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Article

Wildfire affects expression of male sexual plumage through suppressed testosterone circulation in a tropical songbird

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Natural disturbances like drought and wildfires are expected to increase in prevalence, so understanding how organisms are affected is a key goal for conservationists and biologists alike. While many studies have illustrated long-term effects of perturbations on survival and reproduction, little is known of short-term effects to physiology and sexual signal expression. Ornamental traits have been proposed as reliable indicators of environmental health, yet studies are lacking in the context of natural disturbances. Here we present short-term (7–65 days) responses of male red-backed fairywrens *Malurus melanocephalus* to wildfire near the onset of the typical breeding season. Young males of this species are characterized by plastic expression of sexual plumage phenotypes depending on circulating testosterone and body condition. Using two populations with fairywren captures before and after separate wildfires we illustrate that wildfire suppressed molt into ornamented plumage. Neither baseline plasma corticosterone or furcular fat stores were affected by fire. However, fire seemed to interfere with the temporal increase in plasma testosterone during the pre-breeding season, leading to a lower proportion of males molting into ornamented plumage. Collectively, these findings suggest that wildfires inhibit or greatly delay acquisition of ornamentation in males through enduring suppression of testosterone circulation.

Keywords: disturbance, hormones, ornamentation, wildfire

Introduction

As climate change increases the prevalence of drought (Dai 2013, Cook et al. 2014, Trenberth et al. 2014), wildfires are expected to increase in frequency and severity (Flannigan et al. 2013). Understanding the myriad effects wildfires produce for native fauna is thus of utmost importance. Many factors including seasonal timing and interval of fires, as well as whether species evolved in habitats that historically burn, dictate how organisms are affected by wildfire (Hobson and Schieck 1999, Woinarski 1999, Cox and Widener 2008, Stojanovic et al. 2016). Tropical birds are especially vulnerable to the threat of climate change (reviewed by Şekercioğlu et al. 2012), yet few studies have explored how wildfires affect tropical species outside of Amazonian



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forests (Barlow et al. 2002, 2006, Barlow and Peres 2004a, b, Mestre et al. 2013, Lemos Da Silva et al. 2015). Determining how tropical species respond to environmental disturbances can establish which components of phenology are fixed and which are plastic, which has implications for conservation and improves our understanding of life history evolution. For instance, a recent analysis of drought impacts on breeding bird communities in the old and new world tropics revealed that shorter-lived tropical species suffer from decreased survival and continue to breed while longer-lived tropical species delay breeding and thus buffer against detrimental effects to survival (Martin and Mouton 2020). Illuminating the mechanisms underlying the tradeoff between reproduction and survival is thus integral to understanding how organisms respond to natural disturbances such as wildfires.

Testosterone mediates the tradeoff between reproduction and survival in many bird species as it is essential for spermatogenesis and expression of mating behavior, but elevation of testosterone can come with a host of detrimental effects to survival via endogenous costs including immunosuppression and external costs like increased predation and injury (Cawthorn et al. 1998, Peters 2000, Wingfield et al. 2001, Roberts et al. 2004, Reed et al. 2006, McGlothlin et al. 2010, Foo et al. 2017). The expression of secondary sexual characters like plumage ornamentation are stimulated by testosterone in males of many bird species (reviewed by Kimball and Ligon 1999, Hau 2007), and these ornaments can impose costs in the form of increased predation (Møller and Nielsen 1997, Zuk and Kolluru 1998, Candolin 2003, Godin and McDonough 2003, Johnson and Candolin 2017; but see Cain et al. 2019). Signals that are mediated by elevated testosterone can thus impose costs from both increased levels of the hormone and expression of the signal itself. Testosterone-mediated ornaments are often condition dependent (Bókony et al. 2008, McGlothlin et al. 2008), and thus these ornaments represent a potentially fruitful way to assess individual health in response to fluctuating environmental conditions (Hill 1995). Most studies of the effect of perturbations on ornamental traits have been centered around degradation in response to pollution, most notably oil spills and mercury exposure, illustrating the potential for these signals to act as beacons for environmental health (Perez et al. 2010, Pérez et al. 2010, Jacques et al. 2019, Peneaux et al. 2021, Spickler et al. 2020). Determining whether natural disturbances like fire influence signaling traits and the physiological mechanisms underlying these effects, holds promise for informing conservation by revealing the limits of phenotypic plasticity in disturbance-adapted organisms.

Fairywrens (family Maluridae) have emerged as model organisms for studies of the causes and consequences of male ornamentation. Young males of some fairywren species undergo a pre-alternate molt prior to the breeding season in which some remain in drab female-like plumage whereas others molt into a showy ornamental plumage (Peters 2007, Lindsay et al. 2011). In red-backed fairywrens *Malurus melanocephalus*, males adopting the sexually-selected ornamented phenotype circulate significantly higher

testosterone than unornamented males (Lindsay et al. 2009) and testosterone-implantation induces molt into ornamental plumage (Lindsay et al. 2011, Khalil et al. 2020). Molt into ornamental plumage among young males seems to be condition-dependent, as experimentally-reduced condition caused second year males to remain unornamented for their first breeding season (Barron et al. 2013). Interestingly, young males in better condition acquired ornamental plumage absent of significantly greater testosterone circulation (Barron et al. 2013), highlighting the need for additional studies to disentangle these physiological regulators and their roles in phenotypic integration. In addition, resolving how extrinsic factors, including natural disturbances, influence expression of alternate phenotypes in this system could provide a useful test of condition-mediated signaling and its hormonal control in this system.

Here we capitalize on naturally occurring wildfires to determine effects on ornament expression of male red-backed fairywrens in tropical northeast Queensland. We first determine whether a major wildfire prior to the typical breeding season in one of our long-term study populations affects molt into ornamental plumage and breeding readiness. Next, we test whether known physiological mediators of ornamentation in this system, namely testosterone and fat stores (Lindsay et al. 2011, Barron et al. 2013), decrease in response to fire. In addition, we determine whether corticosterone, a glucocorticoid hormone often associated with avian response to environmental stressors (Wingfield et al. 1998, 2017a, Lucas et al. 2006, Bize et al. 2010, Busch et al. 2010, Wingfield 2013) is elevated in response to fire. Finally, we assess which prospective physiological mediators (fat, testosterone and corticosterone) are predictive of alternate phenotype expression in response to a major environmental disturbance.

Material and methods

Study system and timeline

The red-backed fairywren *Malurus melanocephalus* is a small, sedentary, insectivore of Australian savannas. Breeding occurs seasonally, with onset varying from year to year depending on monsoon rains (Webster et al. 2010). Males in their second year adopt one of two plumage phenotypes for breeding: brown (hereafter: unornamented) or black-and-red (hereafter: ornamented), and in rarer cases an intermediate mix of the two (Karubian et al. 2008, Webster et al. 2008). For the present study we employed plumage data from three separate years at our long-term color-banded ‘Donkey Farm’ population (145°23’E, 17°23’S; 250 ha), and one year at a separate newly-banded ‘Sandy Creek’ population (145°23’E, 17°28’S; 220 ha), both near Herberton, QLD, Australia. On 12 October 2012 a large wildfire burned our Donkey Farm field site when fairywrens were beginning to form pairs prior to the typical breeding season in this population (full study timeline: Supporting Information). The Donkey Farm fire burned the entire understory at our study site, leaving only

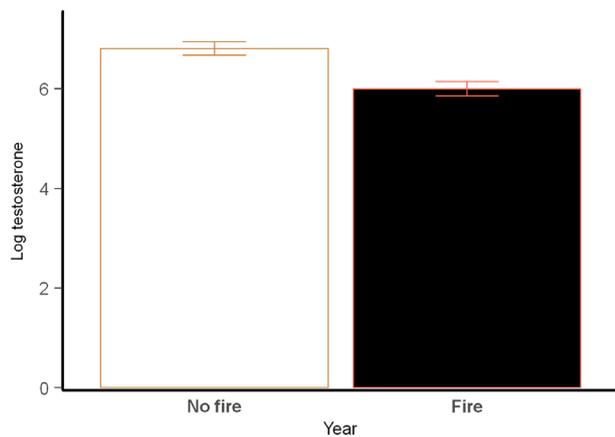


Figure 1. Mean \pm standard error log transformed plasma testosterone by year. Pooled samples from years lacking fire ('No fire') showed elevated testosterone in males relative to date-matched males sampled after wildfire ('Fire') at our Donkey Farm study population ($p=0.018$).

a donkey paddock with short (< 0.75 m) grass that fairywrens typically used sparingly during the non-breeding season. Following this fire, we established nearby (~ 4 km) Sandy Creek as a control site for determining acute effects of wildfire on Fairywren physiology. On 24 November 2012 this site was also burned by a wildfire, providing natural replication of our experiment. The Sandy Creek fire also burned the vast majority of the understory at the site, but left several unburned patches smaller than a typical fairywren breeding territory, and a horse paddock that was unoccupied by fairywrens prior to the fire. Fairywrens in both populations were seen flocking at unusually high numbers in unburned patches, returning to territories at times to forage in the unburned *Eucalyptus* canopy and near unburned or regenerating *Lantana* shrubs. Individuals were caught at both populations in unburned grass and within recently burned habitat near *Lantana* shrubs and short *Eucalyptus* that survived fire. Both fires burned the sites in < 24 hours, and we resumed sampling of Fairywrens 13 days after the Donkey Farm fire and seven days after the Sandy Creek fire (Supporting Information).

Plumage assessment

Percent of ornamental black-and-red plumage (0–100) was assessed both at each capture of males and through continuous sightings of color-banded individuals from August to early January each year. Males with $< 33\%$ ornamented plumage were assigned an 'unornamented' final phenotype, whereas males with $> 66\%$ ornamented plumage were assigned the 'ornamented' phenotype. Males with intermediate scores (33–66% ornamented plumage; $n=2$) were excluded from analyses. We compared males exposed to fire in 2012 to previous seasons at our long-term Donkey Farm study site in which ornamentation was assessed continuously in males and no manipulations were conducted. Two previous field seasons were employed for this purpose: 2009, which was characterized by drought and minimal breeding but no fire, and 2011,

which experienced a typical monsoon and breeding season for this population. This approach allowed us to assess how fire affected acquisition of ornamental plumage relative to both a relatively dry year with minimal breeding and a year with more typical rainfall and breeding.

Field measurements

Red-backed fairywrens were caught in mist nets by flushing or in rare cases, with brief use of playback of in-hand distress calls. We assessed size of furcular fat stores as a measure of condition by half increments from 0 to 3; 0 reflecting no fat and three representing fat protruding beyond the furcular hollow (Barron et al. 2013). Blood was taken immediately upon extraction of the bird from mist nets via the jugular vein, then samples were placed in a small cooler for the remainder of the day. Upon return from the field, we spun blood samples in a centrifuge to separate plasma for hormone analysis. Plasma was stored in liquid nitrogen until shipment to the US where it was stored in a -20° freezer until use in hormone assays. Red blood cells were transferred to 400 μ l of lysis buffer and refrigerated until use in genetic assays.

Testosterone and corticosterone assay

We used a previously validated radioimmunoassay to measure both testosterone and corticosterone simultaneously for 13–50 μ l plasma samples following Lindsay et al. (2011) and Barron et al. (2013). Briefly, we used tritium-labeled testosterone (Perkin Elmer Life Sciences NET-553) with a testosterone antibody (Wien Laboratories T-3003) that cross-reacts with other steroids (100% reactivity with testosterone, 60% with 5α -DHT, 5% aldosterone, $< 15\%$ with other androgens and less than 0.05% with 17β -estradiol and all other steroids), and tritium-labeled corticosterone with a corticosterone antibody (Esoterix Endocrinology B3-163). Samples were randomly assigned to seven separate assays; the between-assay coefficient of variation was 12.96% for testosterone and 14.19% for corticosterone (calculated according to Chard 1995). The detection limit for testosterone was 276.32 pg ml^{-1} , and corticosterone was 0.81 ng ml^{-1} . We back-calculated undetectable testosterone levels from minimal detectable levels (1.95 pg tube^{-1}); all samples had detectable corticosterone.

Sexing methods

Because unornamented males cannot be distinguished from females morphologically, we determined sex genetically. We extracted DNA from blood samples using the Omega Bio-Tek EZ 96 Total DNA/RNA Isolation Kit[®] and amplified an intron within the CHD gene using the primer pair 1237L/1272H (Kahn et al. 1998). Briefly, we PCR-amplified each sample following the protocol of Varian-Ramos et al. (2010), and visualized the PCR products via electrophoresis on a 2% agarose gel. We ran samples alongside a positive and negative control, and visually inspected the gels. We considered individuals with a single band to be males, and individuals with two bands to be females.

Data analysis

All analyses were conducted in R (<www.r-project.org>) studio ver. 1.2.5019 using linear regressions in base R and mixed models in package lme4 (Bates et al. 2015). We used backward stepwise selection following Wang et al. (2008) throughout: the full set of candidate predictors was initially included in each model and any variable with $p \geq 0.4$ was removed.

Effect of wildfire on phenotype and cloacal protuberance expression

We filtered data from years at our Donkey Farm study population that differed in environmental conditions and were otherwise manipulated (2009, 2011 and 2012) to analyze males who were of known age. Because we were interested in determining whether fire affected typical phenology of ornament acquisition, we only analyzed males who were observed after 1 December each year, as males assume their final plumage phenotype before this date in our study population (Barron pers. comm.). We used a binomial generalized linear model for analysis of all known age males adopting ornamented or unornamented phenotypes. The initial model contained age, date of final plumage observation, year (dry, fire, wet year) and the interaction of year and age as fixed predictors. We used post-hoc Tukey comparisons for significant predictors included in the final model.

We used the same dataset employed for final phenotype analysis to determine how years with variable environmental conditions differed in cloacal protuberance development. The dataset was filtered to only include males captured each year after the day of year the 2012 Donkey Farm occurred. We analyzed a binary presence/absence cloacal protuberance variable to assess how varying conditions influenced breeding readiness in males. Year (dry, wet, fire) and day of year were included as fixed effects in the initial model, and Bird ID was included as a random effect to account for repeated measures. We did not include age in models, as filtering this dataset by known age males reduced sample sizes enough to preclude comparisons across years. Post-hoc Tukey comparisons were employed following detection of a significant effect.

Effect of wildfire on physiology

To determine whether fire affected temporal patterns of prospective physiological mediators of phenotype expression, we used linear mixed models comparing the fire year to previous years lacking fire. All captures from previous years were pooled into one 'non-fire' sample set; we use this approach due to limited physiological sampling in years lacking experimental manipulations. All years were filtered to exclude days of the year after the 2012 Donkey Farm fire date. To avoid the confound of potential geographic variation across populations we only analyzed physiological mediators from the long-term Donkey Farm study population. Furcular fat stores and testosterone were log transformed, and corticosterone levels were square root transformed to improve normality. Net-to-bleed time and time bled were included as fixed effects in all initial hormone models and Bird ID was included to account for repeated measures for fat and testosterone models. Each response variable was analyzed with candidate mixed models

initially containing day of year, fire versus no fire and the interaction of day of year and fire versus no fire as predictors.

To assess short-term physiological response to fire, we pooled capture data from the Donkey Farm and Sandy Creek populations, who were exposed to separate wildfires 33 days apart, which resulted in natural replication of our experiment. Because we were interested in how short-term physiological response to fire might affect the phenotypes males adopt, we filtered both populations to only include males who were initially observed as unornamented and were thus able to mount a plastic response to environmental conditions. We used this dataset to determine how furcular fat stores, and plasma testosterone and corticosterone levels were affected by fire among males who were sampled within 30 days before and after onset of fire. Furcular fat stores and testosterone were log transformed, and corticosterone levels were square root transformed as above. We used the same model approach outlined above for the temporal analysis, with population added as an additional predictor. Net-to-bleed time and time bled were included as fixed effects in all initial hormone models as per above temporal analyses. Finally, we assessed whether circulating testosterone and corticosterone were correlated in this dataset with a linear regression.

Effects of wildfire on prospective phenotypic mediators

We assessed what prospective mediators explain variation in male phenotype following exposure to fire. We compiled post-fire data from both populations exposed to wildfire in 2012 and selected males who were first observed as brown and were actively molting at the time of recapture. Consistent with final phenotype analysis, we only analyzed males observed after 1st December as males typically acquire their final phenotype by that time across years. The initial model included fat stores, testosterone, corticosterone, date and population as fixed predictors, with Bird ID as a random effect due to repeated measures. Furcular fat store values were log-transformed, and for both hormones we analyzed residuals from models that included time of day bled, capture to bleed time and day of year as fixed effects according to Vernasco et al. (2020).

Ethics statement

Capture and sampling for this study was done in a safe and humane manner according to procedures approved by the Institutional Animal Care and Use Committees at Washington State University (approval no. 03653-007), Cornell University (2009-0105), the James Cook University Animal Ethics Committee (A1691) and the Queensland Government Environmental Protection Agency.

Results

Effect of wildfire on phenotype and cloacal protuberance expression

Final phenotype expression (ornamented versus unornamented; Table 1) differed by year (dry, wet and fire year; $p < 0.001$) and age ($p < 0.001$), with the interaction of year and

age and day of year as non-significant effects ($p=0.243$ and $p=0.237$, respectively). Post-hoc Tukey tests revealed that males were significantly less ornamented in the fire year compared to the dry year (i.e. drought conditions; $p=0.002$) and wet year (i.e. typical monsoon conditions; $p=0.003$) while final ornamentation did not differ between the wet and dry year ($p=0.160$; full model terms in Supporting information).

Cloacal protuberances also varied by year (full model terms in Table 2; $p < 0.001$), with the fire and dry years showing significantly diminished cloacal protuberance development (Supporting information; fire versus wet: $p < 0.001$; dry versus wet: 0.011). The fire and dry year did not differ in development of cloacal protuberances ($p=0.363$). Day of year had a positive relationship with cloacal protuberance development ($p=0.035$).

Effect of wildfire on physiology

We assessed whether fat stores or circulating hormones differed in the fire year relative to previous years lacking fire (full model terms in Table 2). Day of year was the only significant predictor of furcular fat stores ($p=0.009$), while year and the interaction between year and day of year included as marginally non-significant effects ($p=0.078$ and $p=0.121$, respectively). Day of year showed a positive relationship with furcular fat stores (Supporting information). The fire year was characterized by lower mean testosterone than years lacking fire ($p=0.018$; Fig. 1). Day of year and the interaction between year and day of year were included as non-significant effects in the final model ($p=0.183$ and $p=0.299$, respectively). Square-root transformed corticosterone did not differ by year ($p=0.283$), but day of year was a significant predictor ($p=0.020$), as was net-to-bleed time ($p < 0.001$) and time bled ($p < 0.001$). Day of year and time bled had a positive relationship with corticosterone, while net-to-bleed time had a negative effect.

To determine whether fire produced immediate effects on physiological mediators of ornament expression, we compared samples taken within 30 days prior to and 30 days post fire from males starting the year unornamented in both populations exposed to wildfire (full model terms in Table 3). The final model for log transformed furcular fat stores included the interaction between pre/post-fire and population as a significant effect ($p=0.025$). Log transformed fat stores increased

following fire at the Donkey Farm population (mean: 0.635 pre and 0.741 post) whereas fat decreased following fire at Sandy Creek (mean: 0.781 pre and 0.635 post). Log transformed circulating testosterone was not predicted by sampling pre versus post-fire ($p=0.131$), whereas populations exhibited a marginally non-significant difference ($p=0.060$). Day of year and net-to-bleed time exhibited had positive relationships with circulating testosterone ($p=0.037$ and $p=0.041$, respectively), with time bled included in the final model as a non-significant effect ($p=0.161$). The final model for square-root transformed corticosterone include population as a marginally non-significant predictor ($p=0.059$), with net-to-bleed time and day of year exhibiting a positive relationship with corticosterone ($p \leq 0.001$ and $p=0.004$, respectively). There was no correlation between circulating testosterone and corticosterone residuals ($R^2=0.0085$, $F_{1,119}=1.01$, $p=0.32$; Supporting information).

Effects of wildfire on prospective phenotypic mediators

We tested which components of physiology explained the plumage phenotype (unornamented versus ornamented) males were actively molting into at both populations exposed to fire (full model terms in Supporting information). Testosterone residuals were a significant predictor ($p=0.004$), which were higher in males molting into ornamented plumage.

Discussion

We found that wildfire affected reproductive phenotype expression in male red-backed fairywrens by decreasing the proportion of males molting into the sexually-selected, ornamented red/black plumage (Table 1). Circulating testosterone, which is known to facilitate molt into ornamented plumage in this system (Lindsay et al. 2009, 2011, 2016, Khalil et al. 2020) was lower during the fire year relative to previous years without fire (Fig. 1). The importance of testosterone for ornament production in this species is supported by the fact that males molting into ornamented plumage exhibited higher plasma testosterone levels than did males molting into unornamented plumage following fire (Fig. 2). However, neither testosterone, corticosterone, nor furcular fat stores changed shortly (< 30 days) after fire, indicating that these physiological mediators aren't especially sensitive to this type of disturbance in the short-term.

The current study tested how previously identified physiological mediators of ornament expression were affected by wildfire. Previous correlational (Lindsay et al. 2009) and manipulative studies of testosterone (Lindsay et al. 2011, Khalil et al. 2020) and body condition (Barron et al. 2013) in young males established both as mediators of alternate plumage phenotype expression. Specifically, testosterone levels were higher in males molting into red/black ornamented

Table 1. Contingency table for final phenotype comparison across years varying in environmental conditions and across age classes.

	Final phenotype	
	Unornamented	Ornamented
Year		
Dry	1	23
Wet	37	47
Fire	17	23
Age		
2nd year	51	4
3rd year	9	27
> 3rd year	1	56

Table 2. Summary statistics for physiological comparison of males during fire year relative to previous years lacking fire. Fat stores, testosterone and corticosterone were analyzed in separate models. Significant effects ($\alpha < 0.05$) are bolded; predictors removed from final model depicted with italics.

Fat stores						
Fixed effects	Estimate	SE	Sum of squares	df	F value	p
Year (fire versus no fire)	0.186	0.105	0.281	1	3.127	0.078
Day of year	0.008	0.002	0.623	1	6.932	0.009
Year \times Day of year	-0.006	0.004	0.218	1	2.426	0.121
Random effects	SD					
Bird ID	< 0.001					
Testosterone						
Fixed effects	Estimate	SE	Sum of squares	df	F value	p
Year (fire versus no fire)	-1.472	0.607	1.647	1	5.879	0.018
Day of year	-0.021	0.014	0.508	1	1.813	0.183
Year \times Day of year	0.018	0.017	0.308	1	1.098	0.299
<i>Net-to-bleed time</i>	<i>0.031</i>	<i>0.062</i>	<i>0.057</i>	<i>1</i>	<i>0.246</i>	<i>0.622</i>
<i>Time bled</i>	< 0.001	< 0.001	<i>0.060</i>	<i>1</i>	<i>0.257</i>	<i>0.614</i>
Random effects	SD					
Bird ID	0.687					
Corticosterone						
Fixed effects	Estimate	SE	Sum of squares	df	F value	p
Year (fire versus no fire)	0.31	0.344	0.928	1	1.456	0.236
Day of year	0.002	0.012	3.827	1	6.006	0.020
<i>Year \times Day of year</i>	<i>0.011</i>	<i>0.032</i>	<i>0.072</i>	<i>1</i>	<i>0.109</i>	<i>0.743</i>
Net-to-bleed time	0.699	0.119	22.094	1	34.666	< 0.001
Time bled	-0.002	0.001	10.170	1	15.957	< 0.001

Table 3. Model parameters for comparison of fat stores, log-transformed testosterone and square-root transformed corticosterone for males at two populations < 30 days prior to and < 30 days after fire. Significant effects ($\alpha < 0.05$) are bolded; predictors removed from the final model depicted with italics.

Fat stores						
Fixed effects	Estimate	SE	Sum of squares	df	F value	p
Fire (pre versus post)	0.107	0.078	0.006	1	0.114	0.737
Population	0.146	0.067	0.007	1	0.143	0.707
Fire \times Population	-0.250	0.108	0.277	1	5.314	0.025
<i>Day of year</i>	<i>0.003</i>	<i>0.003</i>	<i>0.023</i>	<i>1</i>	<i>0.434</i>	<i>0.512</i>
Random effects	SD					
Bird ID	0.055					
Testosterone						
Fixed effects	Estimate	SE	Sum of squares	df	F value	p
Fire (pre versus post)	-0.778	0.501	0.356	1	2.411	0.131
Population	-1.105	0.573	0.549	1	3.719	0.061
<i>Fire \times Population</i>	<i>-0.219</i>	<i>0.34</i>	<i>0.065</i>	<i>1</i>	<i>0.417</i>	<i>0.531</i>
Day of year	0.035	0.016	0.692	1	4.683	0.037
Net-to-bleed time	0.255	0.118	0.693	1	4.688	0.041
Time bled	0.056	0.041	0.283	1	1.918	0.186
Random effects	SD					
Bird ID	0.748					
Corticosterone						
Fixed effects	Estimate	SE	Sum of squares	df	F value	p
<i>Fire (pre versus post)</i>	<i>-0.417</i>	<i>0.704</i>	<i>0.098</i>	<i>1</i>	<i>0.227</i>	<i>0.636</i>
Population	-0.618	0.319	1.698	1	3.754	0.059
<i>Fire \times Population</i>	<i>0.293</i>	<i>0.429</i>	<i>0.202</i>	<i>1</i>	<i>0.467</i>	<i>0.499</i>
Day of year	0.019	0.006	4.173	1	9.22	0.004
Net-to-bleed time	0.529	0.127	7.797	1	17.235	< 0.001
<i>Time bled</i>	<i>0.293</i>	<i>0.429</i>	<i>0.286</i>	<i>1</i>	<i>0.649</i>	<i>0.425</i>
Random effects	SD					
Bird ID	0.256					

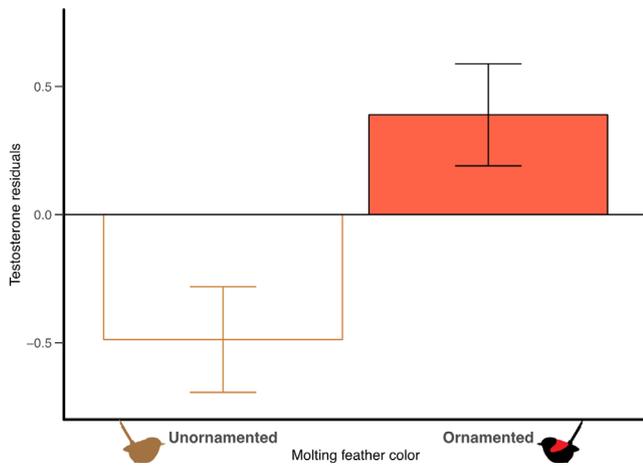


Figure 2. Mean \pm standard error testosterone residuals adjusting for capture parameters (time of day, net-to-bleed time) among males molting in exclusively ornamented (red/black) plumage versus unornamented (brown/white) plumage ($p=0.004$).

plumage compared to males that molted into cryptic brown, female-like plumage during both the pre-breeding and the reproductive period (Lindsay et al. 2009). In separate experiments, testosterone implants induced molt of ornamented plumage (Lindsay et al. 2011, 2016, Khalil et al. 2020). However, experimentally-enhanced body condition resulted in more ornamentation without an associated increase in circulating testosterone (Barron et al. 2013). Adding further complexity to the relationship between testosterone and ornamentation in this system, older, early molting males seem to acquire ornamented plumage without elevating circulating testosterone (Lantz et al. 2017). Results from the present study lend further support for testosterone facilitating molt into ornamented plumage. Lower testosterone during the fire year relative to previous years at our long-term Donkey Farm study population suggest that fire inhibited the seasonal elevation of testosterone that typically occurs during this period as males acquire breeding plumage (Lindsay et al. 2009). Testosterone was predictive of the phenotype males were molting into following fire, and males molting in ornamental plumage had higher plasma testosterone than males molting in unornamented feathers (Fig. 2). Collectively, our testosterone and ornamentation results indicate that the diminished ornamentation seen during that year (Fig. 2) is at least partially the result of suppressed testosterone circulation.

Glucocorticoids have been proposed as mediators of the tradeoff between survival and reproduction in vertebrates (Breuner et al. 2008, Bonier et al. 2009, Almasi et al. 2013, Crespi et al. 2013). Elevated corticosterone, which is the primary avian glucocorticoid, can initiate an emergency life history stage to flee from a natural disturbance, thus interrupting typical phenology (Wingfield et al. 1998, Wingfield and Kitaysky 2002). Many studies of bird species have revealed that corticosterone is responsive to climatic events, and can mediate abandonment of breeding territories when conditions deteriorate (Astheimer et al. 1995, Wingfield

and Kitaysky 2002, Lynn et al. 2003, Wingfield 2013, Krause et al. 2016, Wingfield et al. 2017b). Additionally, one way in which baseline glucocorticoids are thought to mediate the tradeoff between survival and mating is through antagonistic effects on testosterone (Stanczyk et al. 1985, McGuire et al. 2013). In our study, corticosterone was not elevated either relative to previous years lacking fire or in the short-term pre fire versus post fire comparison. Our post fire sampling window corresponded to a time when red-backed fairywrens left their territories to forage in remaining unburned patches of grassland at both populations, however we did not sample males until several days after they left territories, thus precluding our ability to detect a potential corticosterone-mediated emergency life history stage. In addition, our limited sampling window could have kept us from detecting diminished fat stores following fire. Furcular fat stores did not appear to be sensitive to fire in either the comparison to previous study years or in the paired pre fire versus post fire analysis, suggesting that males did not suffer from diminished body condition in response to fire. Finally, we did not find a relationship between corticosterone and testosterone in our dataset (Supporting information), thus adding to a growing list of studies in birds suggesting an absence of antagonism between these two hormones (Davies et al. 2016, Deviche et al. 2017, Abolins-Abols et al. 2018).

Species that evolved in unpredictable environments characterized by regular natural disturbance (e.g. drought, fires) might reasonably be expected to mount an adaptive response to perturbation. Australian tropical savannas are characterized by a history of frequent wildfires, but many species inhabiting these areas are in decline and are negatively-affected by fire (Franklin et al. 2005, Woinarski and Legge 2013). Previous studies of red-backed fairywrens in this context have shown that wildfires lead to decreased reproductive output (Murphy et al. 2010), increased social connectivity (Lantz and Karubian 2017) and shifting habitat use (Sommer et al. 2018) in this species. Although our study did not focus on these characteristics, our observations of red-backed fairywrens support these findings as wildfires forced individuals to leave breeding territories and flock in unusual numbers in the few remaining unburned areas at both study sites (Boersma, pers. obs.). A companion study to ours found reduced dawn singing following wildfire, indicative of a reduction in behavior associated with breeding (Mathers-Winn et al. 2018). We found just one active nest during the study period, which extended through the typical breeding season at our long-term study site, so our findings are consistent with a major reduction or delay in breeding effort following wildfires (Boersma, pers. obs.) as previously reported in this species (Murphy et al. 2010). However, fewer males developed cloacal protuberances during both the fire year and dry year relative to a previous year characterized by more typical monsoon rain and breeding, whereas the fire and dry year did not differ (Supporting information). These results indicate that wildfire does not represent a greater disturbance to breeding than diminished seasonal rainfall. Interestingly, the fire year was an outlier in final phenotype analysis, as it differed both from the

wet and dry year in level of ornamentation. Taken together with the cloacal protuberance results, we conclude that wildfire prior to the typical breeding season interrupted molt into ornamentation, and sustained lack of rainfall precluded males from developing reproductive anatomy.

Conclusions

Wildfires affected young male red-backed fairywrens by suppressing or greatly delaying molt into ornamental breeding plumage and development of cloacal protuberances. Circulating testosterone was lower during the fire year and predictive of the phenotype males were molting into after exposure to fire, consistent with the previously established role for testosterone in production of ornamentation in this system. These results are consistent with this species acting to maximize survival through changes in testosterone when a natural disturbance destroys breeding territories. As the prevalence of wildfires increases, it is important to understand how and to what extent organisms can acutely cope to improve predictive models of response to climate change across diverse taxa. Most studies of response to wildfire have focused on broad and long-term effects to survival and reproduction. Further work is needed to determine how physiological mechanisms underlying the tradeoff between survival and reproduction are affected by fire and other natural disturbances, as presented here.

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Author contributions

Jordan Boersma: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Douglas Barron:** Conceptualization (supporting); Data curation (supporting); Methodology (equal); Project administration (supporting); Supervision (lead); Writing – review and editing (supporting). **Daniel Baldassarre:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **M. Webster:** Conceptualization (supporting); Funding acquisition (equal);

Methodology (supporting); Writing – review and editing (supporting). **H. Schwabl:** Conceptualization (supporting); Funding acquisition (equal); Methodology (supporting); Resources (lead); Supervision (supporting); Writing – review and editing (supporting).

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Data availability statement

All data and code used for this project are available from Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.tb2rbp00r>> (Boersma et al. 2021).

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