

Boersma, J., E. D. Enbody, J. Karubian, H. E. Watts and H. Schwabl. 2022. Drought disrupts year-round breeding readiness in a tropical songbird. *Avian Conservation and Ecology* 17(2):44. <https://doi.org/10.5751/ACE-2343-170244>
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Research Paper

Drought disrupts year-round breeding readiness in a tropical songbird

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ABSTRACT. Climate change is expected to increase the prevalence and severity of extreme weather events like drought. For many opportunistically breeding tropical bird species, precipitation serves as a primary cue for onset of breeding, and sustained drought can have major impacts on reproductive fitness. The physiological effects of drought are poorly understood, but understanding physiological responses can help resolve the mechanisms underlying effects of drought on population demography. We used physiological data collected on a year-round breeding New Guinea endemic passerine, the White-shouldered Fairywren (*Malurus alboscapulatus*), during years with persistent rainfall and during the 2015–2016 El Niño drought event to assess patterns of breeding readiness, body condition, and molt. Many males lost their cloacal protuberances, a sperm storage organ they typically maintain year-round, during the drought period. Body molt, which also occurs year-round in this species, was higher in males during the drought period. Using a sliding-window statistical model approach, we identified a critical precipitation window of 0–40 days prior to capture for cloacal protuberance volume and a window of 8–53 days for molt, with lower precipitation associated with smaller cloacal protuberances and greater molt. Plasma androgens were predictive of variation in male cloacal protuberance volume and molt, thus potentially mediating transitions between life-history stages in response to environmental conditions. Female molt, androgens, and male mass varied with photoperiod, with longer but decreasing day lengths characteristic of the austral summer associated with increasing molt and decreasing androgens. Collectively, our results indicate the potential for photoperiod to cue some life-history stages, whereas reduced rainfall impacts male but apparently not female reproductive physiology and readiness to breed. Improving our understanding of environmental regulation of life-history transitions in tropical taxa is essential for identifying which taxa are most at risk under a changing climate.

La sécheresse perturbe la préparation à la nidification tout au long de l'année chez un passereau tropical

RÉSUMÉ. On prévoit que les changements climatiques augmenteront la prévalence et la gravité des phénomènes météorologiques extrêmes tels que la sécheresse. Pour de nombreuses espèces d'oiseaux tropicaux qui nichent de façon opportuniste, les précipitations sont le principal indice du début de la nidification, et une sécheresse prolongée peut avoir des répercussions importantes sur la capacité de reproduction. Les effets physiologiques de la sécheresse sont mal connus, mais la compréhension des réponses physiologiques peut aider à résoudre les mécanismes sous-jacents aux effets de la sécheresse sur la démographie des populations. Nous avons utilisé les données physiologiques recueillies chez un passereau endémique de Nouvelle-Guinée se reproduisant toute l'année, le Mériion à épauettes (*Malurus alboscapulatus*), au cours d'années avec des précipitations persistantes et pendant l'évènement de sécheresse El Niño de 2015-2016, pour évaluer les tendances de préparation à la nidification, la condition corporelle et la mue. De nombreux mâles ont perdu leur protubérance cloacale – un organe de stockage du sperme qu'ils conservent généralement toute l'année – pendant la période de sécheresse. La mue corporelle, qui se produit également toute l'année chez cette espèce, était plus importante chez les mâles pendant la période de sécheresse. Au moyen d'une approche comportant un modèle statistique à fenêtre coulissante, nous avons identifié une fenêtre de précipitation critique de 0-40 jours avant la capture pour le volume de la protubérance cloacale et une fenêtre de 8-53 jours pour la mue, avec des précipitations plus faibles associées à des protubérances cloacales plus petites et une mue plus importante. Les androgènes plasmatiques étaient prédictifs de la variation du volume de la protubérance cloacale des mâles et de la mue, et pouvaient donc potentiellement réguler les transitions entre les stades du cycle annuel en réponse aux conditions environnementales. La mue des femelles, les androgènes et le poids des mâles variaient en fonction de la photopériode, les journées plus longues mais décroissantes caractéristiques de l'été austral étant associées à une augmentation de la mue et à une diminution des androgènes. Dans l'ensemble, nos résultats indiquent le potentiel de la photopériode pour signaler certains stades du cycle annuel, tandis que la réduction des précipitations a un impact sur la physiologie de la production des mâles, mais apparemment pas sur celle des femelles, et sur la préparation à la nidification. Il est essentiel que nous améliorions notre compréhension de la régulation environnementale des transitions du cycle biologique chez les taxons tropicaux pour identifier les taxons les plus menacés par les changements climatiques.

Key Words: androgens; brood patch; cloacal protuberance; condition; El Niño; molt; phenology; photoperiod; testosterone

INTRODUCTION

Extreme droughts are increasing globally as a result of climate change, especially in the tropics (Neelin et al. 2006, Dai 2013, Cook et al. 2014, Trenberth et al. 2014, Fu 2015). Determining how organisms respond to drier conditions has thus emerged as a key goal for both conservationists and ecologists (Rees et al. 2009, Albright et al. 2010, Brodie et al. 2012). Unlike most temperate zone inhabitants that rely on seasonal changes in photoperiod as a key phenological cue (Dawson et al. 2001, Wingfield 2005, Poissenot et al. 2021), for many tropical species variation in precipitation is used to time breeding (Moreau 1950, Boag and Grant 1984, Shine and Brown 2008, Skagen et al. 2018, Aranzamendi et al. 2019, Halali et al. 2021). Precipitation can serve as a reliable predictive cue of food availability, especially in insectivorous bird species (Poulin et al. 1992, McKinnon et al. 2015, Aranzamendi et al. 2019).

When precipitation is unpredictable, breeding typically occurs opportunistically and reproductive organs must either be maintained year-round or rapidly developed in response to favorable conditions (Hau 2001, Madelaire and Gomes 2016, Aranzamendi et al. 2019). In cases of highly seasonal rainfall, where there are distinct wet and dry seasons, photoperiod may cue timing of breeding despite little variation in day lengths in the tropics (Wikelski et al. 2000, Hau 2001, Hau et al. 2008a, Medeiros et al. 2016). Organisms that use photoperiod as a cue for life-history transitions can suffer from phenological mismatch as a result of climate change (Lof et al. 2012, Zimova et al. 2016, Pedersen et al. 2017). Given that predictability of rainfall in tropical regions is expected to continue declining (Chadwick et al. 2016), determining how tropical species respond to major changes in rainfall is important for establishing which organisms are resilient to climate change.

Drought can shape population trajectories as a major selection event when it affects access to ecological resources (Boag and Grant 1981). Comparative studies of tropical bird species have found severe declines in reproduction during drought periods (Brawn et al. 2017, Martin and Mouton 2020). For instance, Brawn et al. (2017) found that extended dry seasons caused annual recruitment to decrease in 15 of 20 species monitored, although only one of those 20 species suffered decreased survival, suggesting reduced breeding was responsible for declining populations during drought. In another comparative study, Martin and Mouton (2020) found that survival of short-lived tropical species declined during drought, whereas long-lived species were unaffected. This disparity was attributed to short-lived species continuing to breed during poor conditions whereas long-lived species suppressed breeding, therefore buffering against detrimental effects to survival. The paucity of studies of physiological responses to drought limit our understanding of the mechanisms by which drought impacts survival and reproduction (Angelier et al. 2011, McKinnon et al. 2015, Grant et al. 2017).

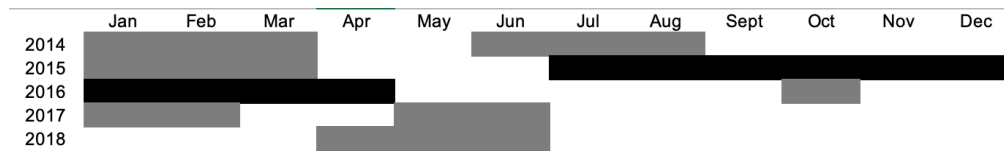
Hormones mediate expression of many morphological and behavioral traits (Ketterson and Nolan 1999, McGlothlin and Ketterson 2008, Kaiser et al. 2014, Lipshutz et al. 2019), and can change rapidly in response to changes in the abiotic (Breuner and Hahn 2003, Lynn et al. 2003, Gill et al. 2008, Hau et al. 2008b, Wingfield et al. 2017, 2018, Boersma et al. 2021) and social environment (Wingfield et al. 1990, Goymann et al. 2004, 2019,

Goymann 2009, Boersma et al. 2022). Gonadal steroid hormones, such as the androgen testosterone and its metabolites (i.e., estradiol), can mediate transitions between life-history stages (Cawthorn et al. 1998, Pärn et al. 2008, Wingfield 2008, Gerlach and Ketterson 2013, Rosvall 2013, Hau and Goymann 2015, de Jong et al. 2016). In males of many temperate bird species, circulating androgens show a seasonal increase at the onset of pair formation when males are initiating spermatogenesis and competing for mates and territories (Wingfield et al. 1990, Goymann 2009, Apfelbeck et al. 2017). The androgen testosterone mediates development of the cloacal protuberance, a bulbous swelling that stores sperm and aids insemination, in seasonally breeding temperate species (Hegner and Wingfield 1987, Schwabl and Farner 1989, Wingfield et al. 1990, Spinney et al. 2006). Comparatively less is known about how androgens are involved in the breeding condition of tropical species that generally experience more stable climates, where males either maintain or rapidly develop a cloacal protuberance to prepare for breeding (Aranzamendi et al. 2019, Enbody et al. 2019, Leitão et al. 2019).

Androgens can cause seasonal molt into breeding (alternate) plumage in males of both temperate and tropical birds (Peters et al. 2000, McGlothlin et al. 2008, Lindsay et al. 2011, Hasegawa et al. 2017), and suppress post-breeding (pre-basic) molt (Nolan et al. 1992). Considerably less research effort has focused on androgens in females, although females can show seasonal variation in testosterone circulation (Ketterson et al. 2005, George and Rosvall 2018, Bentz et al. 2019), differentially allocating androgens to affect offspring phenotypes (Pilz et al. 2004, Strasser and Schwabl 2004, Groothuis and Schwabl 2008), and testosterone can stimulate molt in females (Peters 2007, Lindsay et al. 2016). Assessing androgens and the pleiotropic effects they have on trait expression can illuminate the mechanistic basis of responses to major environmental disturbances (Boersma et al. 2021). By studying both sexes, one can determine whether shared mechanisms allow organisms to avoid costly phenological mismatches by using the same cues to time major life-history events like breeding and molt (Visser et al. 1998, Kucheravy et al. 2021, Williams et al. 2022). Yet most phenological studies are limited to one sex, thus limiting inferences on how changing environmental conditions affect bird populations.

Here we use continuous sampling of tropical White-shouldered Fairywrens (*Malurus alboscapulatus*) during an El Niño-induced drought to determine effects of drought on breeding readiness and physiology in both males and females. This species remains paired and defends territories year-round and appears to breed opportunistically, with males maintaining cloacal protuberances year-round and females caught with brood patches in all months sampled (missing only in December captures; Enbody et al. 2019). We first use a long-term dataset to compare breeding readiness, body condition, and body molt during the drought period relative to periods with sustained rainfall. We then use sliding window models to evaluate the time-scale on which reduced rainfall impacts traits that differ among drought and non-drought periods. In addition, we explore whether photoperiod explains variation in breeding readiness and physiology irrespective of drought conditions. Finally, we assess whether androgens likely mediate physiological responses to drought and photoperiod. We test the hypothesis that this species uses rainfall rather than

Fig. 1. Sampling across months and years of the study. Filled cells indicate months that were sampled. Gray fill indicates non-drought periods and black fill indicates drought periods.



photoperiod as a cue for timing of life-history events. Ultimately, our results suggest that sexes of this year-round breeding species differ in their sensitivity to reduced rainfall and we find some evidence for physiology varying by photoperiod.

MATERIALS AND METHODS

Study system and precipitation measurements

White-shouldered Fairywrens are an insectivorous species endemic to the savannas of New Guinea (Schodde 1982). Here, we studied the *Malurus alboscapulatus moretoni* subspecies, which inhabits areas with moderately seasonal rainfall and is characterized by plumage ornamentation in both males and females (Enbody et al. 2018, 2019). We collected data at two field sites on the mainland of Milne Bay Province, Papua New Guinea, near the villages of Garuahi (150°29' E, 10°13' S, 0–10 m a.s.l.) and Porotona (150°35' E, 10°15' S, 10–20 m a.s.l.) that experienced a severe El Niño drought event in 2015–2016 (Gwahirisa et al. 2017). We used daily precipitation data (in mm) collected by the Papua New Guinea National Weather Service from the nearest weather station (approximately 11 and 17 km, respectively, from field sites) at Gurney Airport in the provincial capital of Alotau (150°20' E, 10°18' S, 18 m a.s.l.) during the 2015–2016 El Niño drought (Gwahirisa et al. 2017).

Physiological measurements

We captured White-shouldered Fairywrens on their territories in mistnets by flushing and occasionally by using conspecific vocalizations (i.e., alarm calls, song). Most captures occurred in the morning between 5:30 AM and 12:00 PM or between 4:00 PM and 7:00 PM, corresponding to peaks in fairywren activity. We captured individuals continuously from January to March and June to August 2014, January to March 2015, July 2015 to April 2016, October 2016, January to February and May to June 2017, and April to June 2018 (Fig. 1). Our sampling window between July 2015 and April 2016 occurred during major drought; individuals captured during this period (N = 163 male captures from 70 individuals and 138 female captures from 63 individuals) were compared to individuals pooled across our other sampling periods (N = 157 male and 153 female captures). Each individual was banded with a unique metal Australian Bird and Bat Banding Scheme (ABBBS) band and a unique combination of three color bands. Upon capture, we assessed presence or absence of a cloacal protuberance (CP) in males and presence or absence of defeathered brood patches (BP) in females to assess breeding readiness. When they were present, we measured length, width, and depth of CPs in males to estimate volume (Fig. A1.1; formula: $\pi [(depth/2)(width/2)] length$, following Tuttle et al. 1996).

Absence of a CP for this study is defined by entirely lacking the bulbous swelling and tip. We systematically searched for nests to assess number of nests per groups monitored (Table A1.1) for females with active (i.e., highly vascularized) brood patches or caught with a developing egg in the oviduct as visible through a distended abdomen. Body mass was measured by using a digital scale, and we adjusted mass by body size by calculating residuals from a linear model of mass by tarsus length as a proxy for body condition (Labocha and Hayes 2012). We assessed body molt by scoring proportion of feathers molting on a 0–3 scale (0 = no molt, 1 = 1–33% feathers molting, 2 = 34–66% feathers molting, 3 = > 67% feathers molting) across head, back, belly, chest, and tail to arrive at a total molt score.

Plasma storage and androgen radioimmunoassay

Upon capture we immediately took a blood sample to minimize the time between capture and assessment of plasma androgen levels (mean net-to-bleed time: 4.79 min, range: 1–10 min). We centrifuged blood samples immediately upon return from the field each day, then stored plasma in 100% ethanol. Plasma androgen concentration was measured by using radioimmunoassay following a protocol validated for this species in a lab at Washington State University (full details: Lindsay et al. 2009, Enbody et al. 2018). Intra-assay coefficients of variation were 4.07 to 14.2%, and the inter-assay coefficient of variation was 8.61%. The minimum detectable level of testosterone was 200.77 pg/ml plasma based on a mean recovery rate of 69.05% and minimum plasma volume of 16.88 μ l (maximum: 53.75 μ l, mean: 41.52 μ l, median: 43.16 μ l). We back-calculated an estimate of androgen concentration for undetectable samples using the minimum detectable level in our assays (1.95 pg/tube; N = 132 of 310 total samples). Our reported androgen values reflect total androgens because the testosterone antibody we used cross-reacts with some closely related androgens, particularly 5 α -DHT (Wien Laboratories T-3003).

Statistical methods

All analyses were conducted in program R (R Core Team 2018) by using sliding window climate analysis in package “climwin” (van de Pol et al. 2016), and linear mixed models in base R and package “lme4” (Bates et al. 2015). For all models, any predictors with $P > 0.2$ were removed from the final model, following Wang et al. (2008). Individual identification was included as a random effect to account for repeated measurements of all response variables.

Models comparing drought and non-drought periods

We first compared breeding readiness (CP presence/absence in males, BP presence/absence in females) between the 2015–2016

El Niño drought period and pooled non-drought periods using binomial models. Then we compared body condition and body molt score between the drought and non-drought period using linear mixed models. To test for photoperiodic effects we included a day length variable, which we calculated from sunrise and sunset times for our study site, a binary daylight trend variable (increasing or decreasing day lengths), and the interaction of the two variables.

Precipitation sliding window models

Following detection of a significant difference ($P < 0.05$) between the drought and pooled non-drought years for a given variable, we used sliding window analysis to search for critical precipitation windows for that variable during the drought sampling period only. We did not include other years because of discontinuous sampling during those periods and our motivation to characterize drought effects specifically. Covariates with $P < 0.2$ in the initial drought versus non-drought model were included as fixed effects in the sliding window model for each response variable. Sliding window analysis compares candidate models with the climate predictor (i.e., daily precipitation) to a null model with no climatic effects, and searches for the critical time window of any climatic effects (van de Pol et al. 2016). We tested both linear and quadratic effects in sliding window precipitation models and selected the best fit based on Akaike Information Criterion corrected for small sample sizes (AICc) scores. Finally, we ran 100 iterations of each sliding window model to account for potential issues with overfitting and generated P values for the effect of precipitation on each response variable.

Body condition as a predictor or cost of breeding during drought

We assessed whether body condition was predictive of breeding during the drought year and whether condition changed from pre-breeding to after a clutch had been initiated. Because of few post-nesting captures we pooled all individuals captured after the initiation of nests (stages pooled: incubation, nestling, fledging, and after nest failure). For these models we included number of days into our drought field season (starting on 15 July) and the interaction between days into drought and breeding status as covariates.

Models of photoperiod in non-drought periods

When photoperiod variables were significant predictors for a response variable in an initial model containing drought and non-drought periods, we ran the same model after excluding the drought year. This was deemed necessary because mean day lengths differed significantly between drought and non-drought periods (mean day length during drought sampling period: 12.14 h, mean day length during non-drought sampling periods: 11.74 h; $P < 0.001$) because of variation in sampling effort (Fig. A1.2); thus, photoperiodic effects were potentially confounded by drought conditions when this period was included in analyses. Therefore, we drew conclusions about photoperiodic effects only when a response variable was predicted by photoperiod in both the full dataset (i.e., the initial model) and in the model for the non-drought dataset. To address potential issues arising from multiple comparisons, we used a Holm-Bonferroni correction to control the family-wise error rate (Holm 1979).

Testing androgens as a mediator of drought and seasonal effects

We first compared log-transformed androgens in males and females across drought and non-drought periods, and tested for photoperiodic effects as described above. To test the potential role of androgens in mediating drought and seasonal effects on breeding readiness and molt, we used linear mixed models with androgens as a candidate predictor of cloacal protuberance volume in males, brood patch presence/absence in females, and molt score in both sexes. Time of day bled and net-to-bleed delay time were included as covariates in all initial androgen models.

RESULTS

Drought effects on breeding readiness

Presence or absence of cloacal protuberance differed significantly between the drought sampling period and non-drought sampling periods (Table A1.2a), with the drought period characterized by more males lacking a cloacal protuberance (13 of 168 captures with no CP during drought vs. 1 of 149 captures with no CP in other periods, Fig. A1.3a). During the drought period, the initial decline in precipitation (Fig. 2a) was associated with diminished cloacal protuberance volumes (Fig. 2b). A sliding window model identified a critical precipitation period of 0–40 days prior to cloacal protuberance measurement (Table 1a, Fig. 3a). The model containing the critical precipitation window outperformed null models according to AICc (-42.68 for model containing 0–40 day precipitation window). Presence or absence of brood patches did not differ significantly across sampling periods (Table A1.1b, Fig. A1.3b).

Fig. 2. Temporal patterns of (a) weekly precipitation immediately prior to and during the 2015–2016 El Niño drought in Papua New Guinea, and (b) male cloacal protuberance (CP) volume during the drought period.

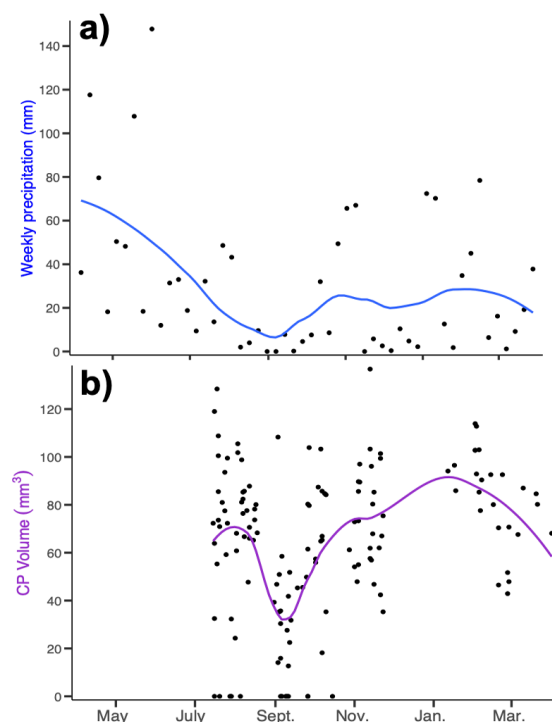
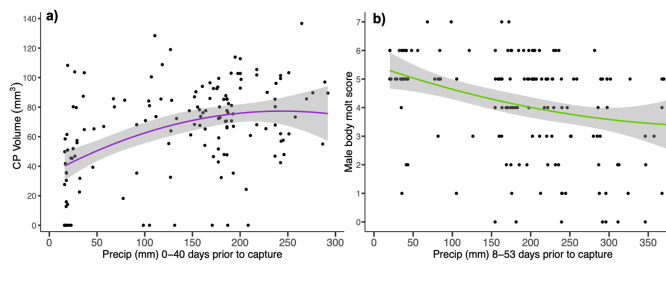


Table 1. Model results for critical climate window analysis for precipitation and (a) cloacal protuberance volume, and (b) body molt in male White-shouldered Fairywrens (*Malurus alboscapulatus*). Sliding window models were used to assess the effect of precipitation on physiological traits that differed between drought and non-drought sampling periods. Bolded terms reflect significant predictors.

Predictor	β	SE	DF	t	P	Random effects	σ
(a) Cloacal protuberance volume (N = 146 captures, 68 males)							
Intercept	46.25	6.95				Male ID	20.50
Precipitation 0–40 days (mm ²)	1.81	0.92	76	1.98	< 0.001		
(b) Male body molt score (N = 164 captures, 71 males)							
Intercept	4.46	0.57				Male ID	0.16
Precipitation 8–53 days (mm ²)	-0.06	0.02	90	-3.59	< 0.001		
Daylight trend (inc)	0.03	0.02	90	-0.03	0.98		

Fig. 3. Quadratic relationship between critical precipitation windows during the drought period and (a) male cloacal protuberance (CP) volume, and (b) male body molt score. Both male CP volume and molt were significantly associated with precipitation windows identified from sliding window models ($P < 0.001$ for both).



Drought effects on body condition

Male body condition (mass/tarsus residuals) showed a non-significant difference across sampling periods ($P = 0.07$, Table A1.2c), although means were nearly identical (mean \pm sd: 0.36 ± 0.71 during drought vs. 0.31 ± 0.55 outside of drought). Body condition in females did not differ across sampling periods (Table A1.2d).

Body condition as a predictor or cost of breeding during drought

Condition was a non-significant predictor for whether females later initiated a nest during the drought period ($\chi^2 = 3.83$, $DF = 1$, $P = 0.05$), with pre-initiation females having higher condition than females who did not attempt to nest (mean \pm sd: -0.29 ± 0.34 pre-initiation females vs. -0.49 ± 0.46 non-nesting females). Among females who nested during drought, condition was lower after nesting ($\chi^2 = 8.39$, $DF = 1$, $P = 0.004$; mean \pm sd: -0.29 ± 0.34 pre-initiation females vs. -0.53 ± 0.37 post-initiation females), and we detected a non-significant interaction between initiation status and days into the drought period ($\chi^2 = 3.51$, $DF = 1$, $P = 0.06$, Fig. A1.4). Body condition in males was not predictive of whether males would nest during the drought period ($\chi^2 = 0.02$, $DF = 1$, $P = 0.89$), nor did mass differ from pre-initiation to post-initiation in nesting males ($\chi^2 = 0.151$, $DF = 1$, $P = 0.22$).

Drought effects on molt

Male body molt differed across sampling periods (Table A1.2e), with the drought period characterized by higher molt scores (mean \pm sd molt: 6.08 ± 2.97 during drought vs. 4.27 ± 1.69 outside of drought). Male body molt was predicted by a critical precipitation window of 8–53 days prior to assessment by using a quadratic model (Table 1b, Fig. 3b). The model containing the critical precipitation window outperformed null models according to AICc (-33.21 for model containing 0–40 day precipitation window). Female molt did not differ across sampling periods (Table A1.2f).

Photoperiodic effects on breeding readiness

Day length was a significant predictor of CP presence/absence in the initial drought versus non-drought model (Table A1.2a), but not in the model with drought period samples removed (Table A1.3a). Presence or absence of brood patches was predicted by day length and daylight trend in the initial model (Table A1.2b), but this effect was absent outside of the drought period (Table A1.3b).

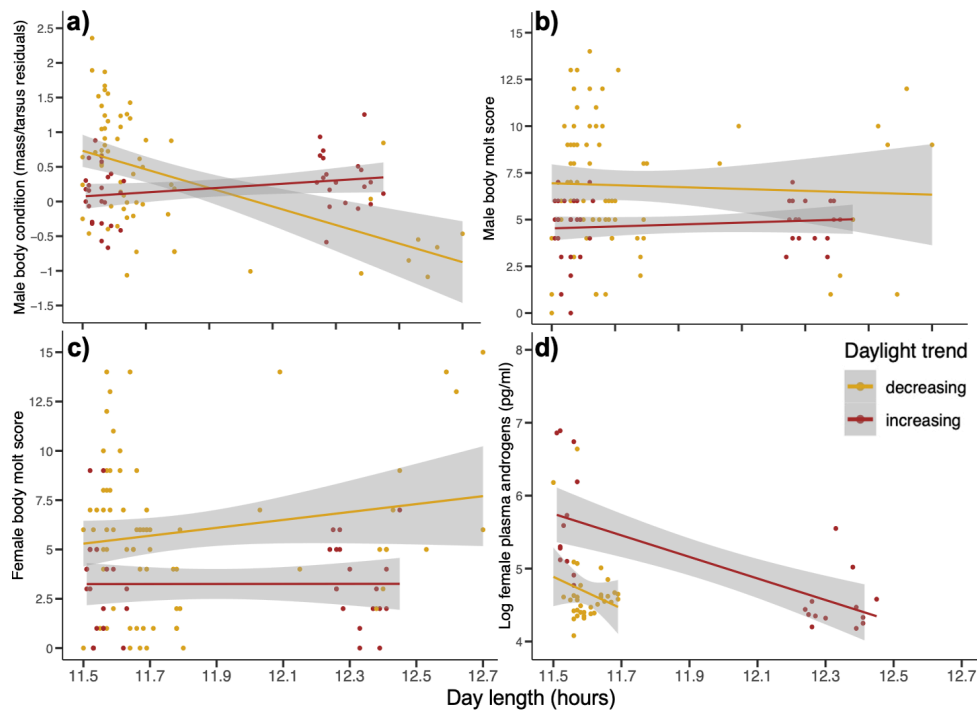
Photoperiodic effects on body condition

Male body condition was predicted by day length and the interaction between day length and daylight trend both in the initial model (Table A1.2c) and in the non-drought only model (Table A1.3c). Male condition decreased under long, decreasing day lengths characteristic of austral summer (Fig. 4a). The initial model for female body condition indicated some seasonal effects (Table A1.2d), although no predictors were significant after excluding the drought period (Table A1.3d).

Photoperiodic effects on molt

Daylight trend was a significant predictor for both male (Table A1.2e) and female molt (Table A1.2f) in the initial model and after excluding drought captures (Table A1.3e, f), with higher molt scores occurring during decreasing day lengths (Fig. 4b, c). Female molt score also differed by day length and the interaction between day length and daylight trend, with long days during a decreasing daylight trend during austral summer associated with higher molt scores (Fig. 4c).

Fig. 4. Relationship between day length and (a) male body condition, (b) male body molt score, (c) female body molt score, and (d) female log transformed plasma androgens. Whether day lengths are in an increasing or decreasing phase is reflected by increasing (red) and decreasing (orange) daylight trend. Day length was a significant predictor for male condition ($P < 0.001$), female molt ($P < 0.02$), and female androgens ($P < 0.001$). Daylight trend was a significant predictor for male ($P = 0.003$) and female body molt ($P < 0.001$), and female androgens ($P = 0.003$). The interaction between day length and daylight trend was a significant predictor for male condition ($P = 0.004$), female molt ($P = 0.04$), and female androgens ($P = 0.03$).



Androgens as a potential mediator of drought and photoperiodic effects

Neither male nor female log-transformed plasma androgen levels differed across drought and non-drought sampling periods (Table A1.2g, h). Daylight trend was a non-significant predictor of male androgens (Table A1.3g), with greater androgen levels measured during increasing (mean \pm sd: 567.90 ± 527.68 pg/ml) versus decreasing daylight (420.54 ± 628.27 pg/ml). Female androgen levels were predicted by day length, daylight trend, and the interaction between the two variables (Table A1.3h). Androgen levels showed a negative association with day length during both increasing and decreasing light phases in females (Fig. 4d). Time of day bled was a significant covariate in males because of higher androgen levels measured in samples collected during late afternoon/early evening (mean \pm sd during AM: 498.44 ± 601.15 vs. 778.31 ± 674.40 pg/ml androgens).

Androgen levels were positively correlated with cloacal protuberance volume in males ($\chi^2 = 14.05$, DF = 1, $P < 0.001$, Fig. A1.5a), and negatively associated with body molt score in males ($\chi^2 = 16.00$, DF = 1, $P < 0.001$, Fig. A1.5b). In females, androgen levels were not predictive of brood patch presence/absence ($\chi^2 = 0.23$, DF = 1, $P = 0.64$) or molt ($\chi^2 = 1.81$, DF = 1, $P = 0.18$).

DISCUSSION

Tropical latitudes are expected to experience less precipitation and more droughts because of climate change (Neelin et al. 2006, Trenberth et al. 2014). We studied how a major El Niño drought event in New Guinea (Gwatarisa et al. 2017) affected breeding readiness and physiology in White-shouldered Fairywrens. Drought was associated with decreased cloacal protuberance presence in males (Fig. 2), with lower precipitation 0–40 days prior to capture associated with smaller protuberance volumes (Fig. 3a). These findings are consistent with those in an opportunistically breeding congener, the Purple-crowned Fairywren (*Malurus coronatus*), in which cloacal protuberances were affected by rainfall within 45 days of capture, shown by using a sliding window model (Aranzamendi et al. 2019). In the Aranzamendi et al. (2019) study, males developed cloacal protuberances and started breeding following rainfall-induced increases in arthropod abundance. Although we did not measure prey abundance in our study, we consider reduced arthropod abundance during drought a likely cause of atrophied cloacal protuberances, which are typically maintained year-round in this species (Enbody et al. 2019).

Several males lost their cloacal protuberance entirely during drought (N = 9 of 68 males), which was only observed once outside of the drought period. Because of slight sampling bias between

drought and non-drought periods (Fig. A1.1), we cannot rule out the possibility that cloacal protuberance volumes declined in early austral spring during drought because of another cue and not because of declining precipitation. However, photoperiod was not predictive of cloacal protuberance volume, and several incidences of atrophy during drought occurred in austral winter ($N = 5$), a period in which we have several years of non-drought sampling without atrophied protuberances. Given the promiscuity of *Malurus* fairywrens (Rowe and Pruett-Jones 2013), diminished cloacal protuberances are likely to be especially costly because they reduce the likelihood of siring young both with social mates and with neighboring groups.

White-shouldered Fairywrens defend territories in pairs year-round and molt throughout the year, with individual variation likely linked to breeding schedule because molt typically does not overlap with nesting (Enbody et al. 2019). We found higher molt scores in males during the drought period, with lower precipitation 8–53 days prior to capture associated with heavier molt (Fig. 3b). Together with our cloacal protuberance results, molt results suggest that males suppressed breeding effort in favor of molt as precipitation declined. Yet female breeding readiness (brood patch presence/absence) was unaffected by drought and many pairs initiated nests during the 2015–2016 El Niño drought period (Table A1.1; $N = 28$ total nests from 67 pairs monitored). That drought affected male but not female breeding readiness suggests possible desynchronization of breeding among sexes. Such desynchronization of male and female breeding physiology might result in reduced reproductive success and contribute to the decline of populations (Visser et al. 1998, Kucheravy et al. 2021, Inouye 2022, Williams et al. 2022).

A previous study of White-shouldered Fairywrens that used data from this drought period found high nest failure (87%) and low adult survival probabilities during drought (Enbody et al. 2019), suggesting that attempts to breed during poor environmental conditions may have negative effects on survival, as has been shown in a comparative study of tropical bird species during drought (Martin and Mouton 2020). We used size-corrected body mass (residuals of mass/tarsus) to test for effects of drought on condition. Size-corrected body mass is a reliable indicator of condition across vertebrates (reviewed in Labocha and Hayes 2012) that often varies with food availability (Brown and Sherry 2006) and can be used as an indicator of declining bird populations (Rioux Paquette et al. 2014). We did not find a difference in body condition between drought and non-drought periods in either sex. However, we found that female who nested during drought started with higher body condition but after nests had been initiated their mass declined to resemble females who did not attempt to nest (Fig. A1.4). In males, however, condition was not predictive of whether a nest was initiated during drought, nor did it differ after initiation among nesting males. Ultimately, our body condition results tentatively support the conclusion that attempts to nest during drought were costly for females but not males.

Determining which species use photoperiod as a cue for life-history events is especially important given that with climate change current conditions are deviating from historical patterns, thus producing costly phenological mismatches (Lof et al. 2012, Zimova et al. 2016, Pedersen et al. 2017). We found that photoperiod was predictive of male body condition, with long, decreasing day lengths (characteristic of austral summer) associated with decreasing

condition. Body molt was greater in both males and females during decreasing daylight trends, perhaps causing the diminished body condition assessed in males under similar photoperiodic conditions. Although breeding readiness was unaffected by photoperiod, we do not interpret these negative results as evidence of an absence of photoperiodic effects on breeding phenology for several reasons. First, our photoperiod models were run by using data from non-drought periods in which only one male was captured without a cloacal protuberance, thus precluding our ability to detect an effect. In females, our metric for breeding readiness (the presence/absence of a brood patch) is a crude assessment of breeding because females seem to retain defeathered brood patches well beyond (i.e., several weeks) the fledging of young (Boersma and Enbody, *personal observation*). Brood patches also typically do not develop until shortly before egg laying, so do not necessarily indicate which females are entering breeding condition (Bailey 1952, Hinde 1962). Consistent year-round nest monitoring is needed to resolve the degree to which photoperiod and/or precipitation serve as cues for life-history transitions in this species.

We used repeat sampling of androgens to assess whether this known integrator of physiological and behavioral traits (Wingfield 2008, Hau et al. 2010, Hau and Goymann 2015, Lipshutz et al. 2019) explained variation in breeding readiness and molt in our dataset. We found that androgen levels were positively associated with cloacal protuberance volume and negatively associated with molt intensity in males. A previous study in this species found that exogenous testosterone caused females that normally do not have a cloacal protuberance to develop them (Boersma et al. 2020), which is consistent with our observations here that androgens regulate the size of the cloacal protuberance in males of this aseasonally breeding species. The negative association between androgens and molt in males could indicate a mechanism for preventing overlap between breeding and molt, as has been proposed previously (Dawson 2004). Androgen levels were also associated with photoperiod in both sexes, with higher androgen levels measured in males during an increasing daylight trend and higher androgen levels in females during short, but increasing, day lengths. The consequences of photoperiod-induced variation in androgens could be a promising avenue for future studies in this system.

Though outside of the scope the present study, social cues are likely to explain variation in how White-shouldered Fairywrens respond to variable precipitation and photoperiod. In other avian species, social cues can initiate release of sex hormones and development of reproductive physiology (Runfeldt and Wingfield 1985, Dufty and Wingfield 1986, Hahn and Silverman 2006, Hau et al. 2008b, Chmura et al. 2020). Sexes can differ in their sensitivity to cues from their mates and other conspecifics (Watts et al. 2016, Chmura et al. 2020, Vernasco et al. 2022), which could explain disparate results among sexes in our study. Continued study of how aseasonally breeding species incorporate information from the physical and social environment to time major life-history events is important, especially in the context of climate change.

CONCLUSIONS

The tropics contain disproportionately high biodiversity and are considered at greater risk of severe impacts from a drying climate

(Neelin et al. 2006, Trenberth et al. 2014). Understanding how drought impacts phenology can resolve which species are most at risk because of climate change. We found that in White-shouldered Fairywrens sexes differ in their response to persistent drought. Whereas male breeding readiness and molt were sensitive to diminished rainfall, females showed no differences in breeding readiness or any physiological measurement across drought and non-drought periods. We found that 13% of males lost their cloacal protuberances during drought conditions, which occurred only once during several years lacking drought. However, many pairs attempted nesting during drought, and females who nested during this period started with greater body mass that declined following clutch initiation. Photoperiod is an alternative driver of changes in reproductive physiology to precipitation that can produce mismatches with current environmental conditions as climate changes (Lof et al. 2012, Zimova et al. 2016, Pedersen et al. 2017). Photoperiod was predictive of some physiological traits in both sexes in our study, which might explain attempts to breed despite drought conditions. Follow-up work is needed in this and other tropical species to establish the extent to which photoperiod and rainfall cues influence life-history transitions and reproductive fitness.

Acknowledgments:

We are grateful to landowners from the Maramatana LLG for granting us access to their land for this research. R. Biggoneau, P. Chaon, and G. Kareba, S. Ketaloya, B. Magnier, D. Nason, and Illa provided expert field assistance. We thank Judit Szabo and two anonymous reviewers for helping improve our initial manuscript. The Papua New Guinea National Weather Service generously provided precipitation data used for this project. This work was supported by a National Science Foundation grants IOS-1354133 to J.K. and 1352885 to H.S., and the Disney Worldwide Conservation Fund to J.K. Additional support came from the Washington State University Elling Research Grant to J.B.

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Drought disrupts year-round breeding readiness in a tropical songbird

Appendix

Table A1. Number of nests found per groups monitored across study years. The drought sampling period is shown by red text, and months for which nest data were not collected are denoted with ‘xx’. Nest searching effort varied across each sampling period and is scored accordingly as low, moderate, or high.

Year	January	February	March	April	May	June	July	August	September	October	November	December
2014												
Active nests	3	xx	xx	xx	xx	0	1	1	0	2	xx	xx
Groups monitored	47	xx	xx	xx	xx	47	47	47	47	47	xx	xx
% Active nests	6.38	xx	xx	xx	xx	0.00	2.13	2.13	0.00	4.26	xx	xx
Search effort	Moderate	xx	xx	xx	xx	Moderate	Moderate	Moderate	Moderate	Moderate	xx	xx
2015												
Active nests	xx	xx	xx	xx	xx	xx	1	0	1	1	3	6
Groups Monitored	xx	xx	xx	xx	xx	xx	67	67	67	67	67	67
% Active nests	xx	xx	xx	xx	xx	xx	1.49	0.00	1.49	1.49	4.48	8.96
Search effort	xx	xx	xx	xx	xx	xx	High	High	High	High	High	High
2016												
Active nests	9	3	4	xx	xx	xx	xx	xx	xx	xx	2	xx
Groups Monitored	64	64	64	xx	xx	xx	xx	xx	xx	xx	64	xx
% Active nests	14.06	4.69	6.25	xx	xx	xx	xx	xx	xx	xx	3.13	xx
Search effort	High	High	High	xx	xx	xx	xx	xx	xx	xx	Low	xx
2017												
Active nests	xx	xx	xx	xx	5	xx	xx	xx	xx	xx	xx	xx
Groups Monitored	xx	xx	xx	xx	31	xx	xx	xx	xx	xx	xx	xx
% Active nests	xx	xx	xx	xx	16.13	xx	xx	xx	xx	xx	xx	xx
Search effort	xx	xx	xx	xx	High	xx	xx	xx	xx	xx	xx	xx

Table A2. Full terms for initial models pooling drought and non-drought sampling periods: **(a)** male cloacal protuberance and **(b)** brood patch presence/absence in females, size-corrected body mass in **(c)** males and **(d)** females, body molt score in **(e)** males and **(f)** females, and log-transformed androgens in **(g)** males and **(h)** females. Bolded terms reflect significant comparisons and italics show terms removed from model ($P > 0.2$). Measurements that differed across drought vs. no drought sample periods were run in a sliding window model (Table 1). When photoperiod was a significant predictor, a separate model was run with data from drought period excluded (Table 2).

(a) Cloacal protuberance (N = 317 captures, 116 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	34.40	15.49				Male ID	21.62
Drought (Y)	-12.78	5.82	1	4.82	0.03		
Day length	-12.78	5.82	1	5.91	0.02		
<i>Daylight trend (inc)</i>	<i>-1.77</i>	<i>13.96</i>	<i>1</i>	<i>0.02</i>	<i>0.90</i>		
<i>Day length x daylight trend</i>	<i>-6.95</i>	<i>14.77</i>	<i>1</i>	<i>0.22</i>	<i>0.64</i>		
(b) Brood patch (N = 230 captures, 109 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	0.48	0.32				Female ID	0.86
Drought (Y)	-0.77	0.46	1	2.75	0.10		
Day length	-0.83	0.37	1	4.98	0.03		
Daylight trend (inc)	0.94	0.34	1	7.45	0.006		
Day length x daylight trend	-0.59	0.37	1	2.53	0.11		
(c) Male mass/tarsus residuals (N = 277 captures, 113 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	0.23	0.07				Male ID	0.45
Drought (Y)	0.13	0.07	1	3.40	0.07		
Day length	-0.05	0.07	1	24.18	<0.001		
Daylight trend (inc)	-0.26	0.05	1	0.44	0.51		
Day length x daylight trend	0.29	0.06	1	23.37	<0.001		
(d) Female mass/tarsus residuals (N = 215 captures, 112 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	8.59	0.07				Female ID	0.37
Drought (Y)	0.02	0.08	1	0.06	0.81		
Day length	-0.23	0.11	1	4.45	0.03		
Daylight trend (inc)	-3.42	1.84	1	3.45	0.06		
Day length x daylight trend	0.28	0.15	1	3.39	0.07		
(e) Male body molt score (N = 307 captures, 114 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	6.26	0.25				Male ID	0.83
Drought (Y)	-1.16	0.34	1	11.57	<0.001		
Day length	-0.4	0.24	1	2.84	0.09		
Daylight trend (inc)	-0.88	0.30	1	8.37	0.004		
Day length x daylight trend	0.45	0.28	1	2.65	0.10		
(f) Female body molt score (N = 279 captures, 124 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	5.32	0.28				Female ID	
<i>Drought (Y)</i>	<i>-0.32</i>	<i>0.46</i>	<i>1</i>	<i>0.50</i>	<i>0.48</i>		
Day length	0.03	0.27	1	0.01	0.91		
Daylight trend (inc)	-1.31	0.36	1	13.13	<0.001		
Day length x daylight trend	-0.55	0.36	1	2.35	0.12		
(g) Male plasma androgens (N = 158 captures, 82 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	5.79	0.29				Male ID	0.23
<i>Drought (Y)</i>	<i>0.06</i>	<i>0.22</i>	<i>1</i>	<i>0.07</i>	<i>0.80</i>		
Day length	0.36	0.08	1	21.87	<0.001		
Daylight trend (inc)	0.27	0.17	1	2.51	0.11		
<i>Day length x daylight trend</i>	<i>-0.15</i>	<i>0.16</i>	<i>1</i>	<i>0.86</i>	<i>0.35</i>		
Time of day bled	-0.71	0.16	1	19.11	<0.001		
Net-to-bleed time (am)	0.07	0.04	1	3.16	0.08		
(h) Female plasma androgens (n = 152 captures, 94 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	5.08	0.14				Female ID	<0.001
Drought (Y)	0.29	0.20	1	2.14	0.14		
Day length	0.2	0.14	1	2.11	0.15		
Daylight trend (inc)	-0.10	0.16	1	0.42	0.52		
Day length x daylight trend	-0.34	0.16	1	4.89	0.03		
<i>Time of day bled (am)</i>	<i>0.02</i>	<i>0.04</i>	<i>1</i>	<i>0.23</i>	<i>0.63</i>		
<i>Net-to-bleed time</i>	<i>-0.15</i>	<i>0.15</i>	<i>1</i>	<i>0.98</i>	<i>0.32</i>		

Table A3. Model results for photoperiodic effects (day length, increasing vs. decreasing light) during pooled non-drought years. Cloacal protuberance presence/absence (**a**) in males and brood patch presence/absence in females (**b**) was used to assess breeding readiness. Mass was assessed in males (**c**) and females (**d**) as a proxy for condition. In addition we sought to determine if photoperiod affects body molt (**e,f**) and plasma androgens (**g,h**) in both sexes. Bolded terms depict significant comparisons and italics show terms removed from final model.

(a) Cloacal protuberance (N = 149 captures, 86 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	16.91	10.40				Male ID	70.14
Day length	0.65	10.84	1	0.004	1.0		
(b) Brood patch (N = 230 captures, 109 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	-0.16	0.29				Female ID	0.68
Day length	0.27	0.32	1	0.7	1.00		
<i>Daylight trend (inc)</i>	<i>-0.11</i>	<i>0.47</i>	<i>1</i>	<i>0.55</i>	<i>0.46</i>		
<i>Day length x daylight trend</i>	<i>-0.65</i>	<i>0.78</i>	<i>1</i>	<i>0.70</i>	<i>0.40</i>		
(c) Male mass/tarsus residuals (N = 128 captures, 85 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	0.17	0.10				Male ID	0.41
Day length	-0.42	0.10	1	19.32	<0.001		
Daylight trend (inc)	0.11	0.13	1	1.76	0.72		
Day length x daylight trend	0.46	0.13	1	12.13	0.004		
(d) Female mass/tarsus residuals (N = 104 captures, 74 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	-0.39	0.06				Female ID	0.25
<i>Day length</i>	<i>-0.20</i>	<i>0.08</i>	<i>1</i>	<i>0.21</i>	<i>0.64</i>		
Daylight trend (inc)	-0.05	0.11	1	0.22	1.0		
<i>Day length x daylight trend</i>	<i>0.13</i>	<i>0.11</i>	<i>1</i>	<i>1.34</i>	<i>0.25</i>		
(e) Male body molt score (N = 149 captures, 86 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	6.68	0.32				Male ID	1.28
<i>Day length</i>	<i>0.03</i>	<i>0.43</i>	<i>1</i>	<i>0.004</i>	<i>0.95</i>		
Daylight trend (inc)	-1.69	0.47	1	13.04	0.003		
<i>Day length x daylight trend</i>	<i>-0.24</i>	<i>0.58</i>	<i>1</i>	<i>0.16</i>	<i>0.68</i>		
(f) Female body molt score (N = 143 captures, 86 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	6.25	0.42				Female ID	2.00
Day length	1.25	0.41	1	9.15	0.02		
Daylight trend (inc)	-2.56	0.60	1	18.46	<0.001		
Day length x daylight trend	-1.66	0.61	1	7.39	0.04		
(g) Male plasma androgens (N = 72 captures, 55 males)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	5.96	0.20				Male ID	0.28
<i>Day length</i>	<i>0.1</i>	<i>0.18</i>	<i>1</i>	<i>0.31</i>	<i>0.58</i>		
Daylight trend (inc)	0.54	0.22	1	6.27	0.06		
Time of day bled (am)	-0.88	0.22	1	15.80	0.001		
<i>Net-to-bleed time</i>	<i>0.02</i>	<i>0.05</i>	<i>1</i>	<i>0.18</i>	<i>0.67</i>		
(h) Female plasma androgens (n = 68 captures, 57 females)							
Predictor	β	SE	DF	X^2	P	Random effects	σ
Intercept	2.69	0.60				Female ID	0.36
Day length	-2.53	0.69	1	13.57	0.002		
Daylight trend (inc)	2.29	0.61	1	14.37	0.003		
Day length x daylight trend	2.02	0.70	1	8.46	0.03		

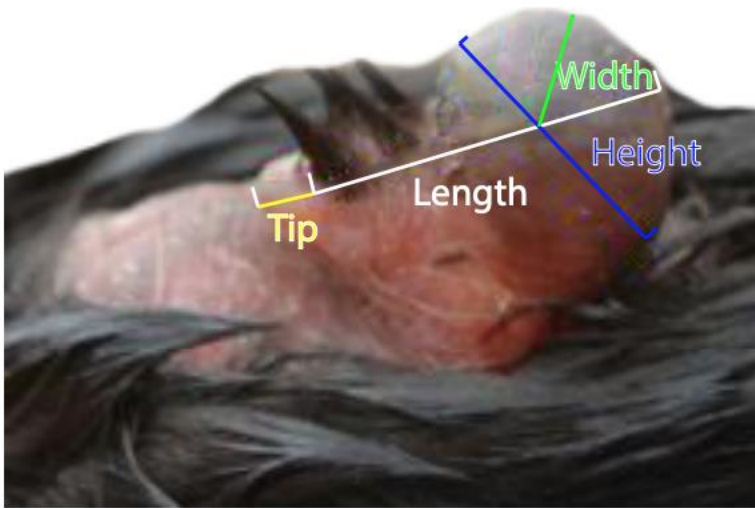


Figure A1. Bulbous cloacal protuberance of a male White-shouldered Fairywren. Each measurement used to calculate total volume is shown.

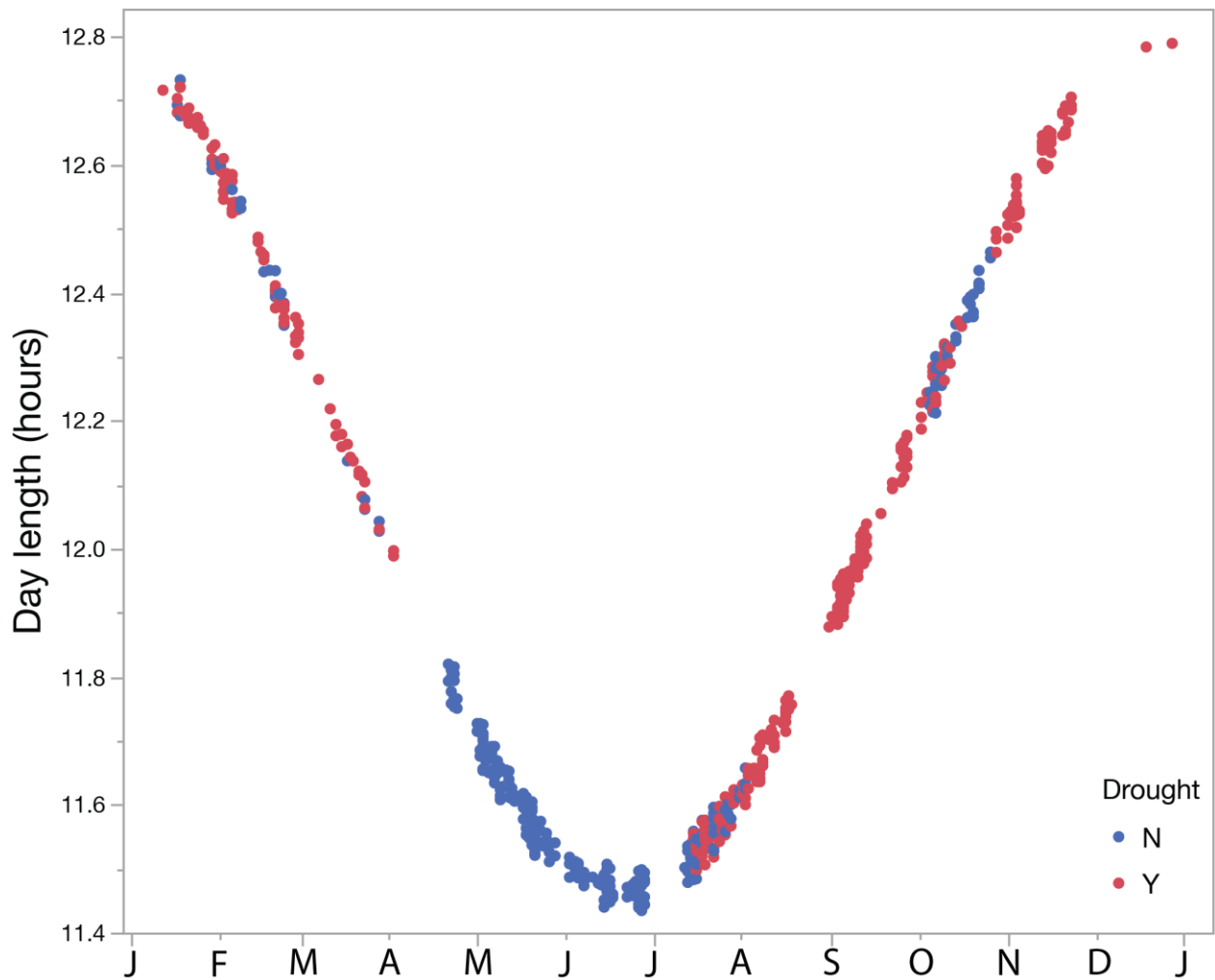


Figure A2. Day lengths across the year at our study site. Points indicate individual captures. The drought sampling period is depicted in red and the pooled non-drought sampling periods in blue.

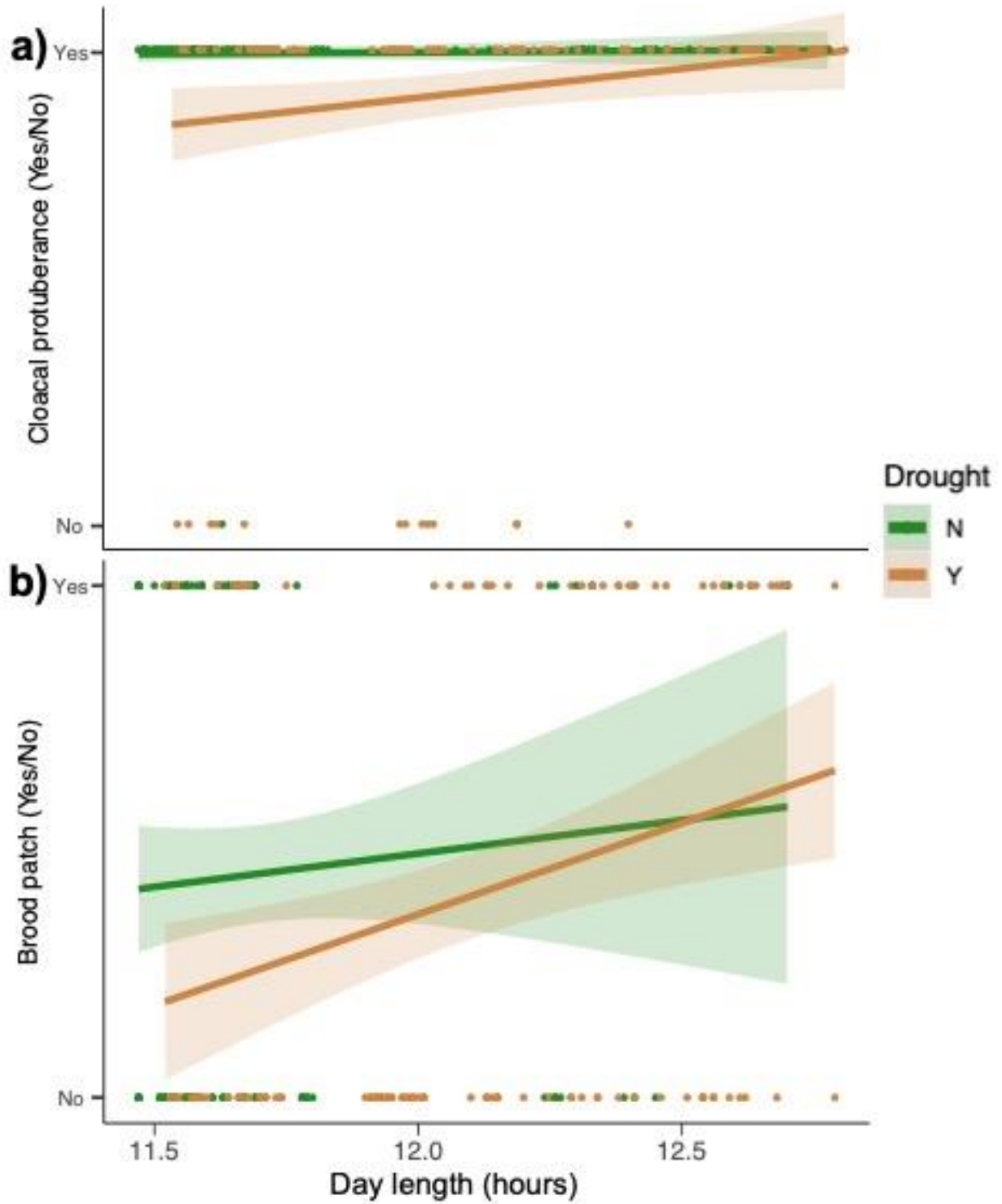


Figure A3. Breeding readiness by day length across drought (brown points and linear fit) and non-drought (green points and linear fit) sampling periods for **a)** male cloacal protuberance presence/absence and **b)** brood patch presence/absence in females.

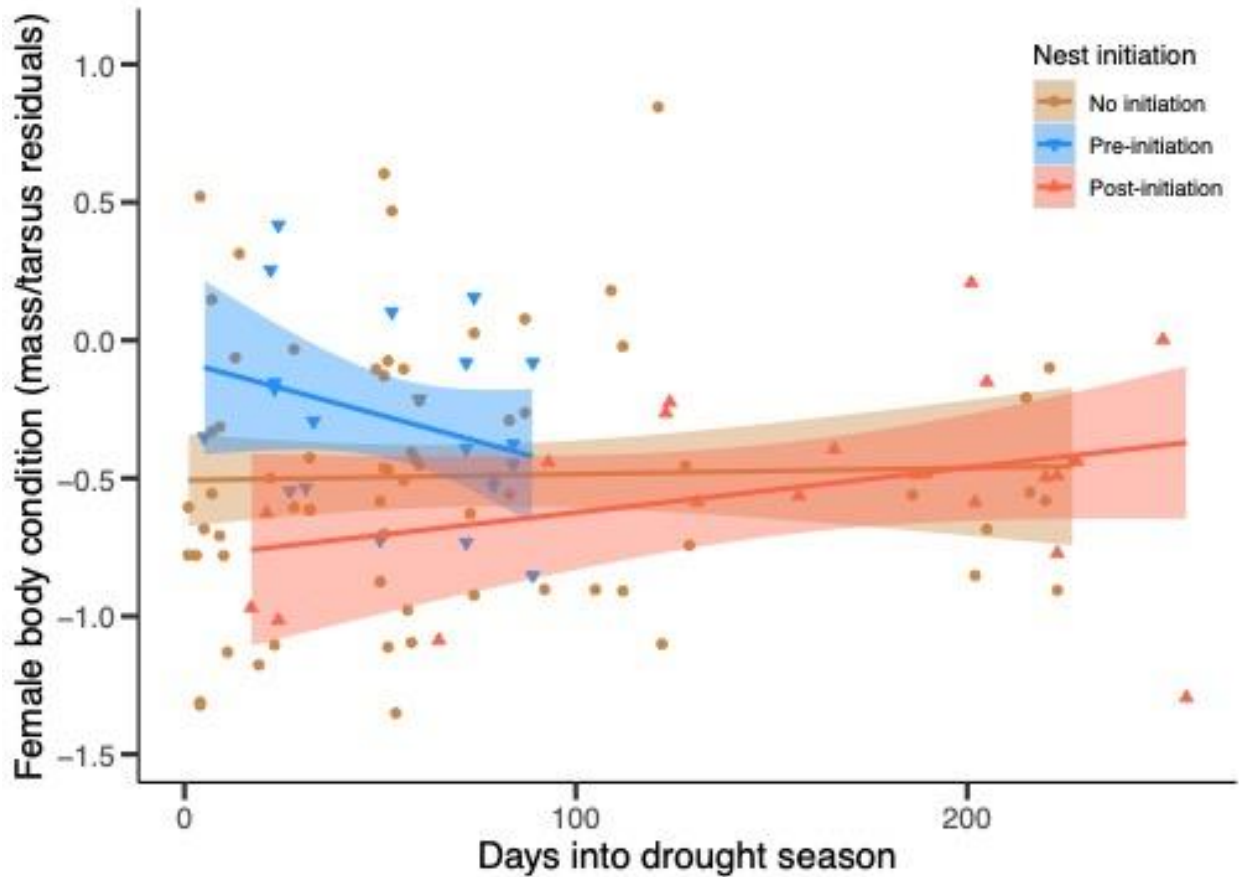


Figure A4. Relationship between days into the drought field season and female size-corrected body mass. Females who did not initiate a nest during drought are shown in brown circles, while pre-initiation nesting females are shown in blue upside-down triangles and post-initiation nesting females in red triangles. Females who did not nest had marginally lower size-corrected mass than nesting females captured before clutch initiation ($P = 0.05$). Among nesters, females had higher mass during pre-initiation relative to post-initiation females ($P = 0.004$), and we detected a non-significant interaction effect between nest initiation status and days into drought season ($P = 0.06$).

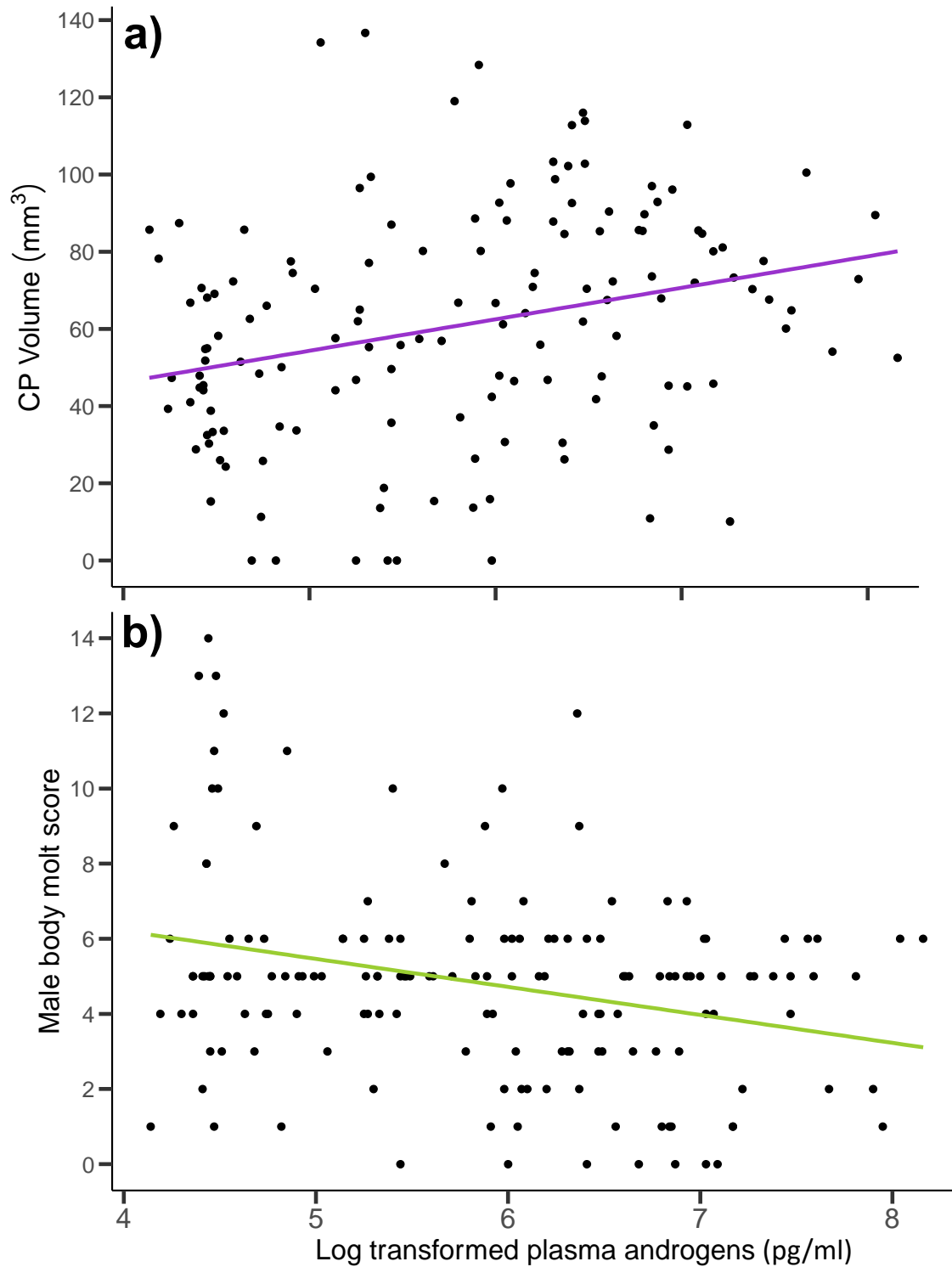


Figure A5. Relationship between log transformed plasma androgens with **a)** cloacal protuberance (CP) volume ($p < 0.001$) and **b)** male body molt score ($p < 0.001$).