1093/icb/ict017>
- Maruska, K. P., Zhang, A., Neboori, A., & Fernald, R. D. (2013). Social opportunity causes rapid transcriptional changes in the social behaviour network of the brain in an African cichlid fish. *Journal of Neuroendocrinology*, 25(2), 145–157. <https://doi.org/10.1111/j.1365-2826.2012.02382.x>
- McQueen, A., Delhey, K., Barzan, F. R., Naimo, A. C., & Peters, A. (2020). Male fairy-wrens produce and maintain vibrant breeding colors irrespective of individual quality. *Behavioral Ecology*, 32(1), 178–187. <https://doi.org/10.1093/beheco/araa128>
- McQueen, A., Delhey, K., Szecsenyi, B., Crino, O. L., Roast, M. J., & Peters, A. (2021). Physiological costs and age constraints of a sexual ornament: An experimental study in a wild bird. *Behavioral Ecology*, 32(2), 327–338. <https://doi.org/10.1093/beheco/araa143>
- McQueen, A., Kempenaers, B., Dale, J., Valcu, M., Emery, Z. T., Dey, C. J., Peters, A., & Delhey, K. (2019). Evolutionary drivers of seasonal plumage colours: Colour change by molt correlates with sexual selection, predation risk and seasonality across passerines. *Ecology Letters*, 22(11), 1838–1849. <https://doi.org/10.1111/ele.13375>
- Mulder, R. A., & Langmore, N. E. (1993). Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, 45(4), 830–833. <https://doi.org/10.1006/anbe.1993.1100>
- Mulder, R. A., & Magrath, M. J. L. (1994). Timing of prenuptial molt as a sexually selected indicator of male quality in superb fairy-wrens (*Malurus cyaneus*). *Behavioral Ecology*, 5(4), 393–400. <https://doi.org/10.1093/beheco/5.4.393>
- Mysterud, A., Meisingset, E., Langvatn, R., Yoccoz, N. G., & Stenseth, N. C. (2005). Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos*, 111(2), 245–252. <https://doi.org/10.1111/j.0030-1299.2005.14197.x>
- Oi, C. A., Wenseleers, T., & Oliveira, R. C. (2021). Causes and consequences of reproductive conflicts in wasp societies. In F. Prezoto, F. S. Nascimento, B. C. Barbosa, & A. Somavilla (Eds.), *Neotropical social wasps: Basic and applied aspects* (pp. 147–178). Cham: Springer International.
- Penn, D. J., & Számadó, S. (2019). The handicap principle: How an erroneous hypothesis became a scientific principle. *Biological Reviews*, 95(1), 267–290. <https://doi.org/10.1111/brv.12563>
- Pérez-Rodríguez, L., Mougeot, F., & Alonso-Alvarez, C. (2010). Carotenoid-based coloration predicts resistance to oxidative damage during immune challenge. *Journal of Experimental Biology*, 213(10), 1685–1690. <https://doi.org/10.1242/jeb.039982>
- Peters, A. (2000). Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immunocompetent. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 267(1446), 883–889. <https://doi.org/10.1098/rspb.2000.1085>
- Peters, A. (2007). Testosterone and carotenoids: An integrated view of trade-offs between immunity and sexual signalling. *BioEssays*, 29(5), 427–430. <https://doi.org/10.1002/bies.20563>
- Peters, A., Kingma, S. A., & Delhey, K. (2013). Seasonal male plumage as a multi-component sexual signal: Insights and opportunities. *Emu*, 113(3), 232–247. <https://doi.org/10.1071/MU12083>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Recher, H. F., Majer, J. D., & Ganesh, S. (1996). Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia. *Austral Ecology*, 21(1), 64–80. <https://doi.org/10.1111/j.1442-9993.1996.tb00586.x>
- Rohwer, S. (1975). The social significance of avian winter plumage variability. *Evolution*, 29(4), 593–610. <https://doi.org/10.2307/2407071>
- Rohwer, S. (1977). Status signaling in harris sparrows: Some experiments in deception. *Behaviour*, 61(1–2), 107–129. <https://doi.org/10.1163/156853977X00504>
- Rohwer, S., & Butcher, G. S. (1988). Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. *American Naturalist*, 131(4), 556–572. <https://doi.org/10.1086/284806>
- Rohwer, S., Fretwell, S. D., & Niles, D. M. (1980). Delayed maturation in passerine plumages and the deceptive acquisition of resources. *American Naturalist*, 115(3), 400–437. <https://doi.org/10.1086/283569>
- Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, 20, 53–65. [https://doi.org/10.1016/0377-0427\(87\)90125-7](https://doi.org/10.1016/0377-0427(87)90125-7)
- Rowe, L., & Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society B: Biological Sciences*, 263(1375), 1415–1421. <https://doi.org/10.1098/rspb.1996.0207>
- Rowley, I., & Russell, E. (1995). The breeding biology of the white-winged fairy-wren *Malurus leucopterus leuconotus* in a Western Australian coastal heathland. *Emu*, 95(3), 175–184.
- Rowley, I., & Russell, E. M. (1997). *Fairy-wrens and grasswrens: Maluridae*. New York: Oxford University Press.
- Ruiz, M., French, S. S., Demas, G. E., & Martins, E. P. (2010). Food supplementation and testosterone interact to influence reproductive behavior and immune function in *Sceloporus graciosus*. *Hormones and Behavior*, 57(2), 134–139. <https://doi.org/10.1016/j.yhbeh.2009.09.019>
- Saino, N., & Möller, A. P. (1996). Sexual ornamentation and immunocompetence in the barn swallow. *Behavioral Ecology*, 7(2), 227–232. <https://doi.org/10.1093/beheco/7.2.227>
- Schodde, R. (1982). *The fairy-wrens: A monograph of the Maluridae*. Melbourne: Lansdowne Editions.
- Shizuka, D., & Farine, D. R. (2016). Measuring the robustness of network community structure using assortativity. *Animal Behaviour*, 112, 237–246.
- Sneath, P. H. A., & Sokal, R. R. (1973). *Numerical taxonomy. The principles and practice of numerical classification*. San Francisco: Freeman.
- Tarvin, K. A., Wong, L. J., Lumpkin, D. C., Schroeder, G. M., D'Andrea, D., Meade, S., Rivers, P., & Murphy, T. G. (2016). Dynamic status signal reflects outcome of social interactions, but not energetic stress. *Frontiers in Ecology and Evolution*, 4, 79. <https://doi.org/10.3389/fevo.2016.00079>
- Therneau, T. M., & Lumley, T. (2014). *Survival* (R package Version 2:3) <https://cran.r-project.org/web/packages/survival/index.html>
- Tibbetts, E. A. (2014). The evolution of honest communication: Integrating social and physiological costs of ornamentation. *Integrative and Comparative Biology*, 54(4), 578–590. <https://doi.org/10.1093/icb/ctu083>
- Tibbetts, E. A., & Dale, J. (2004). A socially enforced signal of quality in a paper wasp. *Nature*, 432(7014), 218–222. <https://doi.org/10.1038/nature02949>
- Tibbetts, E. A., & Izzo, A. (2010). Social punishment of dishonest signalers caused by mismatch between signal and behavior. *Current Biology*, 20(18), 1637–1640. <https://doi.org/10.1016/j.cub.2010.07.042>
- van de Pol, M., Bailey, L. D., McLean, N., Rijdsdijk, L., Lawson, C. R., & Brouwer, L. (2016). Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution*, 7(10), 1246–1257. <https://doi.org/10.1111/2041-210X.12590>
- van de Pol, M., Osmond, H. L., & Cockburn, A. (2012). Fluctuations in population composition dampen the impact of phenotypic plasticity on trait dynamics in superb fairy-wrens. *Journal of Animal Ecology*, 81(2), 411–422. <https://doi.org/10.1111/j.1365-2656.2011.01919.x>
- van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models Supplement. *Animal Behaviour*, 77(3), 753–758.
- Vanpé, C., Gaillard, J. M., Kjellander, P., Mysterud, A., Magnien, P., Delorme, D., Van Laere, G., Klein, F., Liberg, O., & Hewison, A. J. M. (2007). Antler size provides an honest signal of male phenotypic quality in roe deer. *American Naturalist*, 169(4), 481–493. <https://doi.org/10.1086/512046>
- Vergara, P., Martínez-Padilla, J., Mougeot, F., Leckie, F., & Redpath, S. M. (2012). Environmental heterogeneity influences the reliability of secondary sexual traits as condition indicators. *Journal of Evolutionary Biology*, 25(1), 20–28. <https://doi.org/10.1111/j.1420-9101.2011.02399.x>
- Vitousek, M., Zonana, D., & Safran, R. (2014). An integrative view of the signaling phenotype: Dynamic links between signals, physiology, behavior and social context. *Current Zoology*, 60(6), 739–754. <https://doi.org/10.1093/czoolo/60.6.739>
- Webster, M. S., Ligon, R. A., & Leighton, G. M. (2018). Social costs are an underappreciated force for honest signalling in animal aggregations. *Animal Behaviour*, 143, 167–176. <https://doi.org/10.1016/j.anbehav.2017.12.006>
- Webster, M. S., Varian, C. W., & Karubian, J. (2008). Plumage color and reproduction in the red-backed fairy-wren: Why be a dull breeder? *Behavioral Ecology*, 19(3), 517–524. <https://doi.org/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)* (Doctoral dissertation). Ithaca, NY: Cornell University.
- Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: Review and recommendations. *Advances in the Study of Behavior*, 28, 33–74. [https://doi.org/10.1016/S0065-3454\(08\)60215-6](https://doi.org/10.1016/S0065-3454(08)60215-6)
- Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C., & Clutton-Brock, T. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences of the United States of America*, 103(32), 12005–12010. <https://doi.org/10.1073/pnas.0510038103>

Zahavi, A. (1977). The cost of honesty. Further remarks on the handicap principle. *Journal of Theoretical Biology*, 67(3), 603–605. [https://doi.org/10.1016/0022-5193\(77\)90061-3](https://doi.org/10.1016/0022-5193(77)90061-3)

Appendix

Additional Methods

Capture methods

Most adults were captured at least once per year using mist nets. In years that included nonbreeding season work, most adults were captured during the nonbreeding season. Individuals who had not been captured previously were banded with an Australian Bird and Bat Banding Scheme (ABBBS) aluminium numbered band and a unique combination of three plastic colour bands, or two plastic colour bands and one coloured metal band. Nestlings were banded with an ABBBS aluminium numbered band 6 days after hatching. We took standard morphological measurements (Karubian, 2002) and a small blood sample (20–70 μ l) from the wing vein from adults during captures and a smaller blood sample from nestlings from the tarsal vein.

Climate and vegetation data

We obtained rainfall and temperature data from the Australian Government Bureau of Meteorology (Climate Data Online: <http://www.bom.gov.au/climate/data/>). Rainfall recording was inconsistent for the weather station closest to our field site, so we averaged rainfall totals from the three sites closest to our site (Welklin, 2020). Temperature data were collected at the Brisbane Airport, approximately 30 km southeast of our field site, and we obtained daily temperature anomalies by calculating residual daily temperature values from a loess trendline we plotted using the R function 'loess' in the 'stats' package with the span variable set to 0.5 for all temperature data during years 2002–2019. We obtained normalized difference vegetation index (NDVI) data for the area covered by red-backed fairy-wren nonbreeding territories at our study site from Landsat 7 tier 1 surface reflectance satellite images courtesy of the U.S. Geological Survey through Google Earth Engine (GEE) (Gorelick et al., 2017). We calculated NDVI by taking the normalized difference of bands 4 (NIR) and 3 (red) for each image that included no clouds or cloud shadows over the area encompassed by the combined home ranges and used linear interpolation to generate daily values to use in sliding window analyses.

Age and ornamentation

For Fig. 1, we only included males that were recorded in breeding groups during a breeding season. Males that were only seen during the nonbreeding season may not have had time to moult into ornamented plumage.

Whether 1-year-old males paired with a female

We used our long-term breeding data set to determine the broad factors that influenced whether 1-year-old males paired with a female. We asked whether hatch date and the number of male helpers at a male's natal nest influenced whether a 1-year-old male paired or not. We used generalized linear mixed models with binomial distributions and logit link functions to test the importance of these variables. We tested the significance of fixed effects using likelihood ratio tests.

In this analysis and all following analyses for 1-year-old males, we did not include males that received testosterone implants as a

part of a separate experiment. We also did not include 1-year-old males from communities where older males had been removed during our 2017 nonbreeding season for a separate experiment. This change in social environment could have influenced the likelihood a 1-year-old male paired with a female or moulted into ornamented plumage.

Whether males moulted into ornamented plumage

We considered males to be breeders if they ever paired with a female during the breeding season. We considered females to be experienced breeders if we had records of them breeding in previous seasons or if they were first captured as older than 1 year. We considered females inexperienced if they were 1 year old, or if we had records of them acting as helpers and not breeders in the previous breeding season. For analyses using residual condition, if a bird was captured multiple times within a nonbreeding season, we calculated the individual's average residual condition scores for that season to obtain a single value. We tested whether hatch date influenced a 1-year-old male's residual condition score within a year using a linear model where condition score had been centred on year (van de Pol & Wright, 2009).

When testing the importance of hatch date and male helpers at the male's natal nest, we used nest identity (ID) as a random effect. Where possible, we used year as a random effect (when it was not singular), and in some models we used individual ID as an observation-level random effect to improve residual fit (details for each model are available in the Supplementary material). We ran most of these models separately in order to maximize the amount of data available for each question in our data set.

For sliding window analyses measuring the influence of climate on the likelihood of moult, we tested each climate variable separately and used female breeding experience (whether the female had bred previously or not) as a fixed effect. We found that measurements of temperature anomaly and temperature variables produced nearly the same results, so we only report temperature variables here. For each climate variable, we tested whether the observed top window was a false positive by comparing the Δ AIC values of the observed top window to the top windows from 100 permutations. If the observed Δ AIC value was greater than 95% of the randomized values, we considered the top window to not be a false positive (Bailey & van de Pol, 2016). In each permutation, we randomly reassigned the year to which each data point belonged in order to randomize the distribution of ornamented males across years.

Social networks

We built yearly social networks for our 2016–2019 nonbreeding seasons using the 'asnipe' package in R (Farine, 2013). We used permutation tests to confirm that the observed social group structure was more structured than expected by chance. We also measured the robustness of our social groups and social communities to sampling error following Shizuka and Farine (2016) and found that social groups were very robust to sampling error. Further details on social network construction can be found in Welklin (2020).

Identifying when 1-year-old males pair with a female

We were interested in how both interactions with females and other males influenced whether 1-year-old males acquired ornamented plumage. For interactions with females, the most important of these interactions is likely a 1-year-old male's interactions

with his potential social mate in the coming breeding season. Thus, calculating the date the male paired with his female was an important goal, but we found that doing so was fraught with potential error for multiple reasons. First, 1-year-old males and their future paired females typically begin the nonbreeding season in separate nonbreeding social groups. These social groups sometimes interact before the male and female leave their social group and begin forming their own territory. Second, even once a male and female begin forming their own territory and primarily associate with one another, they still often interact with their previous social group, sometimes without their mate. These dynamics can be seen in [Supplementary Fig. S9](#). These dynamics made it difficult to assign a specific pairing date to each male, as it appears that pairing is probably a process that occurs gradually over time. Thus, to test the importance of male's connections to his paired female, we implemented the sliding window approach described in the main text and below, which searches through our raw social network data to find the period with the biggest difference in male–female association scores between ornamented and brown males rather than arbitrarily defining a date for pairing, such as the first date a pair was seen alone. We used this latter method in [Fig. 4b](#) to show the approximate difference in timing of pairing versus moulting into ornamented plumage, but we did not use these dates in our analyses of likelihood of moulting into ornamented plumage.

Whether males moulted and social networks

For the sliding window analysis measuring whether the timing of pairing between a 1-year-old male and a female influenced the likelihood of the male moulting into ornamented plumage, not all pairs were seen in every week from week 28 to week 32. For pairs that were not seen during a week or were seen in fewer than three 5 min points during a week, but had values on either side of the missing weeks, we used linear interpolation to calculate the weighted degree between the male and his female for the missing week. No pairs for which we interpolated data were missing for more than 1 week during this period.

Following [van de Pol et al. \(2016\)](#), we tested whether the observed window was a false positive since we were conducting so many tests. To do this, we conducted permutation tests by randomly reassigning the ornamented/unornamented response variable and its respective year variable among individuals. This process maintained the association between the year variable and the response variable but mixed up their association to each individual's distribution of weekly weighted degree measurements. We did not mix up weekly weighted degree measurements among individuals. We ran this permutation 100 times and compared the Δ AIC of the observed top window to the Δ AIC values of the top windows in each of the 100 permutations ([Supplementary Figs S10–S11](#)). We only used 100 permutations due to the long time frame of running sliding window permutation tests.

We used the same permutation method to calculate the significance of the weighted degree fixed effect during the observed top window, but this time included all individuals we had weighted degree data for during the top window as in the test of the observed data. We ran this permutation 1000 times and compared the observed coefficient for the association variable to 1000 random coefficients ([Supplementary Fig. S12](#)).

We tested whether weighted degree connections differed between paired 1-year-old males that moulted into ornamented plumage and paired 1-year-old males that remained in brown

plumage. We considered males to be paired in this analysis if they were in the same nonbreeding social group as the first female they bred with in the upcoming breeding season. We determined the significance of the plumage variable using permutation tests, where we randomly reassigned the plumage variable among males and compared the observed coefficient to the distribution of 10 000 random coefficients.

Timing of moult into ornamented plumage

For the sliding window analysis testing the influence of rainfall on the proportion of males in ornamented plumage by 1 July, we required individuals to either be seen in ornamented plumage by 1 July or be seen in brown plumage after 1 July to be included in the analysis. For individuals only seen in ornamented plumage after 1 July, we could not be sure when they moulted. We tested whether the top rainfall window was a false positive using permutation tests by randomizing the year to which each data point belonged in order to randomize the distribution of ornamented males across years. We ran 100 permutations and compared the Δ AIC values of the observed top window to the top window from each permutation as described previously.

To understand whether an observation of a male moulting into ornamented plumage (a red-black plumage score between 33% and 85%) was a quality indicator of the approximate date that male achieved ornamented plumage, we measured how quickly males moulted into ornamented plumage once the moulting process began. Specifically, we measured the amount of time males took to transition from intermediate plumage (33–66% red-black plumage) to just short of complete red-black plumage (67–90% red-black plumage). By using 90% rather than 100% as an upper limit for this analysis, we could be sure that nearly all individuals at 90% red-black plumage were still in the process of moulting, whereas if we had used 100% red-black plumage as an upper limit, for individuals that were seen in intermediate plumage, then at 100% red-black plumage, we would not be sure of the date they actually achieved red-black plumage status.

We found that nearly all 2-year-old males took less than 20 days to go from intermediate to red-black plumage, with a mean of 10.9 days ([Figs A1, A2](#)). This gave us confidence, that while approximate, an observation of a male during moult was likely very close to the first date that the male achieved ornamented plumage ($\geq 33\%$ red-black).

For the semiparametric Cox proportional hazards models implemented by the R package 'icenReg' ([Anderson-Bergman, 2017](#)), we used Julian date as our timing variable and left-censored individuals (individuals first seen at 90% red-black plumage or above) were coded as start time = 0, event time = first date observed. For all other individuals, both start and event time were the male's moult date. We used similar models as those described in the main text to measure the influence of previous ornamentation and previous pairing status on the timing of moult to determine whether re-pairing with the same female as in the first breeding season influenced a 2-year-old male's timing of moult. These models were the same as described previously, only we replaced the paired previously fixed effect with a categorical effect of whether the male was paired to the same female or not. To test the significance of each fixed effect, we conducted 1000 permutation tests that randomly reassigned the fixed effect of interest but kept relationships between the response variable and other fixed effects intact.

For the fine-scale climate sliding window analysis using Cox proportional hazard models, we tested that the top climate windows were not false positives by comparing the top Δ AIC value to the Δ AIC of 100 randomizations. For these randomizations, we randomly reassigned moult dates across individuals but kept the other fixed effects associated with their respective moult dates.

Timing of moult and social networks

We again used linear interpolation to calculate missing weighted degree values for 2-year-old males that were not seen for 1 week during the window of weeks 27–33. Males were missing data for no more than 1 week during this window. We only used data from the 2017 season in this analysis and other social network analyses involving 2-year-old males because in all other seasons most 2-year-old males were already ornamented by the time we began collecting social network data. During the 2017 season, we also conducted a removal experiment where we removed old males from two large social communities and kept two other social communities intact to measure the social costs of moult into ornamented plumage (Welklin, 2020). We included mean weighted degree to a male's female, whether the male had been paired previously, treatment group (removal or control) and whether the male was ornamented previously as fixed effects in the Cox proportional hazards models.

For analyses measuring how social environment prior to moult influenced timing of moult in 2-year-old males, we tested each weighted degree variable in a separate Cox proportional hazard model matching the model described above. We determined the significance of each of the weighted degree variables using permutation tests, where we randomly reassigned the weighted degree variable across individuals and compared the observed coefficient for the weighted degree variable to the distribution of random coefficients.

Additional Results

Whether males moulted into ornamented plumage

For 1-year-old males that were in a nonbreeding social group with the female they bred with, those that moulted into

ornamented plumage had lower weighted degree to males (permutation test: $\text{coef} = -1.12$, $N = 10$, $P = 0.013$), lower weighted degree to old males (permutation test: $\text{coef} = -0.29$, $N = 10$, $P = 0.042$), lower weighted degree to 1-year-old males (permutation test: $\text{coef} = -0.83$, $N = 10$, $P = 0.048$) and lower weighted degree to females in different groups (permutation test: $\text{coef} = -0.26$, $N = 10$, $P = 0.057$) prior to moult into ornamented plumage than males that remained in brown plumage (Supplementary Table S14, Fig. S14). Males that were breeders in their first year were not more likely to moult into ornamented plumage in their second year (likelihood ratio test: $\chi^2_1 = 2.72$, $N = 104$, $P = 0.099$; Supplementary Table S27), and staying paired to the same female in their second year was also not important in determining ornament acquisition as a 2-year-old (likelihood ratio test: $\chi^2_1 = 0.01$, $N = 77$, $P = 0.926$; Supplementary Table S28).

Timing of moult into ornamented plumage

We found multiple temperature and NDVI windows that were also important determinants of likelihood of moult into ornamented plumage for 2-year-old males, but all of these windows were strongly correlated with the 216–79 day rainfall window. These correlations showed that warmer periods led to higher rainfall, cooler periods followed rainfall, and rainfall led to higher NDVI scores (Supplementary Figs S21–S22).

Within 2-year-old males that were paired in their first year, staying paired to the same female did not influence timing of moult into ornamented plumage in their second year when all years were measured at the same time (permutation test: $\text{coef} = 0.41$, $N = 45$, $P = 0.167$; Supplementary Table S20, Fig. S23), in wet years (permutation test: $\text{coef} = 0.50$, $N = 25$, $P = 0.157$; Supplementary Table S21, Fig. S24), or in dry years (permutation test: $\text{coef} = 0.58$, $N = 20$, $P = 0.164$; Supplementary Table S22, Fig. S25). The sliding window analysis measuring whether the timing of a 2-year-old male's association to his female influenced the timing of moult into ornamented plumage did not improve upon the baseline model by more than two AIC units (Supplementary Fig. S26), and we found no effect of nonbreeding social connections before moult on timing of moult into ornamented plumage for 2-year-old males (Supplementary Table S23, Fig. S27).

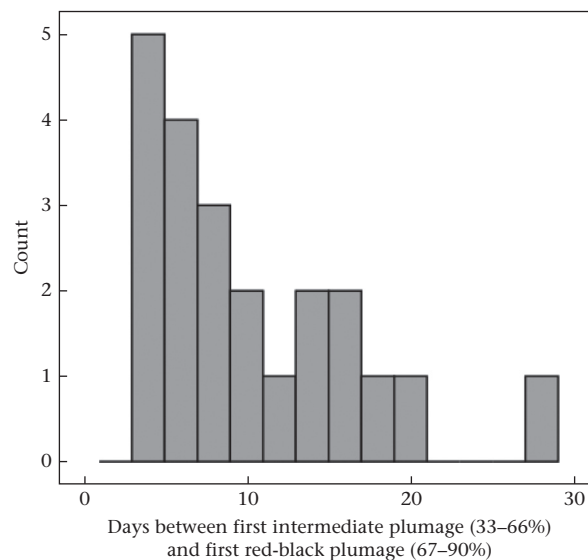


Figure A1. Interval (in days) between the first sighting of each 2-year-old male in intermediate plumage (33–66% red-black plumage) and the first sighting of each 2-year-old male in red-black plumage (67–90% red-black).

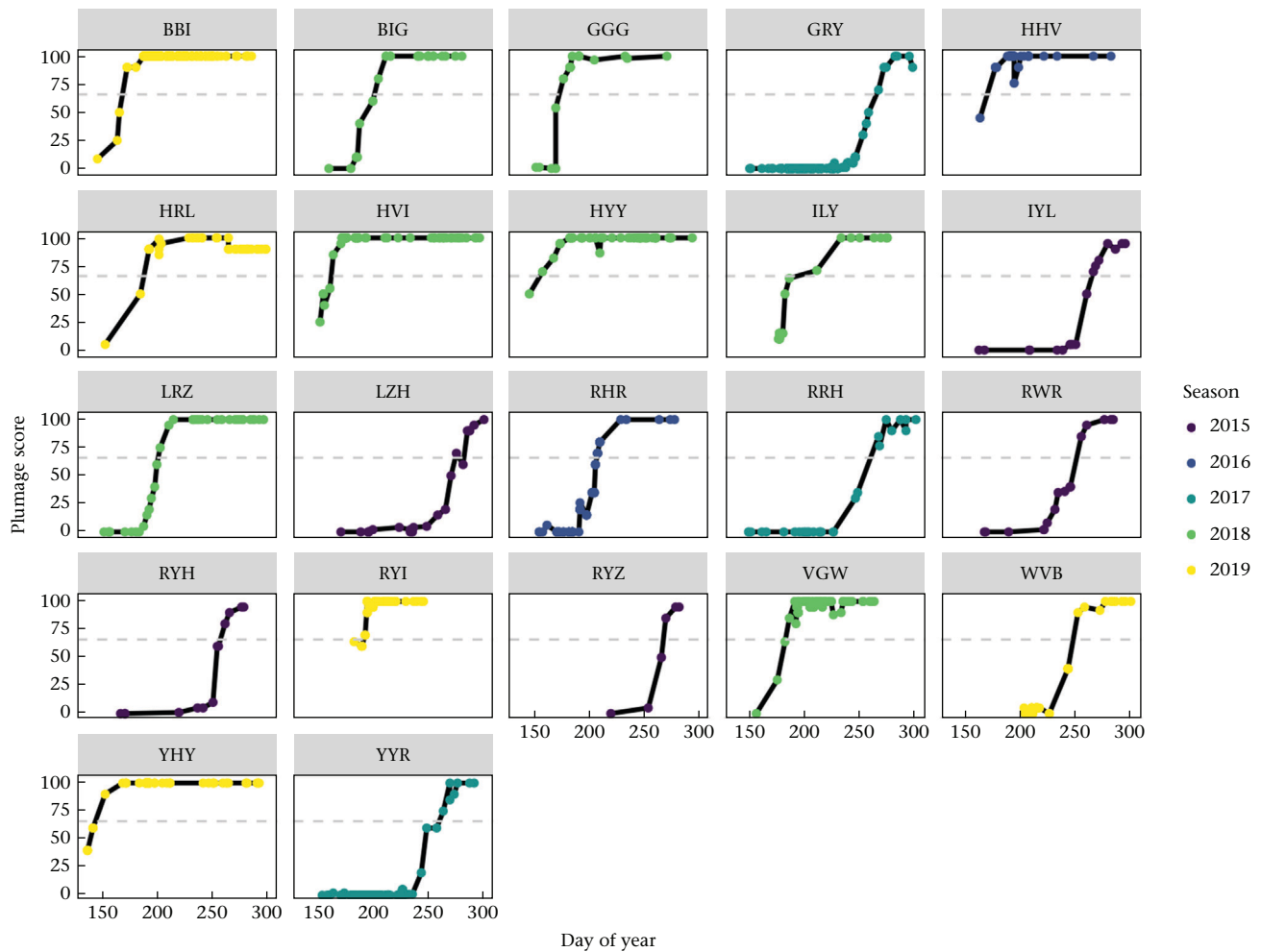


Figure A2. Moult trajectories for 2-year-old males used in the speed of moult analysis. Points are coloured by the season the individual was active. Three-letter combinations at the top of each plot are the individual's colour band combination and the grey dotted lines in each plot show the 66% plumage score. Moult trajectories are not smooth when observers sometimes assigned slightly different moult scores.