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RESEARCH ARTICLE

Male Red-backed Fairywrens appear to enhance a plumage-based signal via adventitious molt

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ABSTRACT

Phenotypically plastic signals that can be altered in response to changing environmental conditions provide animals with the ability to dynamically signal their current condition or status. Such flexibility might also provide a means of avoiding potential trade-offs between signal components. Among birds, for example, both the timing of expression and the coloration of nuptial plumage are often thought to be honest signals of condition. However, because plumage is a relatively static signal type, birds that express condition-dependent plumage signals may face a trade-off between timing of signal production and signal quality, in that signals produced relatively early may be of lower quality because of seasonal constraints. A related cost may be increased fading or wear of plumage associated with extended duration of signal expression. Male Red-backed Fairywrens (*Malurus melanocephalus*) exhibit asynchronous development of nuptial red–black plumage, with some individuals molting into nuptial plumage months earlier than others. We report that male Red-backed Fairywrens that molt into nuptial red–black plumage early during the nonbreeding season appear to increase their plumage coloration by replacing feathers outside of normal molt periods (i.e. adventitious molt). In this way, some male Red-backed Fairywrens may be able to molt into nuptial plumage in the nonbreeding season, which is likely to increase access to mates or resources, and to subsequently enhance the red hue of a plumage-based sexual signal to a putatively more attractive state. We suggest that adventitious molt may be a currently underappreciated mechanism that birds use to improve or maintain the quality of plumage-based signals over time, between periodic full-body molts.

Keywords: adventitious molt, plumage, sexual selection, signal development, trade-offs

El macho de *Malurus melanocephalus* parece mejorar una señal mediada por el plumaje a través de la muda adventicia

RESUMEN

Las señales plásticas fenotípicas que pueden alterarse en respuesta a las condiciones ambientales cambiantes permiten que los animales muestren de modo dinámico su condición o estatus actual. Esta flexibilidad también podría permitirles liberarse de los potenciales costos-beneficios entre los componentes de la señal. En las aves, por ejemplo, los momentos de la expresión y de la coloración del plumaje nupcial son usualmente considerados como señales honestas de la condición. Sin embargo, debido a que el plumaje es un tipo de señal relativamente estático, las aves que expresan su condición a través del plumaje pueden afrontar un costo-beneficio entre el momento de la producción de la señal y la calidad de la señal, ya que las señales producidas relativamente temprano pueden ser de baja calidad debido a restricciones estacionales. Un costo adicional puede darse por el desvanecimiento o el desgaste del plumaje asociado con la extensión de la duración de la señal. Los machos de *Malurus melanocephalus* muestran un desarrollo asincrónico del plumaje nupcial rojo–negro, con algunos individuos mudando al plumaje nupcial algunos meses más temprano que otros. Los machos de *M. melanocephalus* que mudan al plumaje nupcial rojo–negro más temprano durante la estación no reproductiva parecen aumentar la coloración del plumaje mediante el reemplazo de las plumas fuera de los periodos normales de muda (i.e. muda adventicia). De este modo, algunos machos de *M. melanocephalus* pueden ser capaces de mudar al plumaje nupcial durante la estación no reproductiva, lo que probablemente les permite aumentar su acceso a las parejas o a los recursos, y luego aumentar subsecuentemente el tono rojo del plumaje a un estado supuestamente más atractivo de señal sexual. Sugerimos que la muda adventicia puede ser un mecanismo actualmente subestimado que usan las aves para mejorar o mantener la calidad de las señales dadas por el plumaje en el tiempo, entre las mudas corporales completas periódicas.

Palabras clave: costos-beneficios, desarrollo de la señal, muda adventicia, plumaje, selección sexual

INTRODUCTION

The costs associated with producing and maintaining social or sexual signals are often thought to enforce the honesty of these signals, thereby ensuring that they accurately convey information about individual "quality" (Zahavi 1975). For example, the carotenoid-based red plumage in House Finches (*Haemorhous mexicanus*) is commonly cited as an example of an honest signal because it is associated with both diet and condition (Hill 1991, Hill et al. 2002) of males, and females select more colorful males that provide better parental care (Hill 1991). In addition to the size and color of a trait, the timing of signal expression may also convey important information about the condition or status of the bearer. Among birds, considerable intraspecific variation in the timing of development of plumage-based signals occurs both across seasons (i.e. delayed plumage maturation; Lyon and Montgomerie 1986, Hawkins et al. 2012) and within seasons (van Rhijn and Groothuis 1987, Barnard 1995, Omland 1996, Peters et al. 2013). Within-season variation remains relatively understudied, but, in at least some cases, the timing of plumage development appears to be as important as the actual ornament that is produced in determining fitness. For example, among Superb Fairywrens (*Malurus cyaneus*) and Red-winged Fairywrens (*M. elegans*), the only consistent phenotypic predictor of extrapair reproductive success is the duration that males spend in nuptial plumage (Mulder and Magrath 1994, Dunn and Cockburn 1999, Brouwer et al. 2011). Additionally, in African whydahs (Ploceidae: *Vidua*), the temporal variation in ornament development within a season has a higher potential for sexual selection than maximum ornament size (Barnard 1995).

Much as trade-offs may exist between multiple sexual signals (Bro-Jørgensen 2010), trade-offs may also exist between quality and the timing of expression of a given signal, in that the cost of expressing a signal relatively early may lead to production of a smaller or less colorful signal (e.g., del Val et al. 2014). Alternatively, higher-quality individuals may be able to signal their superiority in multiple signal components concurrently; this appears to be the case in Barn Swallows (*Hirundo rustica*), in which individuals in better condition molted earlier and faster to produce higher-quality ornaments (Møller et al. 1995). A third possibility is that individuals might subsequently modify signals that are developed early to effectively avoid a potential trade-off between timing and quality.

In birds, this third possibility has received relatively little attention because plumage has traditionally been considered a static trait, constrained by the timing of the molt cycle (Palmer 1972). However, within-season changes to plumage are known to occur through cosmetic alteration, abrasion, staining, fading, ultraviolet damage, bacterial degradation (reviewed in Montgomerie 2006), or continuous molt (Foster 1975, Kear 2005), which can result in increases or decreases in signal value. Adventitious molt, or replacement of feathers outside of the molt cycle, could also act as a mechanism to allow males to modify a plumage-based signal over time, but this possibility has not been well explored to date. Although replacement of feathers outside of the molt cycle is not well documented, there are reasons to believe that this phenomenon may be more common than is currently appreciated. For example, in a seasonal tropical site in the Brazilian Cerrado, >15% of birds showed continuous year-round replacement of body feathers (Marini and Durães 2001). Indeed, because documenting adventitious molt requires focused attention on molt in combination with year-round data collection, few studies are likely to report this phenomenon when it does occur.

We examined the relationship between timing of development and coloration of a plumage-based sexual signal, the red patch on the back of the Red-backed Fairywren (*M. melanocephalus*). As with other *Malurus* species, Red-backed Fairywrens are well suited for investigating the interplay between timing vs. spectral components of signal quality: Both the timing of molt into nuptial plumage (Peters et al. 2013) and the spectral characteristics of plumage-based signals (Baldassarre and Webster 2013) are variable within populations, and both influence access to mates and fitness (Dunn and Cockburn 1999, Karubian 2002, Webster et al. 2008, Baldassarre and Webster 2013). Our findings indicate that, among a relatively small sample of males, the red patch on the back increases in hue between the nonbreeding and breeding seasons, independent of the periodic molt schedule, which is consistent with the idea that adventitious molt may be driving this pattern.

METHODS

We studied a color-banded population of Red-backed Fairywrens (*M. m. cruentatus*) on Coomalie Farm (13°02′S, 131°02′E) in Northern Territory, Australia, during 2012–2014. We captured individuals during successive nonbreeding (June–August 2012 and 2013) and breeding seasons (December 2012–January 2013 and December 2013–February 2014). We measured morphological traits of all captured birds, including tarsus and mass, but were unable to obtain informative measures of age. We scored molt by estimating the number of growing pin feathers on 6 body parts (head, back, belly, chest, tail, and wing) on a 4-point scale, with a score of zero indicating no molt, and each subsequent point constituting a third of feathers in pin (i.e. birds with 1–33% of feathers in molt in a region would receive a score of 1). As such, a bird experiencing heavy (>66%) molt in all 6 body regions would receive a

FIGURE 1. Male Red-backed Fairywrens in dull eclipse plumage (left) and nuptial red–black plumage (right). Following breeding, most males molt into dull eclipse plumage in the prebasic (postnuptial) molt. The prealternate (prenuptial) molt is asynchronous, such that some males display nuptial red–black plumage for months during nonbreeding periods, whereas others maintain eclipse plumage during the nonbreeding season and molt into red–black right before breeding.

total molt score of 18, the maximum value possible. We focus on back molt in the present study because of the importance of coloration of the red back feathers as a sexual signal, but we present values for total body molt as well, for completeness.

Red-backed Fairywrens undergo 2 molts yr^{-1}, with males acquiring nuptial red–black plumage during a partial prenuptial (i.e. prealternate) molt (body and tail feathers but not flight feathers), and brown eclipse plumage during a complete postnuptial (i.e. prebasic) molt (Rowley and Russell 1997; see Figure 1). The postnuptial molt usually occurs in relative synchrony in a population, but there is considerable variation in the timing of the prenuptial molt, resulting in some males displaying nuptial plumage months in advance of other males (Rowley and Russell 1997, Peters et al. 2013). Individuals in our study population that molted into nuptial red–black plumage during the nonbreeding season were classified as "early" molters, whereas birds that remained in dull brown plumage throughout the nonbreeding season but were in red–black plumage during the subsequent breeding season were classified as "late" molters. Thus, early-molting males were in red–black plumage during 2 capture periods yr^{-1}, whereas late-molting males were in brown plumage during the nonbreeding season and red–black plumage during the breeding season. The prenuptial molt in fairywrens typically lasts about a month (Rowley and Russell 1997); thus, any molt exhibited by these early-molting males during the breeding season would fall well outside the prenuptial molt period. Early-molting birds that we documented as completing the prenuptial molt during the nonbreeding season and that we subsequently observed to have a molt score ≥ 1 on the back during the subsequent breeding season were considered to be exhibiting adventitious molt.

For all red–black males, we collected a small sample of red feathers from the upper center of the back and measured spectral reflectance with an Ocean Optics (Dunedin, Florida, USA) USB2000+ spectrophotometer, using an R400-7 UCV-VIS probe and a PX-2 pulsed xenon light source (following Baldassarre et al. 2013). We mounted 6 feathers from each individual in an overlapping pattern on black cardboard (Crescent ultra-black mounting board) as in other studies focused on this species (e.g., Baldassarre et al. 2013). Although color values can change depending on the number of feathers used (see Quesada and Senar 2006), we confirmed high repeatability of our metrics using 6 feathers across independent spectrophotometry sessions using the same mounted feathers, following the methods in Lessells and Boag (1987; $F = 9.47$, $r_i = 0.81$, $P < 0.001$, $n = 26$). We mounted the probe in a metal block that excluded all ambient light, and the probe light illuminated a ~2 mm diameter circle. We used the program SpectraSuite (Ocean Optics) to calculate reflectance curves, using a white standard (Ocean Optics WS-1) to calibrate the probe. We collected 3 reflectance curves for each sample, moving the probe slightly between measurements; each curve represented the average of 20 scans of the spectrophotometer. We used the average of these 3 curves for each individual to analyze the reflectance in the avian visible spectrum (300–700 nm). Averages of

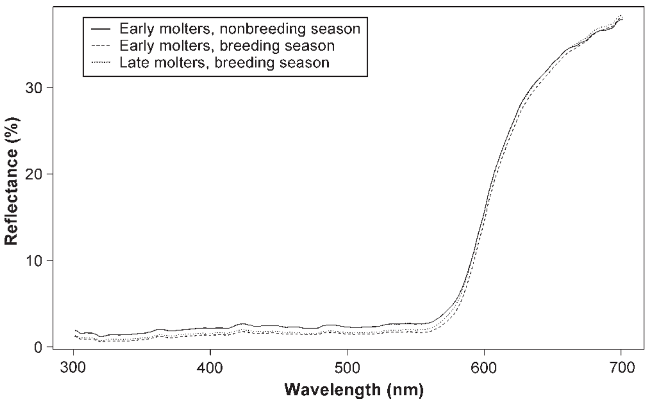

FIGURE 2. Plots of average reflectance spectra for red back feathers of early-molting male Red-backed Fairywrens during the nonbreeding and breeding seasons, and of late-molting males during the breeding season, in Northern Territory, Australia, 2012–2014. Reflectance spectra were averaged across both years for all males within each group. The shapes of the reflectance spectral curves are typical for red plumage, and the relative shape of the curves did not change between seasons. Reflectance spectra are plotted using a smoothing parameter of 0.2 to remove spectral noise while maintaining shape, after comparing smoothing parameters using "plot.smooth" in the R package "pavo."

reflectance spectra across male types (early-molting males in both the nonbreeding and breeding seasons, and late-molting males in the breeding season) are shown in Figure 2.

We used the R package "pavo" (Maia et al. 2013) to analyze the reflectance curves. This program uses tetrahedral color space models (Stoddard and Prum 2008) to plot reflectance spectra modeling avian vision; we used the average avian violet-sensitive (VS) cone-type retina and idealized illumination because Red-backed Fairywrens have a VS visual system (Ödeen et al. 2012). For this analysis, we focus on hue because it is the main colorimetric variable related to differential carotenoid pigmentation (Andersson and Prager 2006). Hue (theta, θ) describes the angle of the color vector and, as such, is a measure of color (capturing variation in the species from orange to red; see Baldassarre and Webster 2013). Plucked feathers are typically replaced within a month (Grubb 2006); thus, plucked nonbreeding-season feathers would not be in pin when we returned during the breeding season several months later. Although we standardized the relative location that we plucked feathers from, it is also unlikely that out of the hundreds of feathers found on the red patch, the same 8–10 feathers would be plucked twice.

Statistical Analyses

We used linear mixed models to assess the relationships between hue, season, and timing of prenuptial molt (i.e. early vs. late). In our first model, we used feather samples from the period when the individuals molted (i.e. nonbreeding-season feathers collected from early-molting birds vs. breeding-season feathers collected from late-molting birds) to assess whether hue varied between early vs. late molters. In the second model, we used breeding-season feather samples collected from both early- and late-molting males to assess whether breeding-season hue differed by molt period. Thus, in both models the predictor variable was molt type (early vs. late) and the response variable was hue, but the models differed in terms of the season in which the feathers of early-molting males were collected. In both models, year and individual were included as random effects to control for potential differences in hue between years and because some individuals were sampled in multiple seasons or years. We fitted models using a normal distribution based on visual inspection of quantile–quantile plots. All analyses were conducted in R 3.0.2 (R Core Team 2013), and linear mixed models were run using the "lmer" function in the "lme4" package (Bates et al. 2015). We tested linear mixed models for significance of molt period on plumage hue using a Wald chi-square test (using the ANOVA [analysis of variance] function in the package "car"; Fox and Weisberg 2011).

For early-molting individuals that were captured in both the nonbreeding season and the subsequent breeding season, we conducted a paired Student's *t*-test to compare hue across these 2 time points. Because late molters were brown throughout the nonbreeding season, we did not have samples of red back feathers for this class of males during both periods and thus were unable to perform the equivalent test on these males. Because data within this subset of individuals were not normally distributed, we transformed hue using the function $\log(x + 0.5)$ to fit assumptions of normality for this test (figures present the untransformed values for easier interpretation).

We calculated male condition as the residuals of a linear regression of mass on tarsus length (ANOVA: $F_{93} = 28.06$, $P < 0.0001$, $r^2 = 0.23$), which reflects fat energy stores in this species (Lindsay et al. 2009). We used a linear mixed model to compare male condition between early- and late-molting males during both the nonbreeding and breeding seasons, with individual and year as random factors. For all adult males captured within a year in both the nonbreeding and the breeding season, we conducted a Student's paired *t*-test using mass between these 2 periods (because tarsus did not change).

RESULTS

Early-molting males, defined as those that molted into red–black plumage during the nonbreeding season,

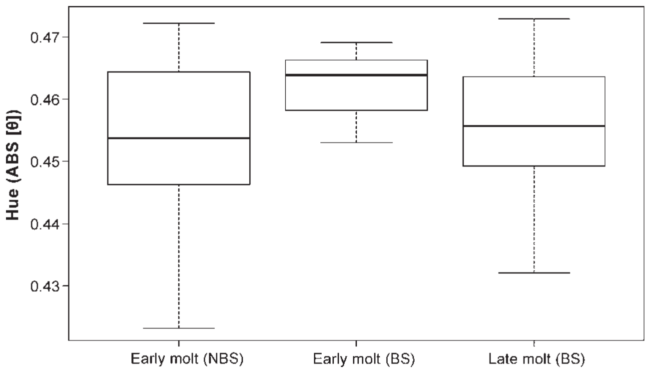

FIGURE 3. Comparisons of red back hue for early-molting male Red-backed Fairywrens during the nonbreeding (NBS, $n = 37$) and breeding (BS, $n = 15$) seasons, and for late-molting males during the breeding season ($n = 27$), in Northern Territory, Australia, 2012–2014. Early-molting males captured during only one period (nonbreeding or breeding) are included in the respective category. Values for plumage hue (θ) have been converted to absolute values (ABS) for visualization purposes, such that a higher value denotes a redder hue, a putatively preferred state. Males that molt early in the nonbreeding season are more red during the breeding season than both early-molting males in the nonbreeding season and late-molting males in the breeding season.

FIGURE 4. Early-molting male Red-backed Fairywrens ($n = 12$) captured in both the nonbreeding and breeding seasons within a single year in Northern Territory, Australia, 2012–2014, increased in redness of back feathers between these 2 periods. Lines between points denote a paired comparison between the 2 time points for the same individual male. Values for plumage hue (θ) have been converted to absolute values (ABS) for visualization purposes, such that a higher value denotes a redder hue.

initially developed red patches during the nonbreeding season that were equivalent to the back hue expressed by late-molting males in the breeding season (Wald chi-square test: $\chi^2 = 0.36$, df $= 1$, $P = 0.55$; early-molting males, nonbreeding season: $n = 36$; late-molting males, breeding season: $n = 27$) (Figure 3). However, early-molting males captured in both the nonbreeding and the breeding season ($n = 12$) tended to increase in redness (i.e. hue) between the nonbreeding and the breeding season (paired $t_{11} = 2.0$, $P = 0.07$; Figure 4). We recorded adventitious back molt for the majority (10 of 12) of these early-molting males during the breeding season, despite the fact that they completed the prenuptial molt months previously (Table 1). Most early-molting males converged upon a very red hue during the breeding season, such that, during the breeding season, early-molting males were significantly more red than late-molting males ($\chi^2 = 3.17$, df $= 1$, $P = 0.05$; early-molting males: $n = 15$; late-molting males: $n = 27$) (Figure 3).

Early-molting males tended to be in better condition than late-molting males during the nonbreeding season (Wald chi-square test: $\chi^2 = 3.11$, df $= 1$, $P = 0.08$; early-molting males: $n = 37$, residual mass -0.03 ± 0.45; late-molting males: $n = 20$, residual mass -0.18 ± 0.28) and in equivalent condition during the breeding season (Wald chi-square test: $\chi^2 = 0.005$, df $= 1$, $P = 0.94$; early-molting males: $n = 15$, residual mass 0.15 ± 0.34; late-molting males: $n = 27$, residual mass 0.06 ± 0.45). Among the males we recaptured in subsequent seasons, we observed a significant increase in mass between the nonbreeding and breeding seasons (paired $t_{33} = -5.94$, $P < 0.0001$; nonbreeding-season mass 6.59 ± 0.38, breeding-season mass 6.94 ± 0.37), including males that were brown (i.e.

TABLE 1. Total and back molt scores for early- and late-molting male Red-backed Fairywrens, by season, in Northern Territory, Australia, 2012–2014. Maximum possible molt score was 18 for total molt and 3 for back molt (see text for details). In the nonbreeding season, early-molting males were completing prenuptial molt from dull to red–black plumage, whereas late-molting males were replacing dull feathers with dull feathers, which we interpret as adventitious molt between the postnuptial and prenuptial molts (or potentially the tail end of the postnuptial molt). In the breeding season, molt by early-molting males during the breeding season represents adventitious molt (replacement of ornamented red–black feathers with red–black feathers); we were unable to determine whether late-molting males were completing the prenuptial molt or exhibiting adventitious molt during this period.

	Nonbreeding season			Breeding season		
	Total molt	Back molt	n	Total molt	Back molt	n
Early-molting males	4.9 ± 3.6	1.4 ± 1.0	37	2.2 ± 1.2	0.7 ± 0.5	14
Late-molting males	1.5 ± 2.2	0.3 ± 0.5	20	1.2 ± 1.6	0.3 ± 0.5	27

late-molting males) and red–black (i.e. early-molting males) during the nonbreeding season.

DISCUSSION

Our results suggest that male Red-backed Fairywrens that develop a plumage-based signal relatively early in the nonbreeding season are able to subsequently modify this signal to attain redder hues during the breeding season. Individual males appeared to achieve this dynamic modification of back coloration via adventitious back molt months after prenuptial molt had been completed. Thus, adventitious molt may allow males to avoid a potential trade-off between signal timing (i.e. early vs. late) and quality (i.e. plumage hue), both of which are thought to be honest signals of quality in this species.

Before discussing these results, we should address potential caveats associated with our study. First, given that the study period was short and that very little breeding occurred on the site during it, we were unable to determine the age or reproductive success of the birds. Hence, the results characterize adventitious molt and signal expression but do not directly address the degree to which this phenomenon may be associated with differences in male age or fitness. Second, the study is based on a relatively small number of individuals; follow-up studies with larger sample sizes would be useful to better determine the generality of the patterns presented here. Third, the study is correlational rather than experimental, which raises the possibility that mechanisms other than adventitious molt may have driven the observed patterns of plumage change. Notably, it is possible that plumage fading, rather than adventitious molt, could cause an increase in plumage hue or brightness, but (to our knowledge) there is no evidence that this occurs in birds. Instead, the relevant studies have found that plumage-signal values decrease over time (e.g., Örnborg et al. 2002, McGraw and Hill 2004, Figuerola and Senar 2005, Evans et al. 2012). Additionally, our reflectance spectra had similar shape across seasons, in contrast to the shift in ultraviolet reflectance associated with fading that was reported by Evans et al. (2012). Also, if fading caused a change in hue, we would expect a uniform change across individuals rather than convergence of early-molting males to a similar hue (below). With these caveats in mind, we'll now discuss the interpretation and potential implications of our findings.

We consider the most parsimonious explanation for the results we obtained to be that adventitious molt allows male Red-backed Fairywrens to modify plumage coloration outside of regular molt periods. The function of adventitious molt has traditionally been framed in terms of replacement of accidentally lost feathers (Ralph et al. 1993). On the basis of the findings presented here, we suggest that the ability to develop new feathers outside of normal molt periods may be adaptive in the context of social or sexual signaling, and may enable individuals to honestly signal quality. The ability to modify plumage-based signals might benefit signalers by allowing them to signal current physiological condition or social status, or both, which may have changed since the molt period. Adventitious molt may also be important in group-living species, in which changes in social or reproductive status can influence optimal behavioral strategies and signals, as appears to be the case in Red-backed Fairywrens (Webster et al. 2010, Karubian et al. 2011). The ability to update signal values outside of established molt periods may be particularly advantageous in unpredictable ecological environments such as the seasonal tropics inhabited by Red-backed Fairywrens, where the onset of breeding can vary by months across different years (Hau 2001, Webster et al. 2010). It is also possible that adventitious molt is adaptive for plumage maintenance in unpredictable or variable environments (e.g., Zann 1985), with enhanced signal quality as a byproduct. The fact that some males exhibited adventitious molt on body parts other than the back, and across seasons, is consistent with the latter hypothesis.

Adventitious molt after the onset of wet-season rains (often associated with the start of breeding; Webster et al. 2010) may allow early-molting male Red-backed Fairywrens to take advantage of increased prey availability (compared to when they completed their initial prenuptial molt) and to honestly signal their current quality in regrown feathers. A counterexample can be found in Northern Flickers (*Colaptes auratus*), a species in which adventitious molt during less favorable periods may result in less elaborate plumage coloration (Wiebe and Bortolotti 2002), the inverse of the pattern we have documented in Red-backed Fairywrens. The increase in mass we observed within individuals between the nonbreeding and breeding seasons is consistent with a change in potential resources or investment of resources and is likely due to seasonal changes in food availability corresponding with rainfall (Hau 2001). The tendency for early-molting individuals to be in better condition, despite presumed costs associated with signal development, corresponds with other *Malurus* studies (Mulder and Magrath 1994, Peters 2000) and suggests that these males may be honestly signaling superior condition by displaying ornamentation relatively early, and/or may have enhanced access to resources through status signaling (Rohwer 1975). The lack of a correlation between condition and molt period in the breeding season is not necessarily surprising, given that individuals of varying condition may have relatively similar degrees of investment in signal quality or may face different costs in relation to molt date (Karubian et al.

2008), or because of higher levels of available prey during the breeding season.

Both signal timing and coloration are associated with reproductive success in *Malurus* (Dunn and Cockburn 1999, Karubian 2002, Webster et al. 2008, Baldassarre and Webster 2013). Molt timing may convey male quality because of the costs associated with molt (King 1980) and/or the social or survival costs of displaying nuptial plumage (Rubenstein and Hauber 2008). Red coloration of the back in Red-backed Fairywrens is produced by carotenoids (Rowe et al. 2008), which are thought to function as an honest signal across taxa because of costs associated with obtaining, metabolizing, and expressing them (Olson and Owens 1998) and potential trade-offs with immunocompetence, parasite resistance, and general health (Hill and Montgomerie 1994, Dufva and Allander 1995, Thompson et al. 1997, Linville et al. 1998). Male Red-backed Fairywrens that were experimentally reddened had higher extrapair reproductive success than control males, indicating that redder hues are preferred by females, although natural variation in redness in the same population was not correlated with reproductive success (Baldassarre and Webster 2013).

Early-molting male Red-backed Fairywrens converged upon a more red hue during the breeding season, which is consistent with the idea that timing of signal development and signal quality are both honest signals. More specifically, early-molting males that achieved more red hues during the nonbreeding season maintained these levels, whereas early-molting individuals that were initially less red increased in hue, resulting in all early-molting males being very red during the breeding season. This finding suggests that adventitious molt allows early-molting males to approach an optimal trait value (Johnstone 1997) or perhaps a physiological limit (McGraw 2006). This pattern—variable plumage during the nonbreeding season converging to similar red hues during the breeding season—may represent a "regression effect," a relatively common statistical artifact when comparing repeated trait measurements with imperfect correlation that can lead biologists to make unfounded interpretations about biological importance (Kelly and Price 2005). However, a possible pattern of regression to the mean among these males does not speak to the basic point of the present study, which is that the birds appeared to increase plumage hue across seasons via adventitious molt (when we would expect no change or a decrease if plumage were static) and that these males (as a group, not just the ones that enhanced their hue the most) were then more red than later-molting birds.

Adventitious molt is not widely noted in the literature but may be more common than is currently appreciated, because documenting it requires recapturing the same individuals multiple times within a year, and most studies documenting molt have been focused on the annual molt cycle (e.g., Johnson et al. 2012). The present results suggest that birds may use adventitious molt for dynamic modification of signals outside of typical molt periods, highlighting the need for increased attention to adventitious molt as a potential mechanism for modifying sexual or social signals.

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