



Original Article

No fitness benefits of early molt in a fairy-wren: relaxed sexual selection under genetic monogamy?

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The evolution of male ornamentation has long been the focus of sexual selection studies. However, evidence is accumulating that sexually selected traits can also be lost, although the process is ill-understood. In male fairy-wrens (*Malurus* spp.), early molt into the seasonal breeding plumage is critical for obtaining extra-pair paternity (EPP), which reaches very high levels in these socially monogamous songbirds. A notable exception is the purple-crowned fairy-wren, *Malurus coronatus*, which, like its congeners, breeds cooperatively, but where EPP is very rare. Nevertheless, males develop a conspicuous seasonal breeding plumage at highly variable times. Based on 6 years of molt data collected for 137 individuals, we investigated the adaptive significance of pre-breeding molt timing as a sexual signal under (near) genetic monogamy. Molt timing varied between and within individuals with age and climate: molt was completed earlier in older males and after wetter years. Despite its potential to act as a sexual signal of male quality, fitness benefits and costs of early molt appear limited: molt timing did not correlate with 1) the likelihood of gaining a breeding position; 2) female mate preference (EPP/cuckoldry, divorce); 3) female reproductive investment (breeding timing, clutch size, number of clutches); 4) breeding performance (hatching success, fledging success, fledgling survival, annual reproductive success); and 5) male survival. However, although molt timing did not predict which subordinates would become breeders, breeders molted earlier than subordinates. The lack of EPP in this species might imply relaxed sexual selection on early molt with potential to lead to trait disappearance.

Key words: evolutionary trait loss, extra-pair paternity, monogamy, pre-breeding molt timing, relaxed sexual selection, seasonal breeding plumage.

INTRODUCTION

A long-standing goal in evolutionary biology is to understand why novel traits arise and how these traits contribute to an individual's fitness. In particular, the evolution of elaborate, conspicuous ornamentation of males has been the focus of many studies in various taxonomic groups (Darwin 1871; Andersson 1994; Andersson and Simmons 2006). Such ornamental traits may signal different types of information related to the bearer's overall body condition and genetic constitution (Zahavi 1975; Hamilton and Zuk 1982; Cotton et al. 2004; Andersson 2006). Males with more elaborate

ornamentation are often of higher quality, being preferred as mates by females or more successful when competing for access to females or resources such as territories (Darwin 1871). As a result, such males are generally thought to achieve higher mating success, a benefit that presumably offsets the apparent survival cost of ornamental expression (Lozano 1994; Hill 2002).

In contrast, far less is known about the evolutionary loss of traits, in particular sexually selected traits, although recent phylogenetic studies have shown it to be taxonomically widespread (Wiens 2001; e.g. insects—Emlen et al. 2005; fish—Basolo 1996; amphibians—Emerson 1996; lizards—Wiens 1999; Quinn and Hews 2000; Ord and Stuart-Fox 2006; birds—Ödeen and Björklund 2003; de Kort and ten Cate 2004). Understanding why and how sexually selected traits are lost is important as it can provide valuable insights into the

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nature and role of various sources of selection and how such sources might interact and affect individual fitness (Wiens 2001; Lahti et al. 2009). However, determining causes and mechanisms of trait loss is challenging, which might explain why this area of research remains relatively unexplored (Wiens 2001; Porter and Crandall 2003; Lahti et al. 2009). Evolutionary loss of traits is assumed to be the result of a weakening or removal of one or several sources of selection maintaining the trait ("relaxed selection"; Lahti et al. 2009). For example, sexually selected male traits may wane when the strength of female choice is overcome by random or environmental effects, such as genetic drift or ecological shifts, resulting in female preferences being reduced, lost or reversed (Basolo 1996; Wiens 1999, 2001; Ödeen and Björklund 2003; Ord and Stuart-Fox 2006; Wong and Rosenthal 2006). Trait loss can occur in various gradations, ranging from complete loss to vestigialization, when the trait is still present in a degraded form. Alternatively, traits can persist due to other remaining sources of selection or positive correlations with other functional traits, although such processes are not always easy to identify (Lahti et al. 2009; Ellers et al. 2012).

Avian species have frequently been used as model systems to investigate the evolution of sexually selected traits as males of many species display colorful sexual ornaments (Owens and Hartley 1998; Dunn et al. 2001; McGraw et al. 2002). In particular, extra-pair paternity (EPP) has been suggested to be an important driver of sexual selection for the evolution of male plumage ornamentation in birds, especially in socially monogamous species that have low apparent variance in male mating success (Møller and Birkhead 1994; Owens and Hartley 1998; Dunn et al. 2001). The ability of pair-bonded males to fertilize females other than their social mate increases this variance (Dunn et al. 2001) and females might receive indirect genetic benefits from these extra-pair fertilizations (although evidence for such benefits remains limited; Griffith et al. 2002; Akçay and Roughgarden 2007; Forstmeier et al. 2014). In some species, females may assess potential extra-pair partners on the basis of their elaborate plumage features, which can therefore be subject to strong directional female preference (Møller and Birkhead 1994; Owens and Hartley 1998; Dunn et al. 2001). If such a selective force is weakened or removed, we expect the balance of selection pressures maintaining conspicuous ornamentation to change, affecting its evolution and maintenance. Several studies based on phylogenetic reconstruction have provided evidence that the loss of ornamental plumage coloration is common across taxa and may occur in either or both sexes within a species, and in one or multiple species within a genus, typically because of a weakening of sexual selection due to ecological constraints (Irwin 1994; Omland 1997; Burns 1998; Omland and Lanyon 2000; Schroeder et al. 2009). As a consequence, we might hypothesize that when female extra-pair mate choice is no longer operating in a monogamous system, evolutionary loss of male ornamentation is likely to occur unless other selective forces are still acting to maintain such ornamentation.

A classic example of male sexual ornaments associated with EPP is found among fairy-wrens (*Malurus* spp.), an Australo-Papuan genus in which males display a conspicuous seasonal ornamental plumage (Rowley and Russell 1997). The fairy-wren mating system is dominated by EPP that has been reported to reach exceptionally high levels in several species (>50% of broods, up to 95% in *M. cyaneus*; Kingma et al. 2009; Peters et al. 2013). Typically, the timing of breeding plumage acquisition is highly variable between males, with some males developing the breeding plumage many months prior to the start of breeding (reviewed in Peters et al.

2013). In several species, including the superb (*M. cyaneus*) and the red-winged (*M. elegans*) fairy-wrens, the timing of breeding plumage acquisition determines the likelihood that a male obtains EPP, and there appears to be strong directional sexual selection for early molt into conspicuous ornamental plumage (at least in some years; Cockburn et al. 2008; Brouwer et al. 2011; van de Pol et al. 2012; Peters et al. 2013). In contrast, very little is known about how molt timing might relate to EPP and more generally to mating success in other groups of sexually dimorphic bird species (e.g. whydahs, *Vidua* spp.—Barnard 1995; mallard, *Anas platyrhynchos*—Omland 1996).

A notable exception to the well-known high EPP levels characterizing Australian fairy-wrens is the purple-crowned fairy-wren *M. coronatus*, in which only 5% of broods have EPP (Kingma et al. 2009; Hidalgo Aranzamendi et al. 2016), despite a broadly similar ecology and social system (Kingma et al. 2009). Similar to other fairy-wrens, the purple-crowned fairy-wren is a cooperative breeder with long-term social partnerships and seasonal plumages, as once a year both (dominant) breeder and subordinate males molt from a dull brown non-breeding plumage into a bright purple-and-black breeding plumage (Rowley and Russell 1997). Interestingly, like other fairy-wrens, the timing of pre-breeding molt shows large variation between and within males (Peters et al. 2013). Because there is virtually no opportunity for female extra-pair mate choice in this species, male pre-breeding molt timing may therefore represent a case of a vestigial sexually selected trait and constitutes a very good candidate for the study of relaxed selection and evolutionary trait loss. Alternatively, molt timing may have been co-opted to signal male quality in another context either to the social female or to potential rivals and this could be the reason for its presence despite low levels of EPP.

Here, we assess this possibility by examining: 1) the nature of the intrinsic and environmental factors underlying variability in pre-breeding molt timing (to test for condition-dependence) and 2) the consequences of this variability on different aspects of male fitness. As sexually selected traits may evolve through inter- and/or intrasexual selection, we systematically test the adaptive hypotheses reflecting how both types of selection can operate in monogamous mating systems and show that none of them is supported in our study species, despite substantial variation in molt timing. Based on a phylogenetic analysis of the genus *Malurus*, we discuss the possibility of a trait loss scenario in *M. coronatus*, which could explain the occurrence of such a variable trait in a genetically monogamous fairy-wren.

METHODS

Study species

We studied a color-banded population of *Malurus coronatus coronatus* resident along Annie Creek and the Adcock River at Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in north-west Australia (17°31'S, 126°6'E) from July 2005 to November 2015. The species is restricted to patchy riparian vegetation of *Pandanus aquaticus* and groups maintain all-purpose territories year-round, linearly arranged along creeks and rivers (Rowley and Russell 1993, 1997). Like most other species of fairy-wren, *M. coronatus* breeds cooperatively. Only the dominant male and female reproduce, and they are often (40–70% of pairs) accompanied by a number of non-breeding male and female subordinates (mostly offspring from previous broods), of which most contribute to nestling feeding (Kingma et al. 2010, 2011a, 2011b). *M. coronatus* can breed year-round with a distinct peak in breeding activity during

the wet season (December–March), and a smaller peak in the late dry season (August–September) in some years (Rowley and Russell 1993, 1997; Hall and Peters 2009; Peters et al. 2013). Unlike other fairy-wrens where EPP rates are very high, *M. coronatus* engages in very limited extra-pair mating (in 5% of broods, and only in 3% of broods from non-incestuously mated pairs; Kingma et al. 2009, 2013; Hidalgo Aranzamendi et al. 2016).

Once per year, males undergo a pre-breeding molt where the brown non-breeding head plumage is replaced by purple and black feathers (Rowley and Russell 1997; Peters et al. 2013; Figure 1). Other plumage patches do not change noticeably in coloration over the year, including the black cheek patches and the blue tail, and the rest of the plumage which is mainly brown above and buff-white below (Rowley and Russell 1993, 1997; Delhey et al. 2013; Figure 1). Most males initiate pre-breeding molt in July–September before breeding starts, but in a proportion of males molt overlaps with the start of the breeding season (Rowley and Russell 1997; Peters et al. 2013; see also results section). It may be noted that females also undertake a pre-breeding molt of the head once per year, where the brown non-breeding head plumage is replaced by slate-grey feathers (Rowley and Russell 1997), although this is not the focus of the present study.

Field data collection

From July 2005 to March 2011, weekly population censuses were conducted year-round to document plumage coloration, group size and social status of each uniquely color-banded male. Each bird could be unambiguously assigned breeder (dominant) or subordinate status from behavioral cues (the most obvious being that only the dominant pair sings duets; Hall and Peters 2008, 2009). At each sighting, plumage coloration of each individual was scored as a percentage of the complete breeding plumage. Throughout the study, birds were routinely captured and tarsus length was measured using

caliper to the nearest 0.1 mm. Tarsus length could be an important indicator of male quality as body size correlates with song frequency (pitch) in male *M. coronatus* and male songs are thought to be sexually selected in the genus *Malurus* (Hall et al. 2013). We used average tarsus length in mm for all available adult captures, adjusted for handler (i.e. predicted values of a model including the identity of the handler as a random intercept).

Nesting activity was monitored by closely following the female, and once found, nests were checked regularly to determine laying date, clutch size (1–4 eggs), hatching and fledging success (for details see Kingma et al. 2011a; Hidalgo Aranzamendi et al. 2016). All nestlings were individually banded on approximately day 7 and parentage of all offspring was determined by genotyping all individuals in our population using 6 or 9 microsatellite loci (for details see Kingma et al. 2009, 2013). After the nestling period, the nest area was monitored to locate the fledglings and determine their survival. Birds captured as adults at the start of the study were classified as “age unknown” with a minimum age based on the presence or absence of offspring (of known age) or the completeness of the breeding plumage. As birds were followed throughout their life, instances of divorce (dissolution of a pair bond where both individuals remain alive) were also documented (for details see Hidalgo Aranzamendi et al. 2016).

From October 2011 to November 2015, biannual population censuses were conducted in November and May–June (for details see Hidalgo Aranzamendi et al. 2016), documenting plumage coloration, group size and social status of all individuals. All new unbanded birds (fledglings, subordinates, or immigrants) were banded, aged by age-specific development of appearance and behavioral cues (tail length, begging behavior, plumage color, bill color) and their parentage was determined using 9 microsatellite loci (Kingma et al. 2013; Hidalgo Aranzamendi et al. 2016). Newly banded birds for which parentage could not be assigned were considered as immigrants and classified as “age unknown”, being at least 3 months old (for details see Hidalgo Aranzamendi et al. 2016).



Figure 1

Non-breeding and breeding plumages in male purple-crowned fairy-wrens. Photographs show a male in non-breeding plumage viewed from the side (a) and from above (b), and a male in breeding plumage viewed from the side (c) and from above (d).

From 2007 onwards, intensive yearly censuses covering almost all suitable habitat along the tributaries that join the study site were conducted to find birds that had dispersed outside the core area (emigrants), providing reliable information on the survival (presence or absence) of all individuals (for details see [Hidalgo Aranzamendi et al. 2016](#)). Birds were declared dead on the basis of failure to sight them in regular surveys and assigned a death date estimate with a given error (mean = 59.6 ± 5.6 days, range: 3–354.5 days; for details see Supplementary Appendix S1).

Territories are stable year-round, and most boundaries remain stable through the years, being easily determined from movement patterns of birds in each group and locations of agonistic interactions between groups. Occasional changes in boundaries (shifts, territory splitting, or establishment of new territories) were recorded throughout the study. Territory quality was assessed based on the proportion of the territory covered by *Pandanus aquaticus* following methods described in [Kingma et al. \(2011a\)](#). *M. coronatus* does not occupy habitat without *Pandanus* and the distribution of *Pandanus* varies considerably between territories. Territories with greater *Pandanus* cover have lower nest failure ([Hidalgo Aranzamendi et al.](#), unpublished data) and more subordinates ([Kingma et al. 2011b](#)), indicating that these territories are more productive or attractive for subordinates. Moreover, dominant females target territories with greater *Pandanus* cover during breeder dispersal (i.e. divorce; [Hidalgo Aranzamendi et al. 2016](#)).

Daily records of rainfall were obtained from a local weather station at Mornington Wildlife Sanctuary from October 2004 to December 2015 (Australian Bureau of Meteorology weather station 002076).

Individual molt profiles

Using the scores of plumage coloration collected from July 2005 to March 2011, molt profiles were derived for each male. A year was defined as starting on 01 July (mid-winter), and ending on 30 June of the following year. The date of pre-breeding molt completion was determined as the date (number of days from 01 July) halfway between 1) the last date an individual was observed with an incomplete breeding plumage (<100% purple) and 2) the first date it was observed with a complete breeding plumage (100% purple). Half the duration between these 2 dates constituted the error of the pre-breeding molt completion date estimate (mean = 14.3 ± 1.1 days, range: 1–170 days). When birds were not observed frequently enough, the obtained estimates were unreliable (error > 21 days, half the average duration of pre-breeding molt) and excluded from further analysis ($n = 85$ of 390 excluded). When birds did not develop a complete breeding plumage (i.e. final percentage of purple <100%), the maximum score was used in a similar manner to determine the pre-breeding molt completion date. Some birds temporarily interrupted the pre-breeding molt at an intermediate coloration score before reaching a complete breeding plumage (mean = $56 \pm 4\%$ of coverage, range: 15–90%), before resuming it subsequently. When this interruption exceeded the average pre-breeding molt duration of 6 weeks, these males were classified as having “interrupted pre-breeding molt” and the profiles were excluded from overall analysis ($n = 9$ first-year males, 14 second-year and older males, and 5 males of unknown age; i.e. a total of 28).

Statistical analyses

We first analyzed (A) whether the timing of molt completion depended on intrinsic and environmental factors. Then, (B) in

order to identify potential benefits and costs associated with early molt, we investigated correlations between molt completion timing and various fitness variables related to both inter- and intrasexual selection. Hereafter we will simply use the term “molt date” to refer to the pre-breeding molt completion date. Details of all statistical models follow below.

(A) Intrinsic and environmental effects on timing of pre-breeding molt

We built a linear mixed model (LMM) with molt date as a response variable, and age, social status (dominant or subordinate), tarsus length, territory quality and group size as fixed effects. Bird identity, territory identity and year were included as random intercepts to account for non-independence in the data. We first restricted this analysis to birds whose age was accurately known ($n = 130$) and showed that the molt date only significantly varied between the first and second years of life, and not beyond (Tables 1 and Supplementary Table S1; for details see Supplementary Appendix S2 (A)). As a consequence, this analysis and subsequent ones were performed using 2 age classes, “1” and “2+”, and birds of unknown age but known to be at least in their second year of life ($n = 120$) were included in the “2+” class. Adjusted repeatability of individual molt behaviour was calculated from the last full model (with 2 age levels, $n = 247$) and the 95% confidence interval inferred from a parametric bootstrap, following [Nakagawa and Schielzeth \(2010\)](#).

As we found that dominant (breeder) males molted earlier than subordinate males, we tested whether this difference was due to within-individual change. To do this, we extracted the molt dates in 2 consecutive years for 1) subordinates who remained subordinate in the second year ($n = 19$) and 2) subordinates who became dominant in the second year ($n = 16$; i.e. a total sample size of $n = 35$ observations), and standardized them relative to the subordinate population for each year (i.e. for a given year we calculated the average date of subordinates and subtracted it from the actual date of each individual). We then built an LMM with the difference between 2 consecutive standardized molt dates as a response variable, and the interaction between the status change (either “from subordinate to subordinate” or “from subordinate to dominant”) and the age class change (either “from 1 to 2+” or “from

Table 1
Older and dominant males produce the annual breeding plumage earlier

Parameter	β	SE	df	<i>t</i> value	<i>P</i>
Fixed effects					
Intercept	173.44	8.58	35.76	20.23	<0.001
Age [†]	−63.55	7.12	235.76	−8.92	<0.001
Status*	−28.81	6.11	174.14	−4.71	<0.001
Tarsus length	−3.50	3.95	77.48	−0.89	0.38
Territory quality	1.08	0.60	52.61	1.80	0.08
Group size	0.69	1.36	223.20	0.50	0.62
Random effects					
$\sigma^2_{\text{individual}}$	249.45				
$\sigma^2_{\text{territory}}$	141.21				
σ^2_{year}	126.60				
$\sigma^2_{\text{residual}}$	680.38				

Shown are results from an LMM examining the effects of age (levels 1, 2+), social status, tarsus length, territory quality, and group size on the date of pre-breeding molt completion in individuals of known age and individuals of unknown age at least in their second year of life ($n = 247$). Significant values ($P < 0.05$) are in bold.

Reference categories are [†]age 1, *subordinate.

2+ to 2+”) as a fixed effect. Bird identity was included as a random intercept.

To determine whether population-level molt completion timing depended on rainfall, we used all the scores of plumage coloration collected from July 2005 to November 2015 and determined for each individual whether it had reached a complete breeding plumage ($\geq 95\%$) by the end of November for each year. Therefore, this approach combined both molt timing and final percentage of purple, which allowed us to use 11 years of data. Specifically, we investigated whether the likelihood of being fully purple ($\geq 95\%$) by the end of November depended on the cumulative rainfall over the past 12 months (from November of the preceding calendar year to October). We built a generalized linear mixed model with penalized quasi-likelihood (GLMMPQL) with the plumage coloration status (fully purple = 1, partially purple = 0) as a binomial response variable, and age, social status and the cumulative rainfall over the past 12 months as fixed effects. Bird identity nested in territory identity was included as a random intercept. Using the cumulative rainfall of the previous wet season (from November of the preceding calendar year to March) gave very similar results (past 12 months *vs* previous wet season: marginal $R^2 = 0.658/0.655$, conditional $R^2 = 0.981/0.980$).

(B) Fitness benefits and costs of early molt

We systematically evaluated all hypothesized sexually selected fitness benefits and costs of early molt that could apply to males in a socially monogamous year-round pair bond.

Gain of a breeder position. We tested whether the timing of molt completion predicted the likelihood of gaining a dominant (breeder) position among subordinates as this is a critical determinant of male reproductive success (subordinates do not participate in reproduction, except for 2 cases recorded in our study population; Kingma et al. 2009). To do so, we built a GLMMPQL with the annual status change (obtained a breeder position within the year = 1, remained subordinate within the year = 0) as a binomial response variable, and molt date (relative to the subordinate population for each year), age and tarsus length as fixed effects. Bird identity nested in territory identity nested in year was included as a random intercept. Cases where such a position was gained by inheritance ($n = 6$) or splitting of the natal territory ($n = 9$) were excluded.

As the opportunity of gaining a breeder position only arises when a dominant male of a territory dies or moves, and because males usually do not disperse far from their natal territory, the opportunity to compete for a vacancy is probably not equal among subordinates. For these reasons, we also performed a case-by-case analysis for each record of a subordinate gaining a breeder position by dispersing in a given year and whose molt date was known for this particular year ($n = 12$). For each case, by using information on territories (group composition and geographical location), we assessed which other males located within the same distance to the vacancy as the “winner” could also compete. Then, we compared the molt date between the competitors using Welch’s *t*-test.

Timing of breeding. We tested whether early molt was related to the quality of the female partner. Because high quality females in other species often start breeding earlier (McGraw et al. 2001; Sheldon et al. 2003; Garant et al. 2007), we tested whether timing of molt completion was correlated to the dominant female’s breeding timing and whether such a correlation differed between

dominants and subordinates. To do this, for territories where the date of the first egg laid by the dominant female was known ($n = 161$), we built an LMM with molt date as a response variable, and age (levels 1, 2+) as well as the interaction between social status and the date of the first egg laid on a territory as fixed effects. Bird identity, territory identity and year were included as random intercepts.

Social female reproductive investment and social reproductive success. Because high quality females in other species also often have higher annual reproductive output (McGraw et al. 2001; Sheldon et al. 2003; Garant et al. 2007), we tested whether male molt timing and female reproductive investment (clutch size and number of clutches) were correlated. Subsequently, we compared male social reproductive success. We also investigated the risk of a male being divorced (females initiate divorce; Hidalgo Aranzamendi et al. 2016) as a proxy for female preference for early molting males.

For all the models described below, we excluded $n = 5$ incestuous pairs of 186 pairs as those have a higher probability to end in divorce for inbreeding avoidance (Hidalgo Aranzamendi et al. 2016) and hatching success in incestuous pairs is known to be much lower ($>30\%$ of reduction compared to non-incestuous pairs; Kingma et al. 2013). We standardized the molt dates relative to the dominant population for each year. In addition, in all models, bird identity, territory identity and year were included as random intercepts (nested in each other if a GLMMPQL was used).

To test whether reproductive investment of a female varied with her partner’s molt date, we built a generalized linear mixed model (GLMM) with the annual number of attempts (0–10) as a count response variable and a zero-truncated Poisson model with clutch size (1–4) as a count response variable. In both models, we fitted molt date, age, tarsus length, territory quality, and group size as fixed effects. Additionally, to determine whether the timing of molt completion predicted the likelihood of experiencing divorce, we built a GLMM with the occurrence of divorce within a year (experienced divorce within the year = 1, did not = 0) as a binomial response variable, and molt date, tarsus length, territory quality and group size as fixed effects. The variance in molt date did not differ between males that divorced and those that did not (Levene’s test for equality of variances, $F_{1,179} = 0.002$, $P = 0.97$). Furthermore, for each record of divorce for which the molt dates of both the previous partner and the new one were known ($n = 18$), we tested whether the new partner completed his molt significantly earlier than the previous partner using Welch’s *t*-test.

To test whether molt date predicted success of breeding attempts—1) hatching success, 2) fledging success, and 3) fledgling survival, we built a GLMMPQL and used the “cbind” function to create a binomial response variable, binding together respectively 1) the number of hatched eggs and the number of unhatched eggs, 2) the number of fledged nestlings and the number of unfledged nestlings, and 3) the number of fledglings that survived for at least 6 weeks and the number of fledglings that did not. Molt date, age, tarsus length, territory quality, and group size were fitted as fixed effects. For the fledging success model, we excluded clutches in which all eggs did not hatch. For the fledgling survival model, we excluded broods with no fledgling. We also tested whether molt date predicted annual reproductive success, assessed as the number of 6-week-old fledglings produced. We built a zero-inflated Poisson model with annual reproductive success as a count response variable. The fixed and random effects listed above were fitted in the

count part of the model and an intercept was fitted for the binomial part of the model (i.e. the zero-inflation did not depend on any explanatory variable).

Extra-pair paternity (EPP) and cuckoldry rates. To determine whether the timing of molt completion predicted the likelihood of obtaining EPP among dominants (as it does in other *Malurus*; Dunn and Cockburn 1999; Brouwer et al. 2011), we built a GLMM with whether a male obtained EPP within a year (obtained EPP within the year = 1, did not = 0) as a binomial response variable, and fitted the same fixed and random effects as in the divorce model above (molt date relative to the dominant population for each year). Although similar results were obtained when including incestuous pairs, we excluded these ($n = 4$) as they have higher EPP for inbreeding avoidance (Kingma et al. 2013). The variance in molt date did not differ between males that obtained EPP and those that did not (Levene's test for equality of variances, $F_{1,166} = 0.65$, $P = 0.42$).

To test whether the timing of molt completion predicted the likelihood of losing paternity among dominants we used a similar GLMM as above, but with the occurrence of paternity loss within a year (lost paternity within the year = 1, did not = 0) instead as a binomial response variable.

Annual survival and remaining lifespan. To assess potential survival costs of early molt (hypothesized to be important in superb fairy-wrens; Peters et al. 2000; Cockburn et al. 2008), we related molt timing to both annual survival and remaining lifespan. Because both response variables could be affected by age, we first restricted the analyses described below to birds whose age was accurately known and showed that neither variable significantly differed between each age class (Supplementary Tables S8 and S9; for details see Supplementary Appendix S2 (B)). Therefore, we expanded these analyses to the age classes "1" and "2+" instead.

To test whether the timing of molt completion correlated with individual annual survival, we built a GLMM with annual survival (survived until the end of the year = 1, died before the end of the year = 0) as a binomial response variable, and molt date (relative to the whole population for each year), age (levels "1" and "2+"), social status, tarsus length, territory quality, and group size as fixed effects. Bird identity, territory identity, and year were included as random intercepts. Birds for which the year of death could not be unambiguously established (i.e. death date estimates with error >183 days or when the error interval included 01 July of a given year) were excluded ($n = 5$ of 205).

To test whether the timing of molt completion correlated with the remaining lifespan among birds that had died by the end of the study, we built a negative binomial model with remaining lifespan (in months) as a count response variable, and fitted the exact same fixed and random effects as in the annual survival model above. Remaining lifespan for a given year was calculated as the number of months between the molt date in the considered year and the death date. Birds whose death date estimate had an error >15 days were excluded ($n = 85$ of 205).

All analyses were done in R 3.2.0 (R Core Team 2015). LMMs were built using the packages "lme4" (Bates et al. 2011) and "lmerTest" (Kuznetsova et al. 2015; for details see Supplementary Appendix S2 (C)). GLMMs were first fitted without random term to estimate dispersion. If data were not over- or underdispersed, GLMMs were built using "lme4"; otherwise we either built 1) GLMMPQLs using the package "MASS" for GLMMs with

binomial response variable, or 2) negative binomial or zero-inflated Poisson models using the package "glmmADMB" for overdispersed GLMMs with count data, or zero-truncated Poisson models using the same package for underdispersed GLMMs with count data (for details see Supplementary Appendix S2 (C)). All continuous variables were centered and scaled. Estimates of model coefficients (β) and their standard error (\pm SE) are presented.

RESULTS

Intrinsic effects on timing of pre-breeding molt

In total, 279 seasonal molt profiles with reliable information on the date of pre-breeding molt completion were obtained from 137 males over a 6-year period. At the population level, pre-breeding molt in male purple-crowned fairy-wrens was on average completed by early October, although the timing of completion was highly variable within and between individuals and within and between years—occurring from May at the earliest to February of the following year at the latest. Only 16% of males (4 of 25) developed a complete breeding plumage in their first year, whereas most (92%, 206 of 224) males in their second year or older reached a complete breeding plumage (all 3-year-old and older males developed more than 98% of the complete breeding plumage; Supplementary Figure S1).

Timing of pre-breeding molt was related to age. A quadratic relationship was observed between age (in months) and the pre-breeding molt completion date (Supplementary Table S1a), with males completing their molt earlier as they aged. This effect appeared to flatten out above 2 years of age, as was confirmed when comparing age categories (Supplementary Table S1b): 1-year-old males completed their molt significantly later than males in older age classes, but timing of molt completion did not differ between 2-year-old males and older males (Supplementary Table S2, Supplementary Figure S2). When using only 2 age classes, "1" and "2+", the strong effect of age on pre-breeding molt completion date remained (Table 1, Figure 2). Timing of pre-breeding

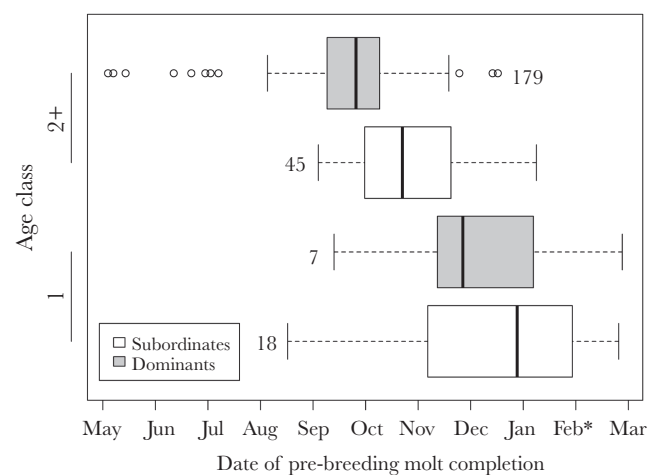


Figure 2

Older and dominant males produce the annual breeding plumage earlier. Shown are the effects of age and social status on the timing of pre-breeding molt completion in male purple-crowned fairy-wrens ($n = 249$). Boxes depict the 25th, 50th, and 75th percentiles, and whiskers the 10th and 90th percentiles. The sample size is indicated for each category. Month of peak breeding initiation is February indicated with an asterisk (*).

molt was strongly related to social status (Table 1), with subordinate males completing their molt significantly later than dominant males in both age classes (Figure 2). Based on the full model with significant fixed terms, adjusted repeatability of individual molt completion timing was 0.21 (95% confidence interval: 0.21–0.33; Table 1), indicating moderately consistent among-individual differences across the years. Individual tarsus length had no effect on the pre-breeding molt completion date (Table 1).

The comparison of within-individual changes in molt timing between subordinates who remained subordinate and subordinates who became dominants confirmed the significant advancement with age, but showed no difference due to the change of social status (Supplementary Table S3b).

Environmental effects on timing of pre-breeding molt

Higher cumulative rainfall in the past 12 months significantly increased the likelihood of males being fully purple ($\geq 95\%$) by the end of November (Table 2, Figure 3). In addition to the effect of rainfall, the likelihood of being fully purple by the end of November was also age- and status-dependent (Table 2, Figure 3), being consistent with the age- and status-dependence of the timing of molt completion reported above. In these analyses, territory quality and group size had no effect on the pre-breeding molt completion date (Table 1).

Fitness benefits and costs of early molt

At the population level, the timing of pre-breeding molt completion in subordinates did not predict the likelihood of gaining a breeder position via dispersal (Supplementary Table S3a, Figure 4a). When we performed a case-by-case analysis, comparing the molt timing of a “winner” of a breeding vacancy and potential competitors located within the same distance to the vacancy, timing of molt completion did not predict success (Welch’s *t*-test, $t = 0.05$, $df = 35$, $P = 0.48$, $n = 19$ pairwise comparisons, including 9 cases of earlier molt completion by the winner and 10 cases of later molt completion).

Over the course of the study, 162 individual molt profiles associated with a reproductive event were recorded in 70 breeder males.

Table 2

By the start of the peak breeding initiation, male breeding plumage is more complete in older and dominant males, and following wetter years

Parameter	β	SE	df	<i>t</i> value	<i>P</i>
Fixed effects					
Intercept	−5.72	0.64	383	−8.94	<0.001
Age†	4.87	0.34	383	14.43	<0.001
Status*	2.99	0.32	383	9.19	<0.001
Rainfall	1.86×10^{-3}	0.58×10^{-3}	383	3.21	0.002
Random effects					
$\sigma^2_{\text{territory}}$	0.77				
$\sigma^2_{\text{individual in territory}}$	2.12				
$\sigma^2_{\text{residual}}$	0.55				

Shown are results from a GLMMPQL examining the effects of age (levels 1, 2+), social status, and cumulative rainfall over the past 12 months (from November of the preceding calendar year to October of the current calendar year) on the likelihood of being fully purple by the end of November ($n = 778$ observations for 300 individuals over 11 years).

Significant values ($P < 0.05$) are in bold

Reference categories are †age 1, *subordinate.

The majority of males (71%) were displaying a complete breeding plumage when the first eggs were laid, while some males (23%) were still undergoing pre-breeding molt, and a few others (6%) were still in non-breeding plumage. No correlation between pre-breeding molt timing of males and timing of breeding initiation by the breeder female (date of first egg) was found (Supplementary Table S4), neither for dominants nor for subordinates.

Among dominants, timing of pre-breeding molt completion was not associated with any component of reproductive success. Specifically, female investment, including the annual number of breeding attempts (Supplementary Table S5, Figure 4b) and clutch size (Supplementary Table S5, Figure 4c) did not vary with molt timing of the breeding partner. Timing of male pre-breeding molt completion was not correlated with hatching success, fledging success and fledgling survival (Supplementary Table S6, Supplementary Figure S3). Finally, the annual number of fledglings produced that survived for at least 6 weeks was not predicted by molt timing (Supplementary Table S5, Figure 4d).

Dominant males who completed their molt earlier were not more likely to gain EPP (Supplementary Table S7, Figure 4e) and those that molted later were not more likely to lose paternity (Supplementary Table S7) or to be divorced (Supplementary Table S7, Figure 4f). In addition, divorcing females did not re-pair with a male that had molted earlier than their previous partner (Welch’s *t*-test, $t = -1.33$, $df = 33$, $P = 0.90$, $n = 18$ pairwise comparisons, including 7 cases of earlier molt completion by the new partner, 10 cases of later molt completion, and 1 case of completion on the same day). Those males that were still undergoing pre-breeding molt or in non-breeding plumage when their partner initiated a clutch, sired 100% of those offspring (32 broods for males in partial breeding plumage, 4 broods for males in non-breeding plumage).

No association between annual survival and timing of pre-breeding molt was found (Supplementary Table S10, Figure 4g). Furthermore, no association between remaining lifespan and timing of pre-breeding molt was found among birds of known lifespan (Supplementary Table S10, Figure 4h).

DISCUSSION

Based on our findings, the timing of acquisition of the purple-and-black breeding plumage in male *M. coronatus* appears to show limited correlations with male quality and environmental conditions: its expression varies with both age and climate, but the age effect is restricted to early life, and the climate effect appears relatively small. In addition, dominants complete their pre-breeding molt earlier than subordinates, suggesting the potential to signal social status and competitive ability among males, although molt timing did not relate to the chances of subordinates to become dominant. Finally, although we investigated numerous reproductive benefits and costs potentially associated with early molt completion, we could not identify any, suggesting weak or even absent female choice acting on this trait in male purple-crowned fairy-wrens.

Pre-breeding molt timing as a signal of male quality? Effects of age and rainfall

The timing of breeding plumage acquisition in male *M. coronatus* is highly variable both between and within individuals. Sexually selected ornaments are often assumed to show high variability, maintained through high condition-dependence (Delhey and Peters 2017), although the latter has proved difficult to test (Cotton et al. 2004; Delhey and Peters 2008; Delhey et al. 2017). Substantial

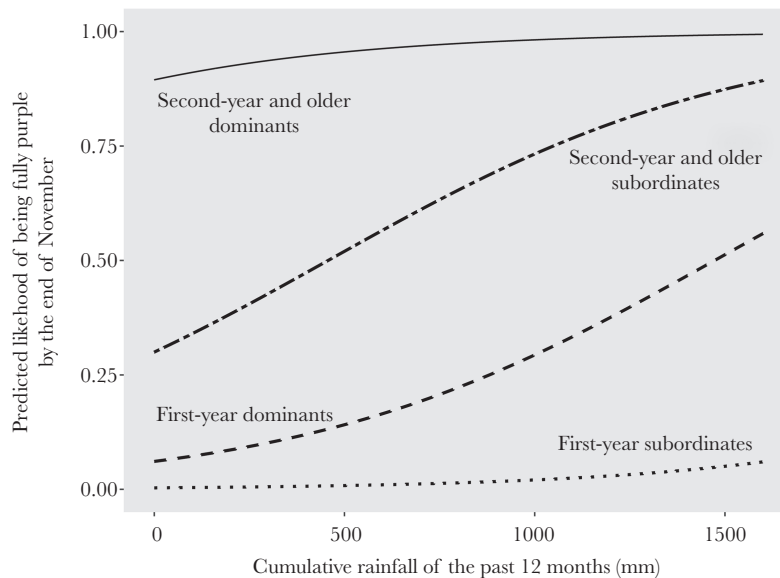


Figure 3

By the start of the peak breeding initiation, male breeding plumage is more complete in older and dominant males, and following wetter years. Shown are the predicted correlations between the likelihood of being fully purple by the end of November and the cumulative rainfall over the past 12 months ($n = 778$ observations) for 1-year-old subordinates (dotted line), 1-year-old dominants (dashed line), 2-year-old and older subordinates (dotted and dashed line), and 2-year-old and older dominants (solid line).

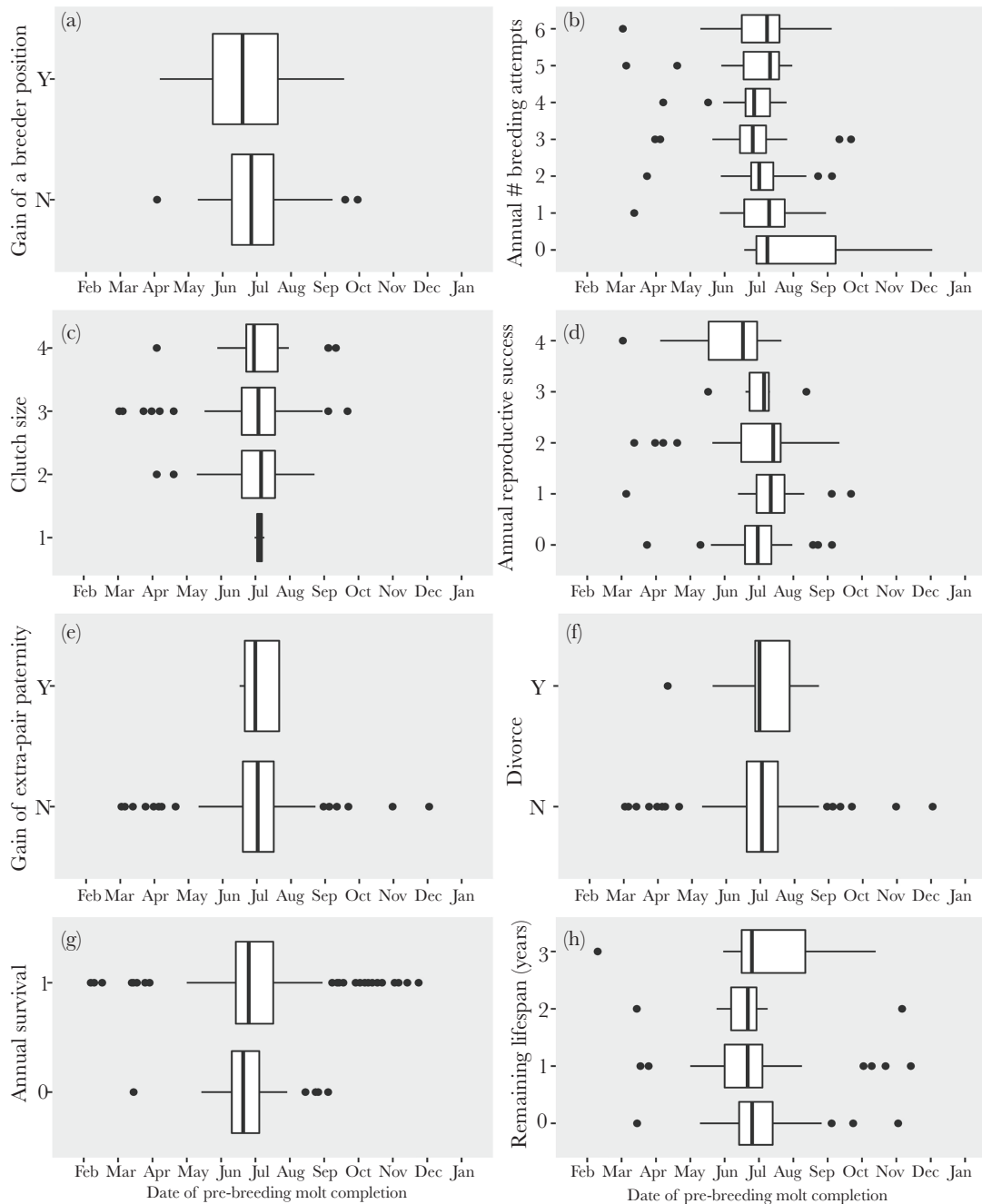
variation in molt timing (range of up to 10 months vs. 3–9 months in other studied fairy-wren species; Peters et al. 2013) therefore provides support for some potential to act as a male quality indicator, either for females in mate assessment or for males when gauging rivals. Moreover, pre-breeding molt timing is moderately repeatable ($r = 0.21$; Table 1), suggesting that it could serve as a reliable signal of male genetic quality (Lynch and Walsh 1998; Bell et al. 2009) and consequently be subject to female preferences (Andersson 1986; Iwasa and Pomiankowski 1994).

The timing of pre-breeding molt shows some degree of age-dependence as a significant advancement occurs within the first 2 years of life (Table 1, Figure 2). Males might benefit from age-dependent investment in their signals, reserving the production of costly traits until older ages (Kokko 1997) and honest signaling should favor delaying development of costly signals and therefore preferences for older males (Brooks and Kemp 2001; Proulx et al. 2002). Age-dependence of molt timing could reflect honest signaling of male quality in *M. coronatus*. However, the observed improvement is restricted to early life, which contrasts with patterns in male superb fairy-wrens that show life-long improvement, with the proportion of early molters increasing linearly with age (van de Pol et al. 2012). In superb fairy-wrens, early acquisition of breeding plumage, months prior to breeding, is critical for obtaining extra-pair fertilizations that dominate the mating system of this species (Dunn and Cockburn 1999). Similarly, male red-winged fairy-wrens acquire their breeding plumage earlier as they get older (Russell et al. 1991) and early molters are preferentially chosen as extra-pair mates by females (Brouwer et al. 2011). That male purple-crowned fairy-wrens do not show further improvement with age is in line with their much lower levels of EPP (Kingma et al. 2009).

The timing of pre-breeding molt in male *M. coronatus* is also sensitive to climate, similar to several other fairy-wrens: higher cumulative rainfall correlates with higher likelihood of displaying a complete breeding plumage by the end of November (Table 2,

Figure 3). This indicates that males complete their molt earlier following wetter years, and this effect appears particularly noticeable in years with extreme climate, especially during drought (e.g. 2005). Molting is energetically and nutritionally demanding in small birds (Payne 1972; Lindström et al. 1993; Murphy 1996; Cornelius et al. 2011). Higher rainfall is likely to result in prolonged vegetation growth and arthropod abundance (Lowman 1982), therefore providing more resources to these insectivorous birds and increasing their ability to undertake their pre-breeding molt early. Such dependence on environmental variability could be interpreted as evidence for condition-dependence. In comparison, in superb fairy-wrens, molt timing shows a strong sensitivity to summer rainfall, and more particularly old males can strongly advance their molt after high summer rainfall (Cockburn et al. 2008; van de Pol et al. 2012).

Both annual survival (reflecting short-term survival) and remaining lifespan (reflecting long-term survival) show no correlation with the timing of pre-breeding molt (Supplementary Table S10, Figures 4g and h). This might suggest that early molt does not entail substantial costs. Cockburn et al. (2008) hypothesized that cold conditions during winter might have detrimental effects on the survival of early molting superb fairy-wrens in temperate SE Australia. In comparison, individuals from our study population experience much milder tropical climatic conditions where temperatures rarely go below 4 °C (vs. −8 °C in Cockburn et al. 2008), which may account for the lack of noticeable survival costs in early molters. However, without experimental data it is hard to interpret this absence of correlation, since only males able to undergo the pre-breeding molt early (and that can absorb the potential costs) might do so (Peters 2000), masking potential survival costs associated with early molt. In addition, it is possible that the selective disappearance of certain phenotypes makes some patterns of survival selection difficult to detect, especially based on the data that were available to us.

**Figure 4**

Molt performance is not related to fitness indicators. Shown is the absence of correlation between the timing of pre-breeding molt completion and (a) the likelihood of gaining a breeder position ($n = 47$), (b) the annual number of breeding attempts (6 and above combined into one class; $n = 166$), (c) clutch size ($n = 259$), (d) annual reproductive success (i.e. number of 6-week-old fledglings produced; 4 and above combined into one class; $n = 151$), (e) the likelihood of gaining EPP ($n = 168$), (f) the likelihood of experiencing divorce ($n = 181$), (g) annual survival ($n = 242$), and (h) remaining lifespan (3 years and above combined into one class; $n = 120$).

Early molt: no fitness benefits through female choice

When investigating an extensive panel of male fitness proxies linked to female choice, we consistently found no evidence of any association with pre-breeding molt timing. Although it is possible that we missed some fitness indicators that are not immediately obvious or easily measured, our data quite strongly suggest weak or absent

intersexual selection favoring early molt in male purple-crowned fairy-wrens.

One potential sexually selected benefit of preferred, more ornamented males, is to pair with females of higher quality, those that start breeding earlier or lay more eggs (McGraw et al. 2001; Sheldon et al. 2003; Garant et al. 2007). We found no evidence for such a process in *M. coronatus*: females paired to an earlier-molting male do not start egg-laying earlier, increase the number

of breeding attempts or lay larger clutches (Supplementary Tables S4 and S5, Figures 4b and c). In agreement with this, our findings did not support any association between molt timing and reproductive success. Early molting males do not achieve greater success of breeding attempts (hatching success, fledging success, fledgling survival) or greater annual reproductive success (Supplementary Tables S5 and S6, Figure 4d and Supplementary Figure S3).

There were no indications that females preferred early molting males as social or EP mates. There was no link between male molt timing and divorce (Supplementary Table S7, Figure 4f). Most divorces are initiated by females that leave their partner to take a breeding position elsewhere (Hidalgo Aranzamendi et al. 2016). This provides an opportunity for females to choose their partner, but pre-breeding molt timing appears not to play a role in such partner assessment by prospecting females. Additionally, late molters do not suffer increased paternity loss and early molters do not increase their chances of gaining EPP (based on the few recorded cases) (Supplementary Table S7, Figure 4e), in contrast to 2 other *Malurus* (Dunn and Cockburn 1999; Brouwer et al. 2011). This is in agreement with the absence in *M. coronatus* of male adaptations that play a central role in the EPP-based mating system of other Australian fairy-wrens (Figure 5; Kingma et al. 2009).

Early molt: a signal of social status or competitive ability?

Independently of the effect of age, the timing of pre-breeding molt in male *M. coronatus* varies according to social status: the dominant male in the group is generally the first to acquire breeding plumage (Table 1, Figure 2). It is possible that, by delaying their molt compared to dominant males, subordinate males attempt

to avoid costly aggressive interactions (Senar 2006; Santos et al. 2011). Alternatively, molt timing might serve as a signal of dominance and competitiveness among males. However, subordinates that molt earlier do not increase their chances to acquire a breeder position (Supplementary Table S3a). Because subordinates do not participate in reproduction (aside from 2 cases of a subordinate male gaining EPP; Kingma et al. 2009), gaining a breeding position is a critical determinant of male success. This can occur by splitting the natal territory, by inheritance (through an orderly, age-based queue) or by dispersal (Kingma 2011; Kingma et al. 2011b; Hidalgo Aranzamendi et al. 2016). In this third case, because breeding vacancies are scarce and male dispersal mostly limited to neighboring territories, the opportunity to compete is rare, which may account for the absence of role of molt timing in the acquisition of such a vacancy.

Timing of pre-breeding molt: the ghost of female EP mate choice past?

We found no association between pre-breeding molt timing and any of the numerous proxies for male fitness we used in this study, suggesting that this trait is currently not under intersexual selection in male purple-crowned fairy-wrens. However, substantial variation exists, partially linked to age and environmental conditions, and it has a potential genetic component (inferred through its repeatability), attributes which are common to sexually selected traits (Cotton et al. 2004; Delhey and Peters 2008). Therefore, the early development of the breeding plumage could be used as a sexual signal, similar to how it functions in other fairy-wrens. Moreover, early molt may function as a social signal of dominance and competitiveness among males, although it is not intuitively clear how this could

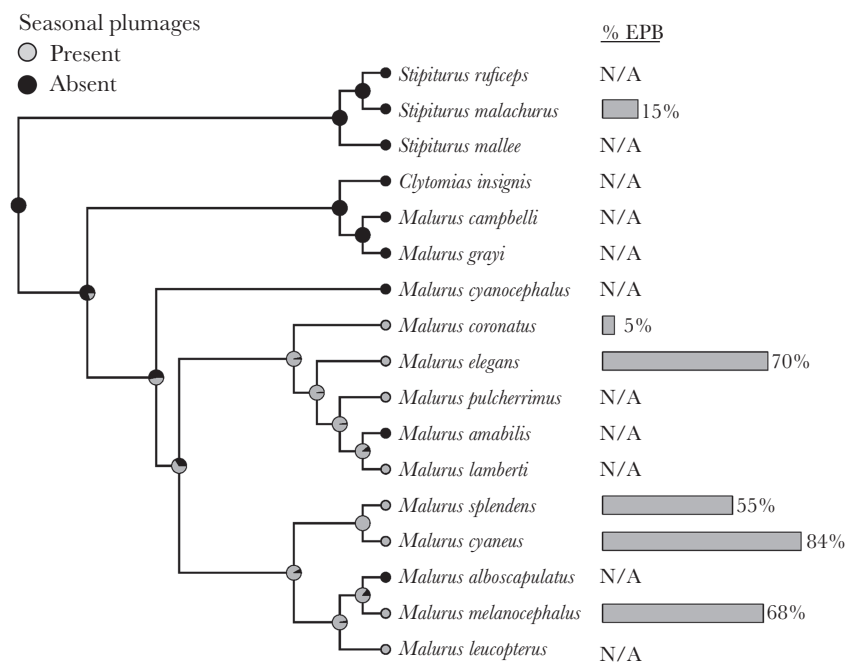


Figure 5

Evolution of seasonal plumages in fairy-wrens and emu-wrens. Shown is the ancestral state reconstruction of changes in seasonal plumages for 17 species of Malurid, using stochastic mapping and based on the supermatrix phylogeny of Marki et al. (2017). Levels of extra-pair paternity expressed as the proportion of broods containing at least one nestling resulting from an extra-pair fertilization (% EPB) are shown for each species (Rowe and Pruett-Jones 2013; N/A: no data available). Reconstruction of ancestral presence/absence of seasonal plumages was done using stochastic mapping using the function “make.simmap” from the R package “phytools” (Revell 2012). We ran 100 stochastic mappings and pie charts in nodes summarize the posterior probability of being one state or the other. For this analysis, we set the root stage as absence of seasonal plumages and we allowed different transition rates between states (model = “ARD”).

work, or could be tested, since males are territorial year-round, whether they are in breeding plumage or not. This raises the question of what is the function of this variation in the timing of breeding plumage acquisition in male purple-crowned fairy-wrens.

Ancestral state reconstruction (Figure 5; based on the recent supermatrix phylogeny by Marki et al. 2017) suggests that variation in pre-breeding molt in male purple-crowned fairy-wrens represents a vestigial trait, on its way to disappearing. Kingma et al. (2009) suggested that *M. coronatus* is derived from an ancestor with high EPP, but subsequently lost the extreme levels of EPP and associated behavioral adaptations that characterize the other *Malurus* (i.e. extra-territorial intrusions, extra-pair courtship displays). According to such a scenario, the highly variable timing of pre-breeding molt is a formerly sexually selected trait that lost its function as sexual selection became weaker (“relaxed” sexual selection; Lahti et al. 2009). This is in agreement with the reduction in the extent of the body covered by breeding plumage in purple-crowned fairy-wrens compared to other species in the genus (Kingma et al. 2009). We hypothesize that the loss of extreme levels of EPP removed the main evolutionary force driving variation in timing of seasonal acquisition of bright male plumage in fairy-wrens, resulting in the loss of its main function. Therefore, this trait could represent an evolutionary vestige that may undergo reduction or even complete loss, unless it acquires a novel function, or is correlated with other traits currently under selection (Lahti et al. 2009). Although traits can persist and continue to be expressed for long periods of time after a source of selection is removed (Lahti et al. 2009), variation in molt timing in male *M. coronatus* appears not to have undergone noticeable reduction, which hints that it may still be under some selection pressures, perhaps difficult to detect if it is only noticeable in specific conditions, or serves other purposes. In particular, molt timing may function as a social signal of dominance and competitiveness among males, which could explain why variation in this trait persists.

CONCLUSION

We found no evidence of sexual selection currently acting on the timing of breeding plumage acquisition, based on the investigation of the male fitness variables presented in this study. However, its strong status-dependence warrants future studies to focus on a potential role in mediating male-male social interactions. Additionally, although the timing of pre-breeding molt is not related to fitness indicators for male purple-crowned fairy-wrens, further work is needed to assess the importance of other signal components, such as variation in the quality of the purple color which represents a unique and highly conspicuous evolutionary innovation in this species (Delhey et al. 2013).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Fan et al. (2017). The data are embargoed for a 12-month period as they are currently being used by the authors in other analyses, and will be made available in the repository at the end of this period.

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