Environmental and genetic components of variation in body size of a cooperative breeder, the purple-crowned fairy-wren

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ABSTRACT

An animal's body size is a trait of major importance for its metabolism, physiology, ecology and fitness. It is thus likely to be under various forms of selection. Climate change is thought to have had various effects on avian body size across the world. However, the intensity and direction of the effect remains controversial. Environmental and genetic variation are likely to influence variation in body size, and measuring their effects with quantitative genetic tools is essential to understand and predict phenotypic temporal trends. Here, I used a 12-year dataset of tarsus length measurements and investigated the effects of environmental factors on this morphological trait in a cooperative breeder, the purple-crowned fairy-wren (*Malurus coronatus coronatus*). I also estimated the genetic component of variation in body size in this species.

Adult tarsus length measurements varied from 20.6 to 26.7mm, and the study population showed a weak increase in size over the study period ($p = 0.02$), but it was not strongly linked with rain- and temperature-related climatic variables. Social group size during the nesting period varied from 2 to 10 individuals, and larger groups were associated with smaller birds. On the contrary, larger brood sizes (ranging from 1 to 4 chicks) consistently yielded larger birds, with broods of 4 having a mean$\pm$SE tarsus of 24.08$\pm$0.08mm and single-individual broods 23.63$\pm$0.09mm.

While the study of climatic effects on animal body size has become increasingly popular in the last decade, the influence of climate change on growth remains poorly understood. The social environment, its interaction with climate and their combined influence on growth should come back to focus for us to understand and predict temporal trends in animal body size.

Environmental factors generally explained a low amount of phenotypic variation, and the heritability of tarsus length after accounting for sex was of 0.48. The cross-sex genetic correlation of male and female tarsus length was 0.63. This estimate and the observed sexual dimorphism suggest that males and females are under contrasting selection pressures and may have a limited possibility to evolve towards their respective optimal body size.

Overall, this study provides a first step towards understanding the evolution of body size in the purple-crowned fairy-wren, and calls for more detailed analyses to determine whether the observed change is a plastic response or a microevolutionary change.

Keywords: body size, tarsus length, heritability, climate change, cooperative breeding, fairy-wren

INTRODUCTION

"Reality is size dependent" (LaBarbera 1989). Steven Vogel's statement highlights the importance of body size as a determining trait of an organism's perception of, and interaction with the physical and biological world. Indeed, this morphological trait affects most aspects of an animal's metabolism, physiology, ecology, and fitness (Peters 1986; LaBarbera 1989; Kingsolver and Huey 2008). Consequently, it is likely to be a trait under various and potentially contrasting forms of selection. For instance, animal body size is often thought to be under selection as an honest signal of fighting ability and a correlate of intrinsic quality as a mate (McGlothlin et al. 2005; Hall et al. 2013; Margraf and Cockburn 2013; Ozgul et al. 2014). Thus, the influence of body size on reproductive success may be particularly pronounced in structured animal societies where only some individuals reproduce, like in cooperatively breeding systems (Ozgul et al. 2014; Kruuk et al. 2015).

In addition to its social functions, body size is known to be of major importance for thermoregulation (Peters 1986; LaBarbera 1989). In the last decade, this trait has been the focus of many studies of climate change effects on animal phenotypes (Gardner et al. 2011; Gardner et al. 2014). A general pattern of shrinking body size as a response to global warming has been observed in several animal taxa with a focus on birds, and has been hypothesized to be an adaptive response to increasing temperatures, in accordance with Bergmann's rule (Gienapp et al. 2008; Teplitsky et al. 2008; Gardner et al. 2009; Olson et al. 2009; Gardner et al. 2011; Gardner et al. 2014; van Gils et al. 2016). Bergmann's rule implies that mean body size increases with latitude, through a genetic adaptation to colder climates (Bergmann 1847; Meiri 2011). Thus, one would expect within-species mean body size to decrease with increasing temperatures. However, all populations do not respond to climate change in the same way and may experience size changes because of other factors that are not accounted for (McKechnie and Wolf 2009; Meiri et al. 2009; Salewski et al. 2014; Collins et al. 2017; Little et al. 2017). Within-population change in body size may represent a response to a wide range of factors such as climatic conditions, but also social conditions, mate choice, competition, predator and parasite abundance or food availability (Gardner et al. 2009; Little et al. 2017). Furthermore, this response may be due to genetic change and/or phenotypic plasticity, and making this distinction is essential in order

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to understand temporal trends in body size (Gienapp et al. 2008; Gardner et al. 2011; Husby et al. 2011; Gienapp and Merilä 2014).

In order to evolve, a morphological trait must be heritable (Kruuk 2004). In other words, the observed phenotypic variation must be at least partly explained by genetic variation (as opposed to environmental variation) for it to respond to natural selection across generations. Consequently, knowledge of the relative contribution of genetic and environmental factors to natural variation is essential in order to assess how phenotypic changes resulting from selection are passed on from one generation to the next (Kruuk et al. 2014). In the past 40 years, substantial progress in the field of quantitative genetics associated with highly accurate parentage assignment have allowed the development of powerful analyses of phenotypic variation in wild vertebrate populations (Kruuk 2004; Kruuk et al. 2008; Wilson et al. 2010; Postma 2014). Particularly, the "animal model" has been repeatedly used to extract variance components of phenotypic traits (Lynch and Walsh 1998; Kruuk 2004; Kruuk et al. 2008; Wilson et al. 2010). This method is based on linear mixed effects models and makes use of the phenotypic resemblance between individuals of known relatedness in complex pedigrees, in order to compute quantitative genetic parameters of ecologically relevant traits (Postma and Charmantier 2007; Postma 2014). Evolutionary biologists are particularly interested in the narrow-sense heritability h^2 (the contribution of additive genetic variance to phenotypic variation), as it is part of the breeders' equation (Falconer and Mackay 1996) that allows to determine the microevolutionary response to selection from one generation to the next: $h^2 \cdot S = R$, where S is the selection differential and R the response to selection (Postma and Charmantier 2007)

The goal of this project was to use the animal model on a long-term vertebrate study in order to estimate the heritability of body size and to test the effect of a suite of environmental factors, both climatic and social, on adult body size. Here, I used an individual-based 12-year dataset of purple-crowned fairy-wren tarsus measurements, a widely used measure of skeletal size in birds.

The purple-crowned fairy-wren (*Malurus coronatus coronatus*) is a passerine bird in decline, endemic of northwest Australia (Rowley and Russel 1997; Skroblin and Legge 2013; BirdLife International 2016). This species is a riparian obligate and its patchily-distributed populations are threatened by

habitat degradation and loss, as well as climate change (Skroblin and Legge 2013). In this species, changing climatic conditions such as higher temperatures and extreme rainfall are associated with lower reproductive success (Hidalgo Aranzamendi et al., in prep), and may also impact body size and its physical and social functions. The importance of this trait in the purple-crowned fairy-wren is supported by a consistent sexual size dimorphism (Rowley and Russel 1997; Kingma et al. 2011a), and by the fact that males advertise their size through their songs (Hall et al. 2013).

First, I show that the study population has been experiencing a weak increase in size over the study period. Then, I analyze the influence of several climatic variables on this morphological trait. I hypothesized that higher mean temperatures and a higher number of extreme days (both temperature- and rainfall-wise) during the nesting period would lead to smaller birds. On the other hand, I hypothesized that higher cumulative rainfall would be beneficial, as it is known that rainfall usually increases food abundance and triggers nesting in this species (Hidalgo Aranzamendi et al., unpublished data). I also analyze the effect of territory quality, social group size during the nesting period, and brood size. I hypothesized that higher territory quality and group size would be associated with longer tarsi, whereas larger brood sizes would result in smaller birds due to intra-brood competition for parental feeding. Then, I use narrow-sense heritability as a crude measurement of evolutionary potential in order to provide a first step to understanding the evolvability of body size in this species. Since males and females may face different evolutionary challenges, the selection pressures acting on their body size may differ in strength and direction. Thus, I finish by calculating the cross-sex genetic correlation of tarsus length, and thereby aim to estimate how independent or constrained the evolution of male and female body size is (Teplitsky et al. 2014).

MATERIALS AND METHODS

Study site and population

The study site is localized at Mornington Wildlife Sanctuary (managed by Australian Wildlife Conservancy), in northern Western Australia (17.51° S, 126.11° E). A local population of purple-crowned fairy-wrens is distributed along approximately 15km of river stretches on Annie Creek and the Adcock River and has been monitored on a regular basis since 2005. Between 2005 and 2010, the population was monitored weekly year round, while from 2011 onward, census was conducted twice a year: in May-June and in November, following the breeding peaks. The population consisted of 117 birds in 2005 and reached 228 in 2016 (247 in June 2017), of which all were banded with unique colour combinations and further identified by a unique band number. Blood samples were taken on most birds for parentage analysis with microsatellite markers.

Purple-crowned fairy-wrens are sexually dimorphic, most notably in plumage colouration (Figure 1). Adult males are slightly larger and have a grey to purple cap and black cheek patches, while females have a grey cap, a white eye ring and rufous cheek patches. Males and females usually pair up for life and breed cooperatively with a social group that occupies a discrete territory (Rowley and Russel 1993; Margraf and Cockburn 2013; Hidalgo Aranzamendi et al. 2016). Territories are always located along river stretches and they vary in length between ~25-380 meters (Kingma et al. 2011a and current situation). Groups are composed of the dominant breeding pair and 0-8 subordinates. The subordinates are mostly (~60%) the offspring of the dominant pair (Kingma et al. 2011b) and may contribute to offspring care and territory/nest defence, thereby improving reproductive success and survival of the breeding pair (Hall and Peters 2008; Kingma et al. 2010; Kingma et al. 2011b). Most of the breeding occurs during and shortly after the wet season (December to March), although nests can be found active at any time point in the year, with a second more minor peak in September-October (Peters et al. 2013).

Field data collection

Tarsus length measurements

Tarsus length is easily measured in the field and it has been used numerous times as a measure of skeletal size in birds (Postma 2014). As opposed to body mass, it is known to be relatively repeatable within individual birds (see section below). In the field, tarsus length was measured with a caliper, from the lower end at the base of the digits to the knob between tarsus and tibia (Figure 2). When time constraints allowed it, tarsus was measured twice at each capture event, and then averaged for that capture before being implemented into statistical analyses. Tarsus length was measured every time a bird was caught, hence the repeated measurements in the dataset.

Aging of measured birds, data inclusion and repeatability

The initial dataset contained all measurements of all fledged birds, regardless of age. Birds that fledged during one of the field seasons were aged with high accuracy, while birds banded later after fledging were aged using morphological and plumage criteria: juveniles maintain flanges until several weeks after fledging, have a brown cap, rufous cheek patches and a growing tail. An estimated hatch date (YY-mm-dd) as well as a hatch year were attributed to each bird. Hatch year follows the austral calendar, starting on July 1 and ending on June 30. In order to determine whether all measurements should be included regardless of age at measurement, the tarsus lengths of fledglings (between 14 and 89 days old) and adults were visually (Figure 3) and formally compared in a linear mixed effects model that included age (fledgling vs. adult), sex and an age:sex interaction as fixed effects, and measurer and individual ID as random effects. For this analysis, only birds that were aged with an accuracy higher than $\pm$ 3 months were included ($n_{measurements}$ = 1130, n_{ind} = 503). The age:sex interaction had little effect on tarsus length (Estimate$\pm$SE (adult:male) = -0.039$\pm$0.062mm, p=0.53), and the tarsi of adults were slightly longer than those of fledglings, but the difference was not significant (Estimate$\pm$SE (adult) = 0.061$\pm$0.048mm, p=0.20). As a result, all birds caught and measured after fledging were included in the final dataset.

The repeatability of tarsus length measurements was 0.87 (CI: [0.84, 0.89]), calculated as $V_{ID}/(V_{ID} + V_{residual})$ with a simple linear mixed model run on the entire data set: $n_{males} = 372$, $n_{females} = 344$, measured by 16 measurers (number of measurements by measurer ranged between 1 and 489) between 2005 and 2016. The model included sex and measurer as fixed effects, and individual ID as a random effect. As I expected a higher within-individual repeatability, I kept using measurer as a random term in all my models, to account for between-measurer differences.

Territory quality

In the study region, purple-crowned fairy-wrens solely reside in close association with riparian vegetation containing the palm-like tree *Pandanus aquaticus* (Kingma et al. 2011a). Purple-crowned fairy-wren territories vary in the density, width and height of *Pandanus* patches, and territories with greater *Pandanus* cover sustain larger groups, indicating that these territories are more productive (Kingma et al. 2011a). Furthermore, a vast majority of nests are built in the crowns of that plant species (Kingma et al. 2011a, Niki Teunissen, pers. comm.), emphasizing the importance of this association. Thus, *Pandanus* cover was used as a measure of habitat quality for each individual territory. It was quantified along the territory by one observer assigning a score between 0 (absence) and 10 (extremely dense and high patch) every 50m (2005-2008, 2013) or every 25m (2015) on each side of the river/creek. The scores for both sides were added up to a maximum score of 20. If a territory was longer than 50m/25m, all scores within the territory were averaged to a single score per territory.

In years when *Pandanus* cover was not quantified in the field (2009-2012, 2014, 2016), the missing values were estimated from a straight line drawn between the closest field measurements, assuming the change in territory quality followed a linear trend, as shown by long-term data (Supplementary Figure 1). When only earlier or later measurements were available, the missing value was replaced by the closest field measurement (e.g. 2016 territory qualities are approximated by the 2015 measurements).

Social group size and brood size

Social group size was defined as the number of adult and fledged birds present in the territory at the time of hatching. This includes parents, adult subordinates and fledglings of previous broods. The group size at hatching of each individual bird was extracted from long-term data files in two different ways for two time periods:

– 2005-2010 (continuous monitoring): all birds whose presence was recorded in the territory of interest before and after the hatch date were counted.

– 2011-2016 (biannual monitoring):. all birds observed by the end of the closest field season to the hatch date were counted. Given the slow turn-over in group composition, this is mostly accurate.

Group size ranged from 2 to 10 birds within a territory.

Brood size was defined as the number of fledglings emerging from the same nest as the individual of interest. That variable could only be attributed to a limited subset of the dataset (i.e. when nests were monitored regularly: 2005-2010, some nests in 2015-2016) and is thus only included in models that focus on accurate hatch dates. Brood size ranged from 1 to 4.

Field season of April-June 2017

The most recent field season at Mornington Wildlife Sanctuary started on 28 April 2017 and ended on 23 June 2017. During this two-month period, we set out to perform the annual monitoring tasks of the local purple-crowned fairy-wren population. These included (1) daily census of selected occupied territories, (2) assessment of habitat quality along Annie Creek and the Adcock River, (3) long-distance (~20km radius) counts of the peripheral populations of purple-crowned fairy-wrens along the tributaries that join the study area (including the Adcock, Fitzroy, Hann and Throssell rivers, Roy, and Spider creeks), (4) banding of all unbanded individuals in the study population (recent fledglings and immigrants), and (5) blood sampling of unbanded individuals for parentage assignment and of selected banded individuals for an immunological study. Although the data set was enriched with a new generation of tarsus length measurements, the measurements made in 2017 were not included in the

present analysis because parentage assignment could not be done on time. For further support of current results, the data we collected in 2017 may be included in a future publication of my findings.

Climate data

Daily climate records were obtained from the Australian Bureau of Meteorology (BoM: http://www.bom.gov.au/climate/). For rainfall, I used data from the weather station at Mornington (number 002076). In cases where rainfall records were missing (e.g. October-November 2006, 2008), the data set was completed as much as possible using the closest weather station, at the Old Mornington Homestead, about 17km away (number 002036; 17.39° S, 126.23° E). 28 days in 2006 and 120 days in 2008 had no measurement of daily cumulative rainfall.

Daily temperature minima and maxima were unavailable for the Mornington station. As a result, data from the Fitzroy Crossing (station number 003093; 18.19°S, 125.56 °E), about 95km South-West from the study area, were used. The Fitzroy Crossing data are highly correlated with data from Mornington (Hidalgo Aranzamendi et al., in prep). A total of 33 temperature records (maxima or minima) were missing from the database: I decided to approximate them by averaging the value of the previous day and that of the next day. Daily average temperature was defined as the midpoint between minimum and maximum daily temperatures.

I defined extreme climatic conditions as rainfall/temperatures exceeding the 95th percentile of daily records between 2004 and 2016 (following a definition from van de Pol et al. 2017), as these were the conditions that birds included in the analysis experienced. Following this logic, daily rainfall was considered extreme if exceeding 44.1mm, while days were considered extremely hot when their maximum exceeded 42.6°C.

Climate variables were calculated for different time intervals that I considered important for skeletal growth:

- Hatch date - 14 days: incubation lasts about 12-14 days,
- Hatch date + 14 days: nestlings fledge at 12-14 days of age, and their growth is close to being finished,

- Hatch date - 30 days: arbitrary period that should include conditions influencing female investment in eggs,

- Hatch date + 60 days: period at the end of which fledglings should have reached an adult size and start dispersing.

Climate variables of a given type (temperature or rainfall) were highly correlated, and thus only one of each was included in each model to avoid colinearity and overparametrisation (Hidalgo Aranzamendi et al., in prep).

Yearly climate trends are shown on Figure 4.

Data analysis

All analyses were conducted in R (R Core Team 2016). First, a simple linear mixed-effects model with sex and hatch year (as a linear covariate) as fixed terms and individual ID as a random term was run with lme4 (see procedure below) in order to determine whether a temporal change was detectable over the study period. Then, the significance of fixed effects (sex, climatic variables, territory quality, group size and brood size) on tarsus length was tested with (1) simple linear mixed-effects models, and (2) the animal model. The former method allows to quickly compute estimates and *p*-values, while the latter is more computationally intensive and allows to confirm the conclusions reached previously. With both methods, the models were separated into two batches, the first analyzing data form birds aged with high accuracy, while the second made use of the data from birds aged with lower accuracy. This allowed to test for the effects of climatic variables measured within different time windows around hatching time.

Linear mixed-effects models using lme4

The significance of fixed (and random) effects was first tested in a series of linear mixed effect models using the function lmer of the R package lme4 (Bates et al. 2015). All fixed effects were not tested within the same model to avoid strong correlations between environmental predictors. All *p*-values were obtained from F statistics (fixed effects) and likelihood ratio tests (random effects) using

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lmerTest (Kuznetsova et al. 2016). The homoscedasticity of residuals was assessed visually, and none of the models deviated strongly from this assumption. The continuous fixed terms (group size, brood size, territory quality and climate variables) were scaled and centred to improve model convergence and to increase the comparability of estimates (Schielzeth 2010). Indeed, the estimates then represent the change in tarsus length for one standard deviation of the predictor. Random effects in all models consisted of individual ID, nest ID (only available for a subset of the data) or natal territory ID, measurer, hatch year, genetic mother ID and genetic father ID.

Animal models using MCMCglmm

Following the methodology described by Wilson et al. (2010) and the tutorial by Pierre de Villemereuil (available on: http://devillemereuil.legtux.org/wp-content/uploads/2012/12/tuto_en.pdf), several animal models were run to confirm the trends unveiled by the linear mixed models. The animal model makes use of all the information present in a pedigree by computing the relatedness of each individual to all other individuals in the dataset (Kruuk 2004; Wilson et al. 2010). The pedigree used in all animal model analyses is illustrated on Supplementary Figure 2 and includes 6 generations of measurements.

I took a Bayesian approach and implemented Markov Chain Monte Carlo general linear mixed effect models (MCMCglmm). All models were fitted with relatively uninformative priors: inverse-gamma distributed priors (variance V=1, nu=0.002). Fixed effects were considered significant when the 95% credible interval of their posterior mean did not overlap 0, which was further supported by low pMCMC values. pMCMC is the posterior probability that the parameter is not different from zero (it is not a p-value but provides a similar kind of information) (Wilson et al. 2010). The relative contribution of random terms to tarsus length was assessed using the posterior mean and credible intervals of their variance component. Random terms in all models included breeding values (computed from the pedigree), nest ID/natal territory ID, individual ID, hatch year and measurer.

All models with only sex as a fixed effect were run with the following parameters: number of iterations = 1001000, burnin = 1000 and thin = 1000. Models with more fixed effects were run for a

longer time and with a longer burnin, to make sure they would converge and sample uncorrelated iterations: number of iterations = 2005000, burnin = 5000, and thin = 1000. All MCMCglmms were checked for problems arising from autocorrelation of iterations and model convergence. The former was done visually by looking at the track and the posterior distribution of estimates and variance components, and numerically by calculating the autocorrelations between successive samples (autocorrelations between -0.05 and 0.05 were considered acceptable). The latter was tested using a Heidelberg stationarity test, where *p*-values above the arbitrary threshold of 0.05 mean that the hypothesis of convergence cannot be rejected.

All models were robust to prior modification: altering priors following the example from Wilson et al. (2010) did not change the qualitative conclusions drawn from the original analyses.

Narrow-sense heritability, after accounting for sex

The narrow-sense heritability measures the proportion of phenotypic variance (V_P) attributable to additive genetic variance (V_A). The remainder is, in simplest cases, fully attributed to environmental variance (V_E) (Postma 2014). I calculated the heritability of tarsus length from an MCMCglmm that had only sex as a fixed term (and all random terms), as it was the most influential significant factor among fixed effects in earlier analyses. The heritability after accounting for sex is thus:

$$h^2 = \frac{V_A}{V_A + V_{ID} + V_{measurer} + V_{territory} + V_{year}}$$

where V_A is the additive genetic variance component (associated with the pedigree), $V_{measurer}$ is the variance component associated with measurer effects, $V_{territory}$ is the variance component associated with natal territory effects, and V_{year} is the variance component associated with hatch year effects.

Cross-sex genetic correlation

The cross-sex genetic correlation was calculated as the cross-sex covariance divided by the geometric mean of the variances for male tarsus length and female tarsus length:

$$genetic\ correlation = \frac{cov(tarsus_{male}, tarsus_{female})}{\sqrt{var(tarsus_{male}) \cdot var(tarsus_{female})}}$$

The covariance was obtained from a bivariate MCMCglmm with male and female tarsus length as two distinct traits. The prior distribution was specified following the example of Pierre de Villemereuil (V=diag(2)/2, nu=2; see link above). The model did not include any fixed effects, and included individual breeding values (the pedigree), individual ID, measurer, natal territory ID and hatch year as random effects.

RESULTS

The full dataset included 1701 tarsus length measurements done on 716 individual birds (372 males and 344 females). Males had a mean$\pm$SE tarsus length of 24.36$\pm$0.03 mm, while for females it was 23.45$\pm$0.04mm. A simple linear mixed effects model was able to detect a positive effect of hatch year on tarsus length (Estimate$\pm$SE = 0.021$\pm$0.009, $p = 0.02$), with birds born more recently reaching larger sizes (Figure 5). Hatch year was thus included in all models as a random term in combination with nest ID or natal territory ID in order to account for common permanent environmental effects (Wilson et al. 2010).

Environmental factors influencing tarsus length

    Linear mixed effects models with lmer4

Estimates, standard errors and *p*-values of fixed effects are summarized in Tables 1 and 2. Variance components, χ^2 and *p*-values of random effects are summarized in Supplementary Tables 1 and 2. Models 1 and 6 did not include climate-related fixed effects, in order to maximize the sample size of tarsus measurements (Table 1 and 2). In contrast, models 2-5 only included measurements on birds whose hatch date was estimated with an accuracy of < 1/2 month (Table 1). In the latter models, brood size and precise climate variables (hatch date $\pm$14 days) were included as fixed effects. Finally, models 7-10 included fixed effects that could only be estimated for birds with a relatively high hatch date accuracy (< 1 month) (Table 2).

Across all models, sex had a consistent large effect on tarsus length, with males being larger than females (Tables 1 and 2). Territory quality had no significant effect in models 1 and 6 (Figure 6A), and was therefore removed from the models that included climate variables. Across all models, group size had a negative effect on tarsus length (Figure 6B), although effect sizes were larger and *p*-values smaller in models 1-5, where this variable was calculated with greater accuracy and the sample size was smaller (Table 1). Brood size had a consistent positive effect on tarsus length (Table 1). The

mean$\pm$SE tarsus length measurement of birds who fledged alongside with no, 1, 2 or 3 broodmates was 23.63$\pm$0.09mm, 23.81$\pm$0.06mm, 24.06$\pm$0.05mm, and 24.08$\pm$0.08mm, respectively (Figure 6C). Across models 2-5 and 7-10, climate variables had very little effect on tarsus length (Tables 1 and 2). Cumulative rainfall, mean temperature and the number of extremely hot days had no detectable effect on tarsus length. The number of extremely rainy days had a detectable negative effect on tarsus length when longer pre- and post-hatching time periods were considered (Table 2), however these effects were not strong enough to reach significance when only considered at a scale of hatch date $\pm$ 14 days (Table 1). The relationship between tarsus length and climatic conditions at hatch -30/+60 days are shown on Figures 7 and 8 (for rainfall and temperature, respectively). The same plots for climatic conditions at hatch $\pm$ 14 days is shown on Supplementary Figures 3 and 4.

Animal models

Posterior means of the model estimates of fixed effects, their credible intervals and pMCMC values are summarized in Tables 3 and 4. Posterior means of the variance components of random effects and their credible intervals are summarized in Tables 5 and 6.

Models had the same structure as that of the earlier linear mixed effects models. Models 11 and 16 did not include climate-related fixed effects (Tables 3 and 4). Models 12-15 only included measurements on birds whose hatch date was estimated with an accuracy of < 1/2 month (Table 3). In the latter models, brood size and precise climate variables (hatch date $\pm$14 days) were included as fixed effects. Finally, models 17-20 included fixed effects that were calculated for birds with a lower hatch date accuracy (< 1 month) (Table 4).

The results obtained from earlier linear mixed effects models were confirmed with this Bayesian approach. Sex had a consistent large effect on tarsus length in the same direction as above (Tables 3 and 4). Territory quality had no significant effect in models 11 and 16, and was therefore removed from the models that included climate variables. Group size had an inconsistently significant negative effect on tarsus length, only detected in models 11-15 (Table 3). Brood size had a consistent positive effect on tarsus length (Table 3).

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Across models 12-15 and 17-20, the effect of climate variables on tarsus length was rarely detectable (Tables 3 and 4). Similar to earlier models, cumulative rainfall, mean temperature and the number of extremely hot days during growth had no detectable effect on tarsus length. The number of extreme rainy days had a detectable negative effect on tarsus length when longer pre- and post-hatching time periods were considered (Table 4).

Heritability and cross-sex correlation

The additive variance V_A consistently contributed to a high proportion of the total phenotypic variance (Tables 5 and 6), even higher as the number of fixed effects in the model increased. This trend is expected as adding fixed effects reduces V_P and thereby increases the result of $h^2 = V_A/V_P$ (Wilson 2008) . Individual ID, measurer, nest ID/natal territory ID and hatch year had more minor contributions to the total variation.

The heritability and credible interval calculated on the base of model 21 with only sex as a fixed effect and all random effects were 0.48 [0.37, 0.61] (Tables 4 and 6). The cross-sex genetic correlation calculated based on a model without fixed effects and all random effects was of 0.63 [0.41, 0.82] (full model output in supplementary material).

DISCUSSION

Here, I use a 12-year data set of tarsus length measurements of purple-crowned fairy-wrens to show that a limited set of environmental factors influence variation in body size. Over the study period, body size has increased, despite a lack of obvious change in climatic conditions. Environmental sources of variation included extreme rainfall events during the breeding season, social group size and brood size. The heritability and cross-sex genetic correlation suggest a potential for selection pressures to act on this trait on both sexes together and separately, and for a microevolutionary response to develop over time.

Environmental components of variation in body size

Climate

Surprisingly, cumulative rainfall in periods before and after hatching had no detectable effect on tarsus length. In the purple-crowned fairy-wren, nesting is triggered by rainfall and food availability is highest during the wet season (Hidalgo Aranzamendi et al., unpublished data). Thus, one would expect precipitation to positively affect individual growth. The breeding and population growth of tropical birds is highly sensitive to changes in the amount and timing of rainfall regimes (Brawn et al. 2016). Higher rainfall is often associated with higher breeding success in tropical insectivorous birds, as it is tightly linked with invertebrate abundance (Brawn et al. 2016, Hidalgo Aranzameni et al., in prep.). Precipitations are also beneficial in some temperate species, as it has been shown for the closely related superb fairy-wren (*Malurus cyaneus*), where rainfall favours breeding initiation and larger juveniles (Cockburn et al. 2008; Kruuk et al. 2015). One possible reason for this lack of effect of cumulative rainfall on a fitness-related trait is the selection of specific time windows that may not be the most influential. Indeed, purple-crowned fairy-wrens are long-lived and rainfall may play a role in shaping fitness-related traits at other times in their (or their parents') life. Selecting the appropriate time-window for climatic variables is challenging and renders that type of analysis complicated (Kruuk et al. 2015).

Although cumulative rainfall does not seem to affect tarsus length, higher frequencies of extreme rainfall events during critical periods can be detrimental, as shown here where the number of extremely wet days before and during skeletal growth had a detectable negative effect on tarsus length. In the purple-crowned fairy-wren, it has been shown that extreme rainfall (computed in the same way) reduces fledgling survival and the number of recruits produced per nest (Hidalgo Aranzamendi et al., in prep.). Extreme rainfall events noticeably decrease invertebrate abundance temporarily in the study area (Niki Teunissen, pers. comm.). Furthermore, feeding adults tend to be less active during rainfall events and may decrease provisioning (Hidalgo Aranzamendi, in prep.), which may explain the observed detrimental effects. Since extreme rainfall events will become more frequent in the tropics, including northern Australia (Lehmann et al. 2015; Moise et al 2015), it is possible that further phenotypic consequences will be observed in the near future.

As opposed to extreme rainfall, the above analysis did not detect any effect of mean or extreme temperatures on body size, despite strong yearly variation in these climatic variables (Figure 4). Interestingly, Hidalgo Aranzamendi et al. (in prep.) and Kruuk et al. (2015) found little or contrasting effects of temperatures on nest success of purple-crowned fairy-wrens and juvenile tarsus length of superb fairy-wrens, respectively. This suggests that the effect of temperature on nestling growth and success is either non existing, or more complex than we imagine, and further investigation with precise temperature measurements in the nest is needed.

If the effect of temperature is real but was not detected, several explanations can be brought up for the observed lack of phenotypic response. First of all, it is possible that the influence of temperature on skeletal growth is buffered by a compensation mechanism (plasticity) so that the end result of growth - adult size - is not strongly affected by variation in temperature. One example of such plasticity is the behavioural adjustments of parents when they initiate nest building and need to select an appropriate nesting site (Hidalgo Aranzamendi et al., in prep.). Nest placement can be a critical player in mitigating the impacts of environmental variation on nestling fitness-related traits (Leighton 2016; Mainwaring et al. 2016; van de Pol et al. 2017). Thus, if parents can adjust nest location to suit their

environment, the effect of climatic conditions on body size, such as precipitation and temperatures, may be buffered and hard to detect. However, behavioural plasticity can be costly (DeWitt et al. 1998) and in this case limited by the abundance of optimal nesting sites. As global climatic conditions become more hostile, the microclimate provided by well-managed habitat and vegetation will be essential for this population to mitigate climatic selection pressures on nestling growth.

A second possible explanation is that the time period covered by the dataset is not long enough to capture the effect of variation in temperatures on body size. Indeed, the most powerful analyses of long-term phenotypic variation on wild vertebrate populations were done on datasets that had been enriched by three to five decades of data collection (e.g. Sheldon et al. 2003; Mccleery et al. 2004; Postma and van Noordwijk 2005; Charmantier et al. 2006; Postma 2014; Kruuk et al. 2015), and their power to detect environmental effects on phenotypes was far greater.

Finally, it is also possible that the temperature measured at the Fitzroy Crossing weather station (see materials and methods) does not faithfully reflect the temperatures experienced by nestlings in the nest and thus adds noise to the data. More precise investigations of the effect of nest temperature on nestling growth and survival are about to start in the lab and will confirm or rule out this explanation.

Territory and social environment

Territory quality measured as the density of *Pandanus* plants had little to no effect on body size. It is likely that *Pandanus* cover is important for fitness-related traits other than body size during the nesting period. Indeed, territory quality had strong effects on risk of nest failure due to predation or floods in another study (Hidalgo Aranzamendi et al., in prep.). Knowing that floods are likely to become more frequent in the future (Lehmann et al. 2015; Moise and et al 2015), it is still a relevant factor to include in analyses of ecologically-relevant traits. It is worth noting that the study population has almost doubled since the start of the study. This population increase may be due to an increase in other aspects of habitat quality and resource availability, not accounted for with *Pandanus* cover. The slight increase in body size observed over time (Figure 5) may be linked with an increase in food availability. Testing this hypothesis would require invertebrate surveys in feeding grounds and/or

alternative measures of food abundance. A temporal decrease in body size has been associated with a decrease in food availability in some other Australian bird species, although this relationship cannot be generalized (Little et al. 2017).

Counter to my expectations, social group size during growth had a weak negative effect on body size, although inconsistent. As the number of helpers often improves nestling provisioning and growth (te Marvelde et al. 2009; Kingma et al. 2010; Liebl et al. 2016), I expected the social group size during growth to have a positive association with body size. Nevertheless, social group size as calculated here (all adult and fledged individuals present in the territory during the nesting period) does not necessarily reflect the number of birds contributing to nestling feeding in the group (Kingma et al. 2011b). A more detailed analysis of social group composition (sex and age of group members) during nesting and its effect on feeding rates and the offspring's body size would certainly help explain the observed trend. It has been previously shown that males provide more care than females in the purple-crowned fairy-wren (Kingma et al. 2011b; Margraf and Cockburn 2013). In addition, juvenile subordinates may not start helping until a certain age (145 days according to Kingma et al. 2011b), and adult birds do not necessarily help feeding (23% of subordinates did not feed nestlings in the study by Kingma et al. (2011b)). A large group size may thus not be as beneficial as a large group of helpers would. Social interactions between group members and competition for limited food resources may decrease provisioning, leading to decreased offspring growth and smaller fledglings. In closely related red-winged fairy-wrens (*Malurus elegans*), where males and females provision at comparable rates, Brouwer and colleagues (2014) found that nestlings were fed and grew more in the presence of female than male helpers. Particularly, they show that group members reduced their individual provisioning rate as the number of male helpers increased, while they kept it constant when the number of female helpers increased. Thus, the composition of the social environment within a territory during nesting may have dramatic effects on offspring phenotypic traits.

Once again, my expectations were contradicted by the data and birds that fledged with more broodmates were notably larger than birds from smaller broods (Figure 6). The trade-off between "many small and few large" offspring has been known by animal ecologists for several decades (Smith and Fretwell 1974; Brockelman 1975), and is derived from the limited allocation of resources by parents between the quantity and quality of offspring. The correlation between the number and size of offspring is thought to be negative, even at the genetic level (e.g. Garant et al. 2008). However, this trade-off is often difficult to show empirically, and a positive relationship between quantity and size of offspring has been observed repeatedly (>23% of studies in the review by Christians 2002). Interestingly, a handful of recent studies found that the relationship between offspring (or egg) size and number can be modulated by maternal body condition/environmental conditions in both intensity and direction (Schroderus et al. 2012; Lim et al. 2014; Pellerin et al. 2014). Purple-crowned fairy-wrens are opportunistic breeders, and offspring quickly transition from the egg to fledging, in less than a month (Rowley and Russel 1993). Parents are highly responsive to environmental cues of food availability and initiate breeding shortly after rainfall, matching peak food abundance (Hidalgo Aranzamendi et al., unpublished data). Thus, it is likely that the good conditions that allowed a female to lay four eggs that hatched successfully will allow the resulting nestlings to grow into large birds. In contrast, a small clutch produced by a female in poorer condition may have to deal with relatively poor conditions during the entire growth period. This hypothesis should be formally tested by taking measures of food abundance, parental and helper condition and by trying to relate them to offspring growth and body size.

Genetic component of variation in body size

Although several environmental factors were associated with adult body size in this study, about half of the phenotypic variation was explained by additive genetic variance. The heritability of tarsus length calculated here is comparable to previous estimates obtained with the animal model in other species: Postma (2014) looked at 22 different heritability estimates of tarsus length heritability in various bird species, and found a mean $\pm$ SE h^2 of 0.54$\pm$0.033. The estimate presented here accounts

for sex effects, and does not consider any other fixed effect. The nature and number of fixed effects included in models used to calculate heritability estimates are often overlooked and can change the value of h^2 and its evolutionary interpretation (Wilson 2008). As the sexual dimorphism was already observed by others before me (Rowley and Russel 1997; Kingma et al. 2011a; Hall et al. 2013) and confirmed here, I think it appropriate to include sex in the calculation. A sexual size dimorphism was consistently observed across all models, with males having longer tarsi than females. This may mean that the body size of each sex has been under contrasting intensities/forms of selection over time. For a morphological trait, the cross-sex genetic correlation of tarsus length calculated here is relatively low. Poissant and colleagues (2010) reviewed the cross-sex genetic correlation of a suite of phenotypic traits in 114 studies, and found a mean $\pm$ SE correlation coefficient of 0.80 ± 0.03 for morphological traits (n=352 coefficients). From their meta-analysis of the relationship between cross-sex genetic correlations and sexual dimorphism, they conclude that a low correlation is associated with a strong sexual dimorphism. Thus, a relatively low cross-sex genetic correlation may allow for independent microevolutionary adjustments towards each sex's evolutionary optimum. Over the study period, males and females do not show a strong sign of differential responses to selection (Figure 5), although this may be detectable over longer time periods, with more variation in environmental conditions, and with a formal selection analysis. Whether the overall increase in tarsus size over time observed here is due to a microevolutionary response or to phenotypic plasticity requires further investigation.

The likelihood that wild animal populations can respond fast enough to changing environmental conditions will ultimately depend on whether their response is genetic or plastic. As of yet and to my knowledge, only three studies have determined whether the observed change in body size was due to microevolutionary change or to plasticity (Teplitsky et al. 2008; Husby et al. 2011; Gienapp and Merilä 2014), and all three concluded that the change in body size was due to plasticity. Phenotypic plasticity is very unlikely to provide long-term solutions to continued, directional change in climatic conditions (Gienapp et al. 2008; Visser 2008; Gardner et al. 2011), as it can be costly and has a limited scope. Consequently, in order to understand and predict future evolutionary trajectories of fitness-related traits such as body size, it is essential that researchers focus their attention on the complexity

underlying the effects of climatic conditions on such traits, take other environmental variables into account, and develop analytical tools to distinguish plasticity from microevolutionary responses.

Overall, this study provides a stepping stone for further investigation on the evolution of body size in the purple-crowned fairy-wren and calls for detailed selection and fitness analyses on this important trait.

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FIGURES AND TABLES

Figure 1 - Adult pair of purple-crowned fairy-wrens. Female (left panel) and male (right panel). Unbanded members of the same dominant pair along the Throssell River. Size dimorphism is not visible to the naked eye, but sexual dichromatism is obvious. Both individuals are on the same branch, for comparison. Credits: Mehdi Khadraoui 2017.
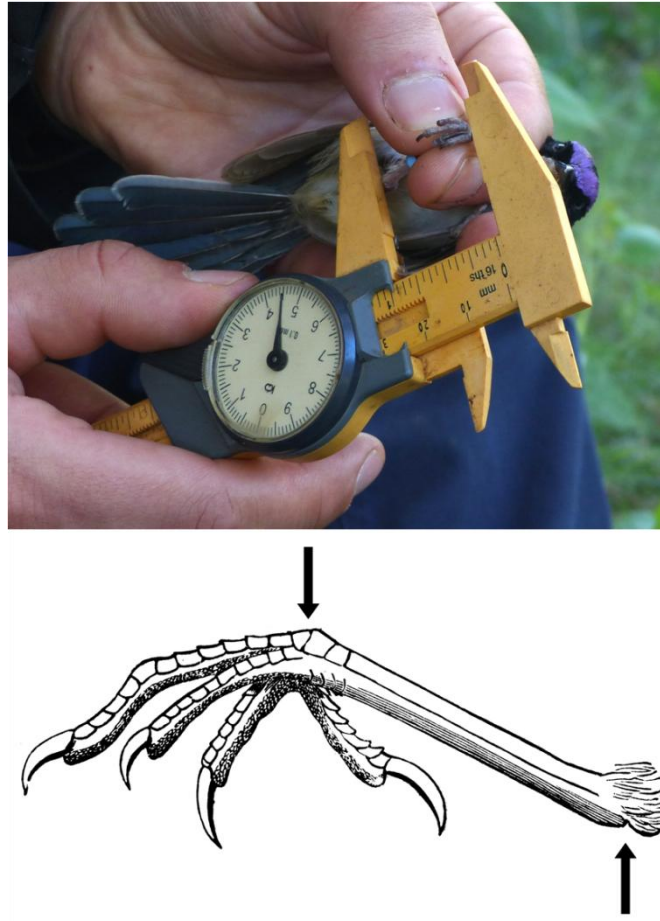
Figure 2 - Tarsus length measurement. Above: field measurement of an adult male's tarsus. Below: illustration of tarsus length limits, from the base of the digits (left) to the knob at the upper end of the tarsus (right) (adapted from Coues 1884).
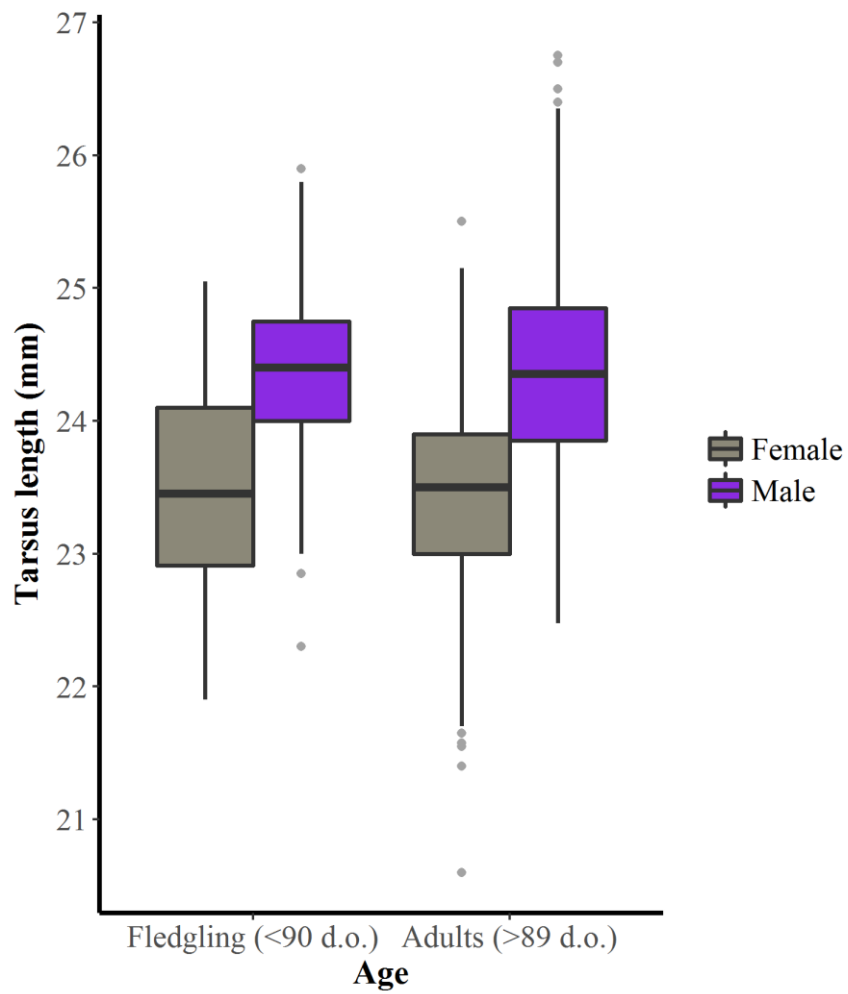
Figure 3 - Comparison of tarsus length between fledglings and adult birds. The difference is minor and not significant (p=0.218). Sample sizes: fledglings: 78 females (78 measurements) and 85 males (87 measurements); adults: 196 females (396 measurements) and 243 males (569 measurements).
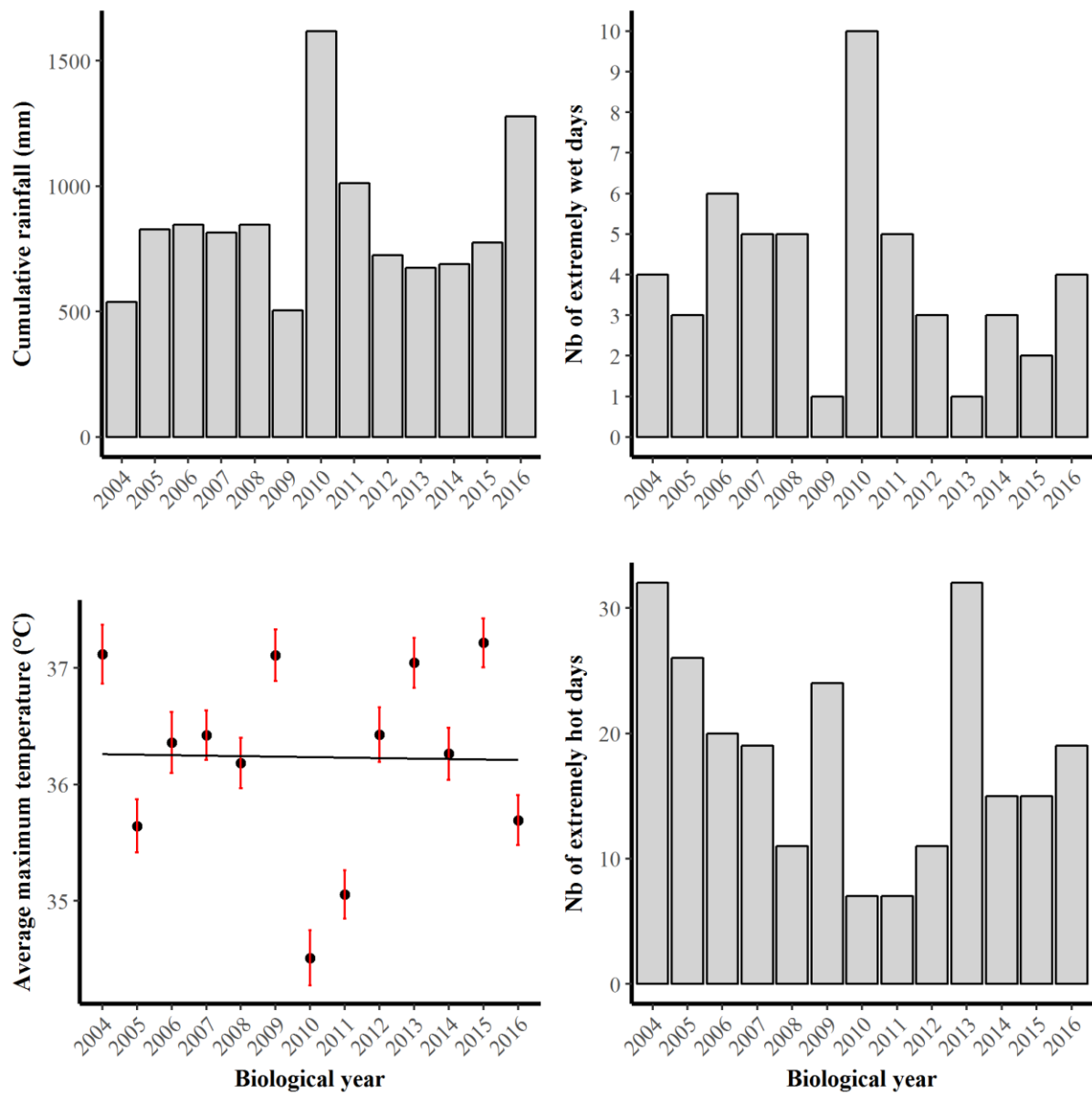
Figure 4 - Yearly trends of climate variables of interest during the study period. Top left: cumulative precipitation per biological year (July 1-June 30). Top right: number of extremely wet days with precipitations exceeding 44.1mm, per biological year. Bottom left: average daily maximum temperature and standard error per biological year, with regression line. Bottom right: number of extremely hot days with temperature maxima exceeding 42.6°C, per biological year.

Figure 5 - Effect of hatch year on tarsus length measurements in males and females. Tarsus length as a function of hatch year, defined as a biologically relevant yea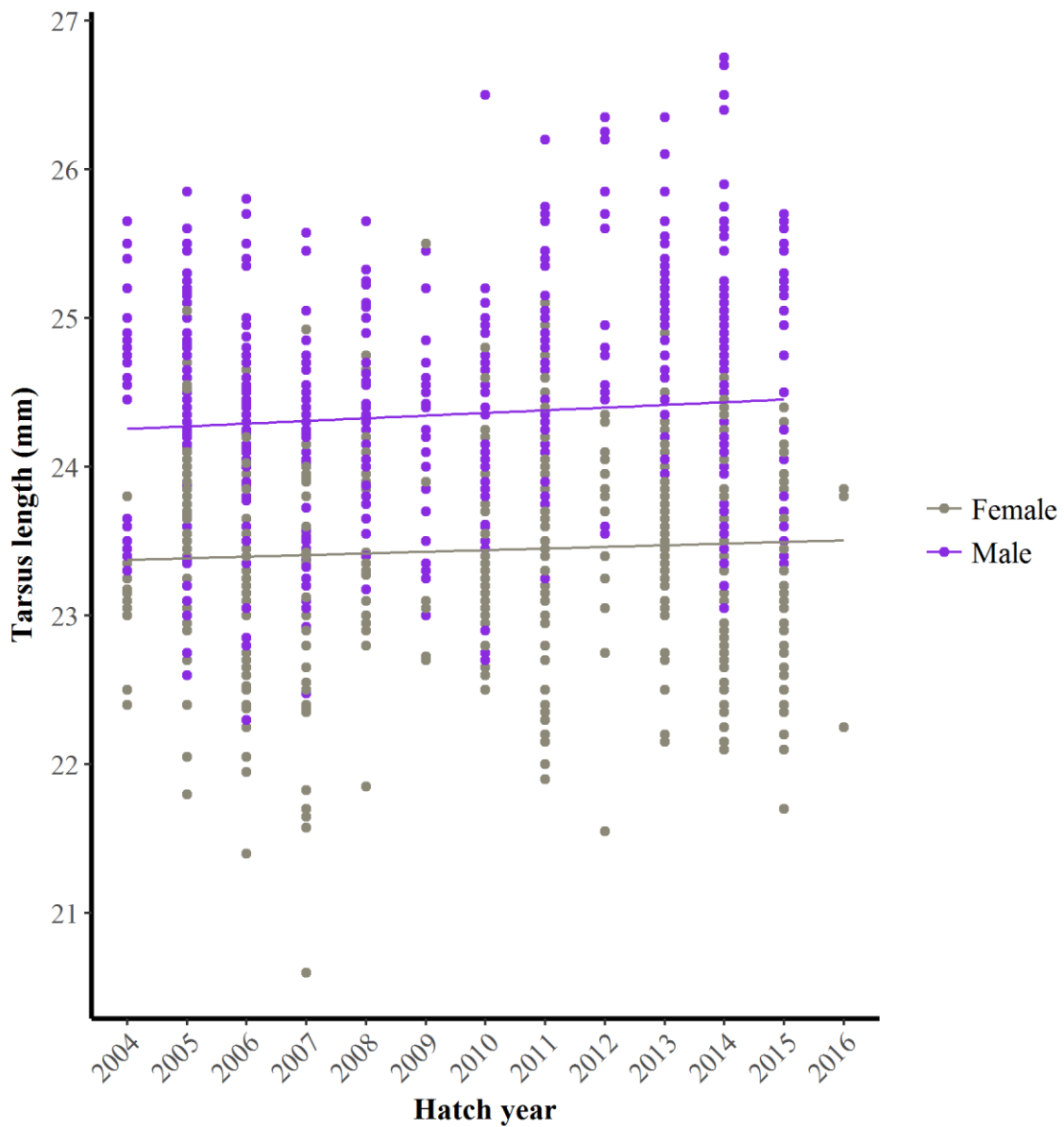r (2005 starts on 1 July 2005 and ends on 30 June 2006); regression lines are plotted separately for each sex; all birds are included except immigrants and founders of the population, whose hatch date is unknown ($n_{measurements}$ = 1235).
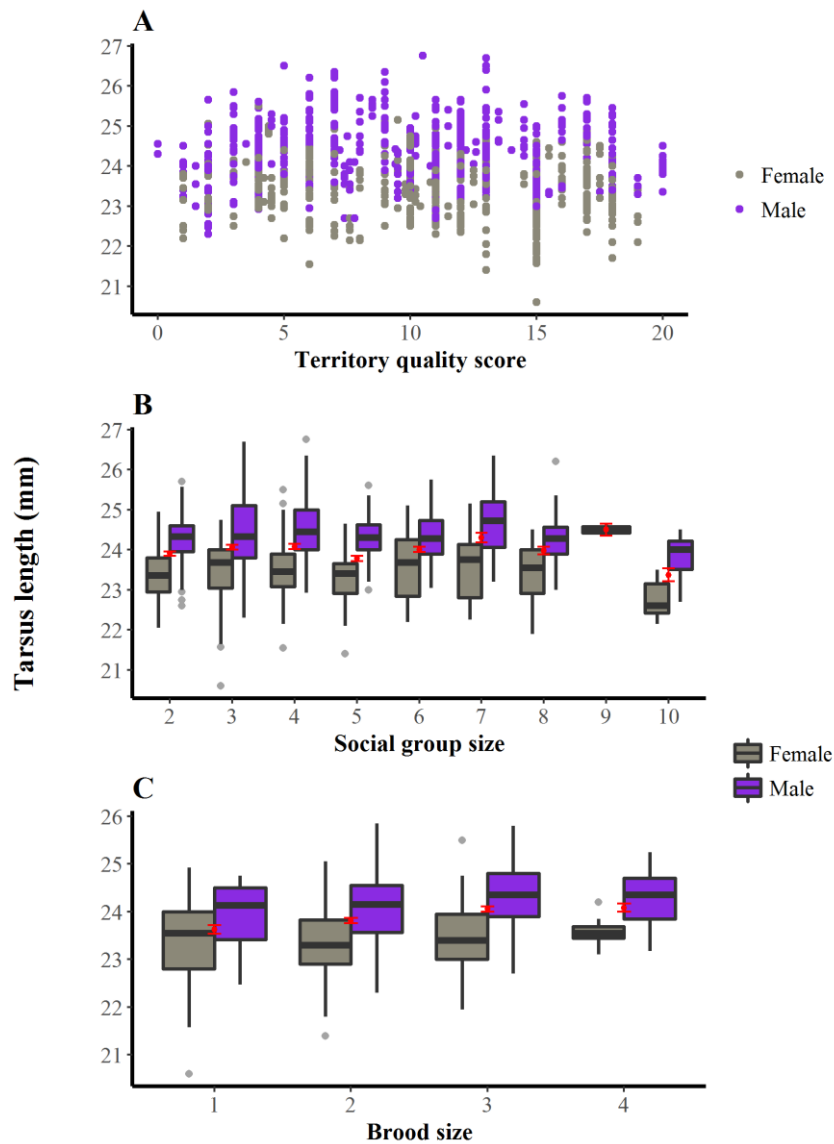
Figure 6 - Association of tarsus length and territory quality, social group size and brood size, by sex. (A) Tarsus length measurements in relation to natal territory quality in hatch year, measured as *Pandanus* cover. (B) Box plot of tarsus length measurements in relation to social group size at hatching, red dots and error bars are the mean$\pm$SE tarsus length measurement by group size, regardless of sex. (C) Box plot of tarsus length as a function of brood size, red dots and error bars are the mean$\pm$SE tarsus length measurement by brood size, regardless of sex, ($n_{measurements}$ ($n_{individuals}$) : 40 (15), 111 (46), 139 (47) and 11 (35) for males fledged in a brood of 1, 2, 3, and 4 birds, respectively; 51 (22), 75 (34), 68 (30) and 16 (11) females fledged in a brood of 1, 2, 3, and 4 birds respectively).

Figure 7 - Association of tarsus length measurements and rainfall variables, by sex. Left: tarsus length as a function of cumulative rainfall (including regression line and SE) and number of days with extreme rainfall during the 30 days before hatching. Right: cumulative rainfall (including regression line and SE) and number of days with extreme rainfall during the 60 days after hatching.

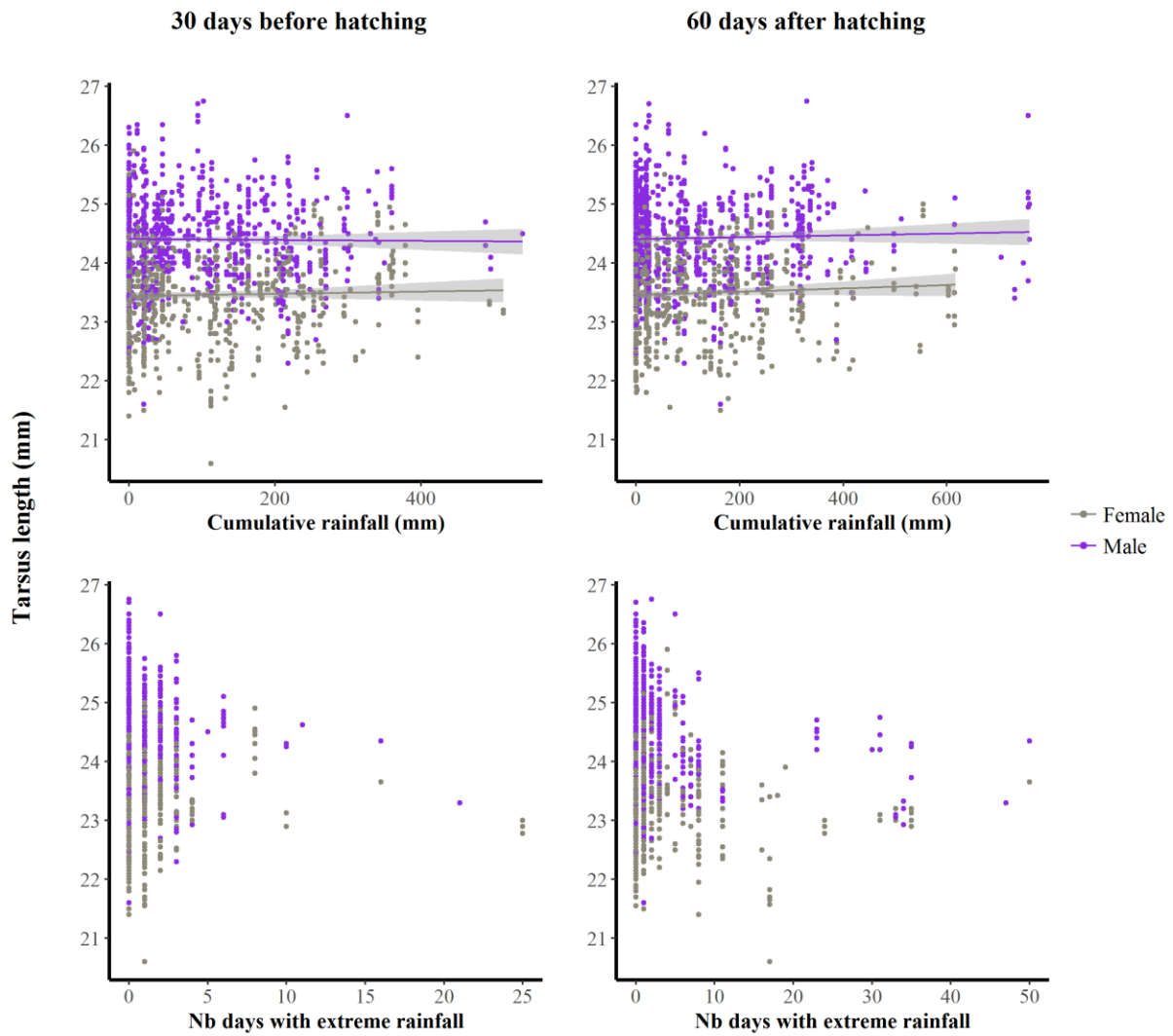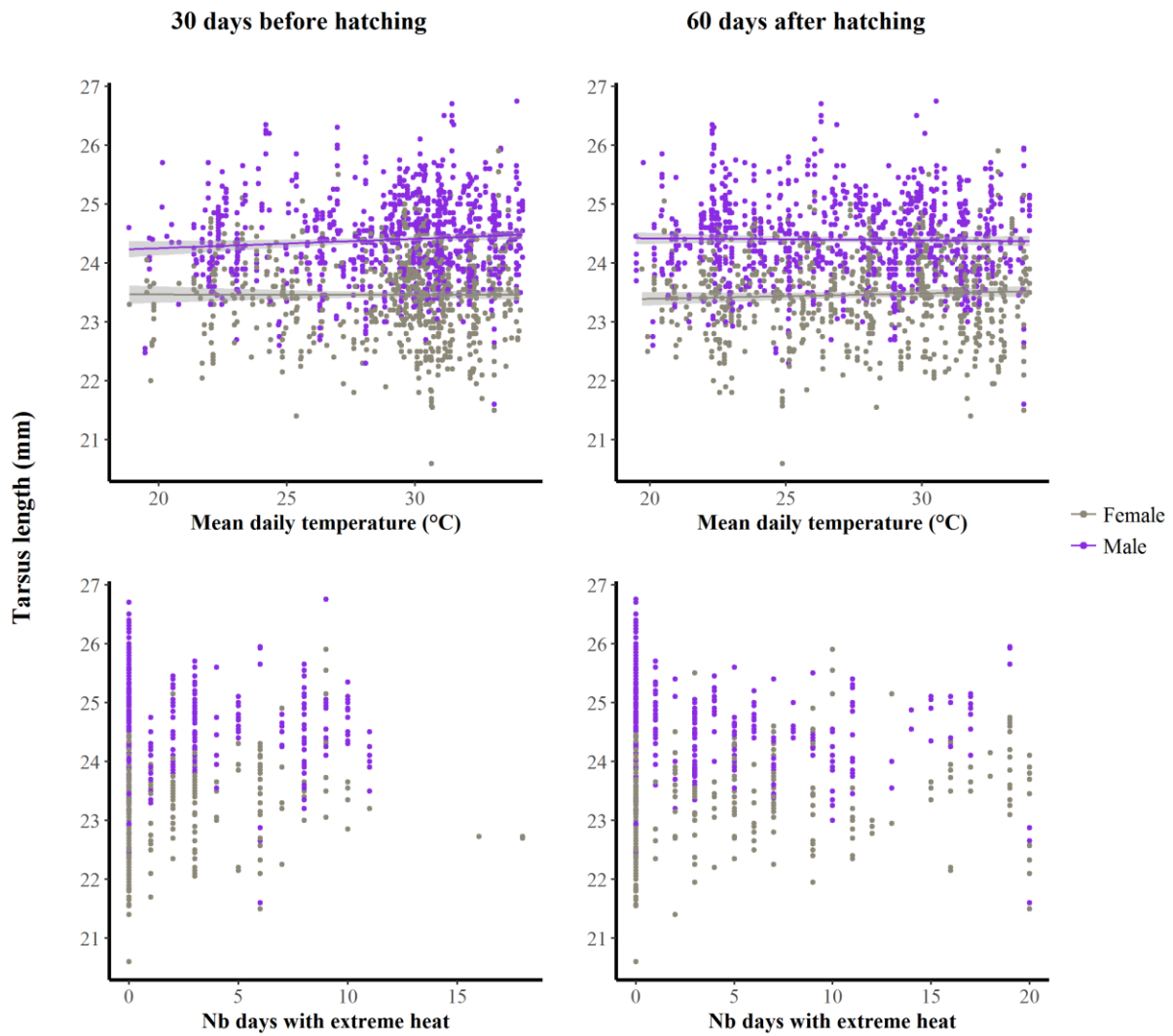**Figure 8 - Association of tarsus length measurements and temperature variables, by sex.** Left: tarsus length as a function of mean daily temperature (including regression line and SE) and number of days with extreme heat during the 30 days before hatching. Right: mean daily temperature (including regression line and SE) and number of days with extreme heat during the 60 days after hatching.

Table 1 - Estimates and associated standard errors (in mm) and *p*-values for the fixed effects of models 1 to 5. All continuous fixed effects were scaled prior to analysis. All models include birds whose hatch date accuracy is < 1/2 month. *p*-values ≤ 0.05 are in bold. Sample sizes for models 1, 2, 3, 4 and 5: 501, 481, 460, 501, 501, respectively.

Model	1	2	3	4	5
Rainfall	-	cumulative	cumulative	nb extreme days	nb extreme days
Temperature	-	mean	mean	nb extreme days	nb extreme days
Intercept	23.265±0.111	23.296±0.109	23.334±0.116	23.295±0.109	23.297±0.109
Sex (reference: female)	0.833±0.081 $p = $ <2e-16	0.929±0.086 $p = $ <2e-16	0.858±0.089 $p = $ <2e-16	0.899±0.085 $p = $ <2e-16	0.899±0.086 $p = $ <2e-16
Territory quality	-0.084±0.069 $p = 0.22$	-	-	-	-
Group size	-0.143±0.073 $p = 0.05$	-0.092±0.065 $p = 0.16$	-0.067±0.065 $p = 0.31$	-0.112±0.068 $p = 0.10$	-0.097±0.067 $p = 0.15$
Brood size	0.146±0.050 $p = 0.004$	0.010±0.053 $p = 0.06$	0.101±0.055 $p = 0.07$	0.123±0.054 $p = 0.03$	0.138±0.056 $p = 0.02$
Rainfall 14 days before hatch	-	0.039±0.058 $p = 0.51$	-	-0.065±0.041 $p = 0.11$	-
Rainfall 14 days after hatch	-	-	0.040±0.043 $p = 0.36$	-	-0.026±0.042 $p = 0.53$
Temperature 14 days before hatch	-	0.018±0.049 $p = 0.72$	-	0.001±0047 $p = 0.99$	-
Temperature 14 days after hatch	-	-	-0.003±0.052 $p = 0.95$	-	-0.040±0.055 $p = 0.47$

Table 2 - Estimates and associated standard errors (in mm) and *p*-values for the fixed effects of models 6 to 10. All continuous fixed effects were scaled prior to analysis. Model 6 includes all birds, while models 7-10 include all birds whose hatch date is known with an accuracy of < 1 month. *p*-values $\leq$ 0.05 are in bold. Sample sizes for models 6, 7, 8, 9, and 10: 1056, 1035, 943, 1056, and 1056, respectively.

Model	6	7	8	9	10
Rainfall	-	cumulative	cumulative	nb extreme days	nb extreme days
Temperature	-	mean	mean	nb extreme days	nb extreme days
Intercept	23.288$\pm$0.090	23.373$\pm$0.092	23.284$\pm$0.096	23.377$\pm$0.093	23.279$\pm$0.089
Sex (reference: female)	0.897$\pm$0.054 p = <2e-16	0.911$\pm$0.060 p = <2e-16	0.881$\pm$0.063 p = <2e-16	0.887$\pm$0.060 p = <2e-16	0.888$\pm$0.060 p = <2e-16
Territory quality	-0.056$\pm$0.043 p = 0.20	-	-	-	-
Group size	-0.021$\pm$0.034 p = 0.55	-0.002$\pm$0.040 p = 0.96	-0.003$\pm$0.042 p = 0.94	-0.014$\pm$0.041 p = 0.73	-0.014$\pm$0.039 p = 0.71
Rainfall 30 days before hatch		0.020$\pm$0.037 p = 0.59	-	-0.059$\pm$0.026 p = **0.025**	-
Rainfall 60 days after hatch		-	-0.030$\pm$0.048 p = 0.54	-	-0.100$\pm$0.030 p = **0.001**
Temperature 30 days before hatch		0.032$\pm$0.038 p = 0.39	-	-0.021$\pm$0.032 p = 0.51	-
Temperature 60 days after hatch		-	0.026$\pm$0.048 p = 0.59	-	-0.010$\pm$0.030 p = 0.74

Table 3 - Posterior means, credible interval lower and upper limits, and *p*MCMC for fixed effects of MCMCglmm models 11 to 15. These models include birds with hatch date accuracy < 1/2 month. *p*MCMC ≤ 0.05 or for which the credible interval does not overlap 0 are in bold. Sample sizes for models 11, 12, 13, 14 and 15: 501, 481, 460, 501, 501, respectively.

Model	11	12	13	14	15
Rainfall	-	cumulative	cumulative	nb extreme days	nb extreme days
Temperature	-	mean	mean	nb extreme days	nb extreme days
Intercept	23.341 [23.098, 23.581]	23.325 [23.078, 23.565]	23.351 [23.096, 23.602]	23.348 [23.125, 23.603]	23.334 [23.079, 23.581]
Sex (reference: female)	0.878 [0.700, 1.043] $p = <0.0005$	0.938 [0.783, 1.108] $p < 0.0005$	0.878 [0.687, 1.048] $p < 0.0005$	0.885 [0.722, 1.063] $p < 0.0005$	0.890 [0.735, 1.055] $p < 0.0005$
Territory quality	-0.047 [-0.178, 0.085] $p = 0.48$	-	-	-	-
Group size	-0.107 [-0.221, -0.003] $p = 0.06$	-0.087 [-0.193, 0.012] $p = 0.10$	-0.054 [-0.166, 0.046] $p = 0.325$	-0.116 [-0.221, 0.001] $p = 0.04$	-0.102 [-0.217, -0.003] $p = 0.06$
Brood size	0.128 [0.026, 0.220] $p = 0.01$	0.100 [0.002, 0.205] $p = 0.06$	0.107 [0.007, 0.221] $p = 0.06$	0.114 [0.018, 0.218] $p = 0.03$	0.137 [0.036, 0.240] $p = 0.006$
Rainfall 14 days before hatch	-	0.037 [-0.053, 0.132] $¨p = 0.42$	-	-0.051 [-0.140, 0.031] $p = 0.23$	-
Rainfall 14 days after hatch	-	-	0.052 [-0.033; 0.147] $p = 0.26$	-	-0.012 [-0.095, 0.077] $p = 0.81$
Temperature 14 days before hatch	-	0.015 [-0.078, 0.114] $p = 0.76$	-	0.027 [-0.068, 0.132] $p = 0.57$	-
Temperature 14 days after hatch	-	-	-0.014 [-0.120, 0.092] $p = 0.80$	-	-0.035 [-0.142, 0.072] $p = 0.50$

Table 4 - Posterior means, credible interval lower and upper limits, and *p*MCMC for fixed effects of MCMCglmm models 16 to 21. Models 16 and 21 include all birds, while models 17-18 include birds with hatch date accuracy < 1 month. *p*MCMC ≤ 0.05 or for which the credible interval does not overlap 0 are in bold. Sample sizes for models 16, 17, 18, 19, 20, and 21: 1056, 1035, 943, 1056, 1056, and 1701, respectively.

Model	16	17	18	19	20	21
Rainfall	-	cumulative	cumulative	nb extreme days	nb extreme days	-
Temperature	-	mean	mean	nb extreme days	nb extreme days	-
Intercept	23.402 [23.205, 23.611]	23.390 [23.179, 23.598]	23.413 [23.220, 23.623]	23.402 [23.194, 23.613]	23.404 [23.192, 23.616]	23.449 [23.308, 23.603]
Sex (reference: female)	0.903 [0.900, 1.000] *p* < 0.0005	0.908 [0.795, 1.022] *p* < 0.0005	0.882 [0.762, 0.995] *p* < 0.0005	0.888 [0.786, 1.009] *p* < 0.0005	0.887 [0.777, 0.996] *p* < 0.0005	0.915 [0.835, 1.006] *p* < 0.0005
Territory quality	-0.007 [-0.083, 0.083] *p* = 0.86	-	-	-	-	-
Group size	-0.011 [-0.077, 0.045] *p* = 0.72	-0.009 [-0.077, 0.061] *p* = 0.77	-0.005 [-0.075, 0.068] *p* = 0.92	-0.015 [-0.089, 0.058] *p* = 0.71	-0.018 [-0.087, 0.053] *p* = 0.61	-
Rainfall 30 days before hatch	-	0.010 [-0.060, 0.070] *p* = 0.75	-	-0.056 [-0.103, -0.008] *p* = 0.03	-	-
Rainfall 60 days after hatch	-	-	-0.049 [-0.139, 0.038] *p* = 0.28	-	-0.096 [-0.151, -0.039] *p* = 0.001	-
Temperature 30 days before hatch	-	0.004 [-0.061, 0.075] *p* = 0.93	-	-0.010 [-0.069, 0.047] *p* = 73	-	-
Temperature 60 days after hatch	-	-	0.022 [-0.065, 0.110] *p* = 0.62	-	-0.021 [-0.078, 0.034] *p* = 0.47	-

Table 5 - Posterior means with lower and upper limits of credible intervals for variance components of MCMCglmm models 11-15. Models include birds whose hatch date accuracy is <1/2 month.

Model	11	12	13	14	15
V_A	0.312 [0.150, 0.492]	0.344 [0.205, 0.484]	0.354 [0.219, 0.475]	0.338 [0.159, 0.488]	0.325 [0.156, 0.488]
Individual ID	0.062 [0.0003, 1.162]	0.032 [0.0002, 0.106]	0.026 [0.0002, 0.092]	0.049 [0.0003, 0.139]	0.058 [0.0002, 0.156]
Nest ID	0.0275 [0.0002, 0.089]	0.017 [0.0002, 0.057]	0.014 [0.0002, 0048]	0.025 [0.0002, 0.082]	0.027 [0.0002, 0.087]
Hatch year	0.015 [0.0002, 0.052]	0.008 [0.0001, 0.031]	0.015 [0.0002, 0.052]	0.012 [0.0002, 0.042]	0.013 [0.0001, 0.047]
Measurer	0.049 [0.009, 0.111]	0.046 [0.011, 0.103]	0.047 [0.010, 0.105]	0.048 [0.009, 0.104]	0.048 [0.012, 0.106]
Residual	0.051 [0.042, 0.060]	0.052 [0.042, 0.061]	0.054 [0.044, 0.063]	0.051 [0.042, 0.060]	0.051 [0.042, 0.060]

Table 6 - Posterior means with lower and upper limits of credible intervals for variance components of MCMCglmm models 16-21. Models 17-20 include birds whose hatch date accuracy is < 1 month.

Model	16	17	18	19	20	21
V_A	0.370 [0.247, 0.496]	0.372 [0.245, 0.478]	0.376 [0.281, 0.472]	0.344 [0.202, 0.468]	0.349 [0.211, 0.481]	0.244 [0.169, 0.316]
Individual ID	0.045 [0.0002, 0.109]	0.031 [0.0003, 0.090]	0.016 [0.0003, 0.056]	0.058 [0.0002, 0.129]	0.052 [0.0002, 0.122]	0.132 [0.089, 0.178]
Natal territory ID	0.012 [0.0003, 0.035]	0.014 [0.0002, 0.048]	0.014 [0.0003, 0.048]	0.018 [0.0002, 0.059]	0.018 [0.0003, 0.058]	0.013 [0.0003, 0.041]
Hatch year	0.014 [0.0003, 0.037]	0.011 [0.0003, 0.034]	0.009 [0.0002, 0.033]	0.015 [0.0004, 0.041]	0.009 [0.0002, 0.025]	0.010 [0.001, 0.025]
Measurer	0.052 [0.017, 0.109]	0.044 [0.012, 0.088]	0.041 [0.011, 0.082]	0.044 [0.014, 0.090]	0.045 [0.013, 0.091]	0.036 [0.010, 0.065]
Residual	0.061 [0.055, 0.069]	0.063 [0.055, 0.071]	0.065 [0.057, 0.074]	0.061 [0.054, 0.069]	0.062 [0.054, 0.069]	0.062 [0.056, 0.068]

SUPPLEMENTARY MATERIAL
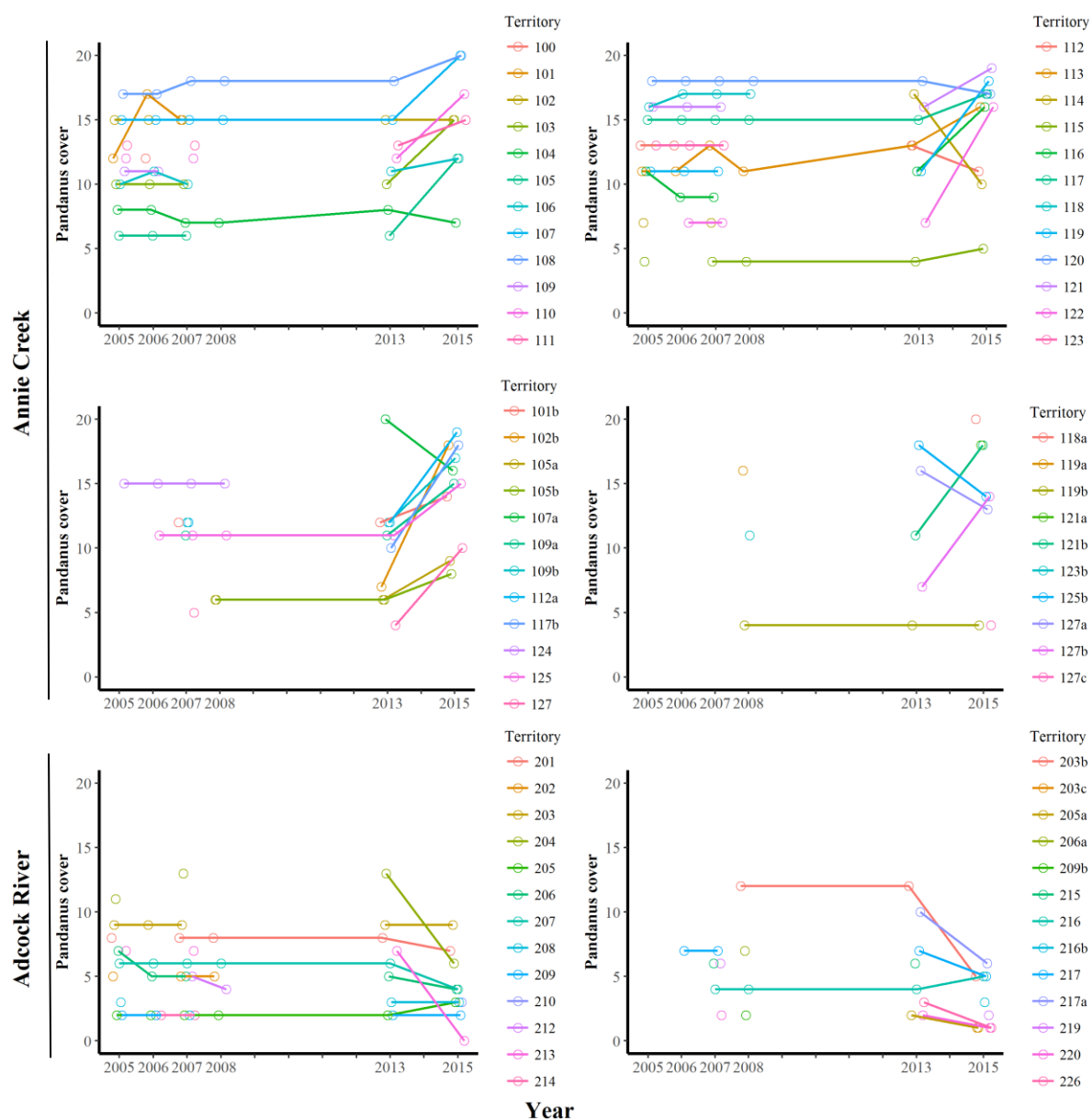
Supplementary Figure 1 - Territory quality measured as *Pandanus* cover over the study period.
Pandanus cover was measured in 2005, 2006, 2007, 2008, 2013 and 2015 (labeled years on x-axes).
The top four plots are drawn for territories located along Annie Creek (territory names starting with
"1"), the bottom two plots are drawn for territories located along the Adcock River (territory names
starting with "2"). Within plots, different colours identify different territories.
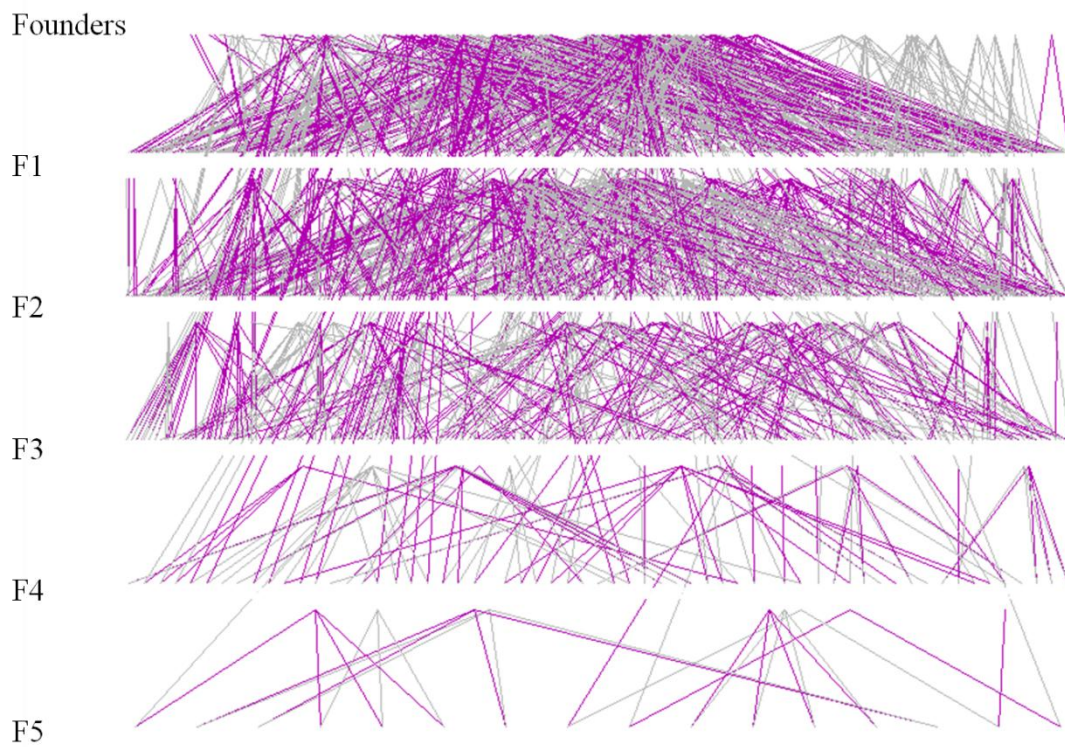
Supplementary Figure 2 - Pedigree of birds caught between 2005 and 2016. Six generations are displayed. Paternal lines are drawn in purple, maternal lines are drawn in grey. Drawn with Pedigree Viewer (Kinghorn 2011).
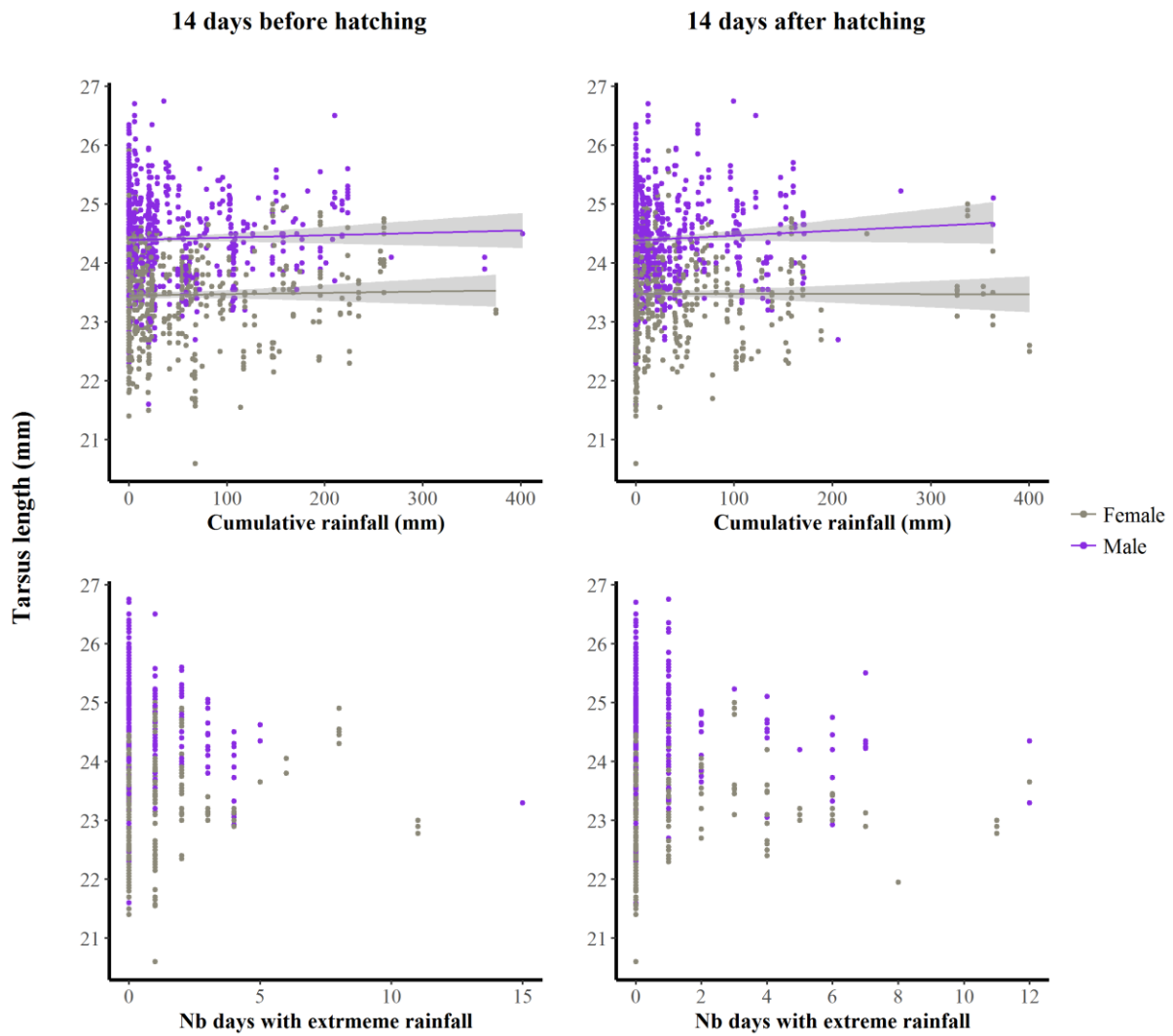
Supplementary Figure 3 - Association of tarsus length measurements and rainfall variables, by sex. Left: tarsus length as a function of cumulative rainfall (including regression line and SE) and number of days with extreme rainfall during the 14 days before hatching. Right: cumulative rainfall (including regression line and SE) and number of days with extreme rainfall during the 14 days after hatching.
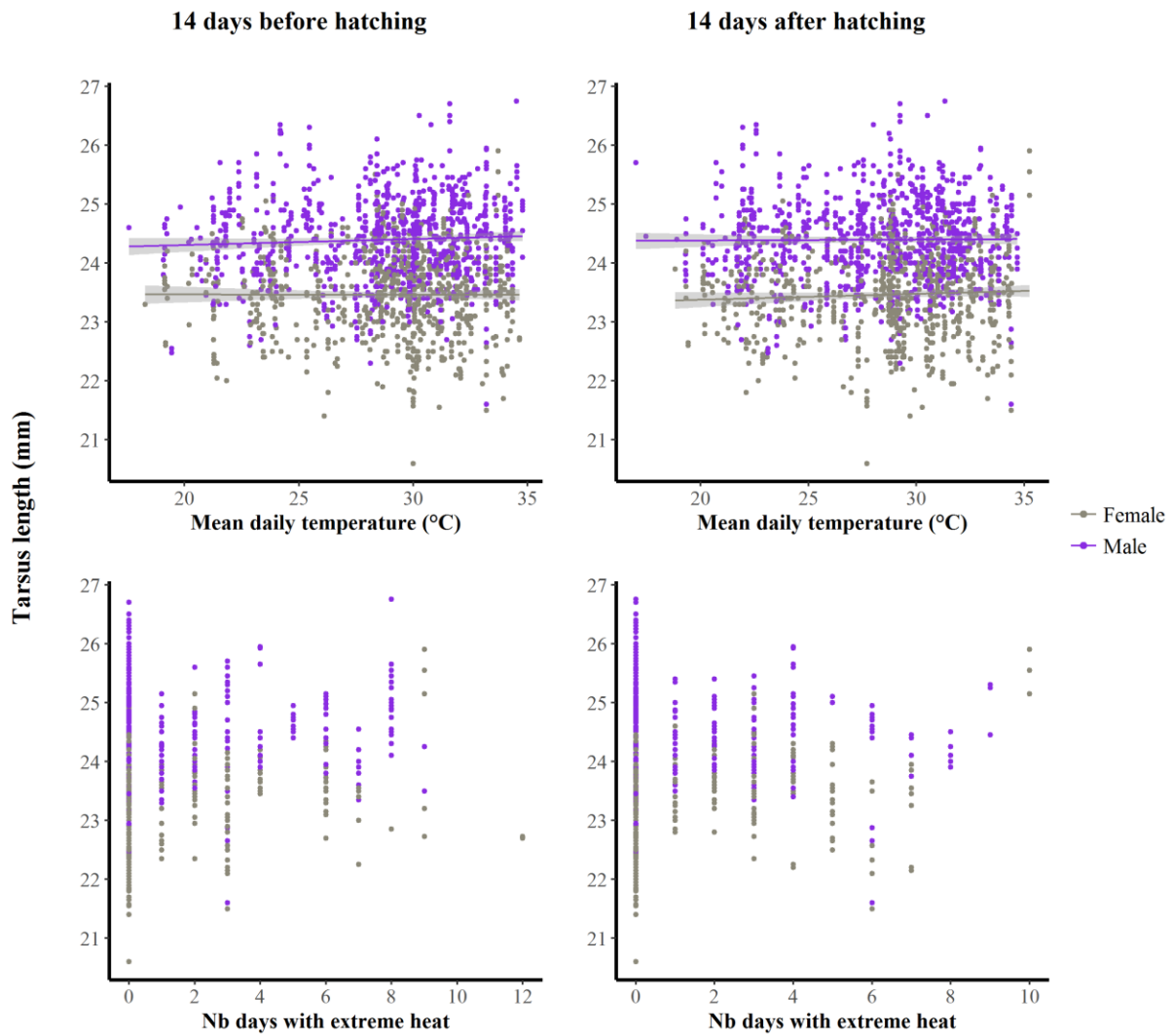
Supplementary Figure 4 - Association of tarsus length measurements and temperature variables, by sex. Left: tarsus length as a function of mean daily temperature (including regression line and SE) and number of days with extreme heat during the 14 days before hatching. Right: mean daily temperature (including regression line and SE) and number of days with extreme heat during the 14 days after hatching.

Supplementary Table 1 - Variance components of the random effects of models 1 to 5. χ^2 and p-values from the likelihood ratio tests are provided as well. p-values ≤ 0.05 are in bold.

Model	1	2	3	4	5
Individual ID	$v = 0.207$	0.191	0.194	0.195	0.195
	$\chi^2 = 205.076$	148.197	132.582	153.922	153.498
	p <2e-16	**<2e-16**	**<2e-16**	**<2e-16**	**<2e-16**
Nest ID	$v = 0.056$	0.026	0.001	0.053	0.062
	$\chi^2 = 1.436$	0.471	0.001	1.467	1.864
	$p = 0.23$	0.49	0.98	0.23	0.17
Hatch year	$v = 0.0005$	0.000	0.005	0.000	0.002
	$\chi^2 = 0.004$	0.000	0.152	0.000	0.034
	$p = 0.95$	1.00	0.70	1.00	0.85
Genetic mother ID	$v = 0.015$	0.044	0.060	0.013	0.013
	$\chi^2 = 0.088$	0.659	0.895	0.058	0.049
	$p = 0.77$	0.42	0.34	0.81	0.82
Genetic father ID	$v = 0.109$	0.143	0.156	0.152	0.140
	$\chi^2 = 5.276$	6.717	6.378	6.632	6.109
	$p = 0.02$	**0.01**	**0.01**	**0.01**	**0.01**
Measurer	$v = 0.038$	0.038	0.038	0.039	0.039
	$\chi^2 = 58.243$	46.378	45.863	48.915	49.186
	$p = 2e-14$	**1e-11**	**1e-11**	**3e-12**	**2e-12**
Residual	$v = 0.049$	0.052	0.053	0.050	0.050

Supplementary Table 2 - Variance components of the random effects of models 6 to 10. χ^2 and p-values from the likelihood ratio tests are provided as well. p-values ≤ 0.05 are in bold.

Model	6	7	8	9	10
Individual ID	$v = 0.237$ $\chi^2 = 486.955$ $p = $ **<2e-16**	0.214 356.110 **<2e-16**	0.208 291.06 **<2e-16**	0.233 404.390 **<2e-16**	0.233 390.881 **<2e-16**
Natal territory ID	$v = 0.016$ $\chi^2 = 0.168$ $p = 0.682$	0.051 1.250 0.26	0.075 2.030 0.15	0.068 2.400 0.12	0.071 2.759 0.10
Hatch year	$v = 0.011$ $\chi^2 = 3.336$ $p = 0.068$	0.010 2.200 0.14	0.013 1.400 0.24	0.012 2.600 0.11	0.006 0.781 0.38
Genetic mother ID	$v = 0.089$ $\chi^2 = 6.763$ $p = $ **0.009**	0.079 5.200 **0.02**	0.080 5.210 **0.02**	0.054 2.910 0.09	0.047 2.289 0.13
Genetic father ID	$v = 0.067$ $\chi^2 = 4.518$ $p = $ **0.03**	0.069 3.950 **0.05**	0.043 1.370 0.24	0.060 3.330 0.07	0.061 3.540 **0.02**
Measurer	$v = 0.043$ $\chi^2 = 195.554$ p **<2e-16**	0.038 129.250 **<2e-16**	0.034 104.780 **<2e-16**	0.038 130.430 **<2e-16**	0.038 130.380 **<2e-16**
Residual	$v = 0.061$	0.063	0.066	0.061	0.062

CROSS-SEX GENETIC CORRELATION - MODEL SUMMARY OUTPUT

Here is the raw output of the summary call on the model that was used to calculate the cross-sex
genetic correlation:

```
> summary(model_crosssex)

 Iterations = 5001:2004001
 Thinning interval  = 1000
 Sample size  = 2000

 DIC: 669.9898

 G-structure:  ~us(trait):animal

                                     post.mean l-95% CI u-95% CI eff.samp
traitTarsusM:traitTarsusM.animal   0.2155  0.14342   0.3024     2000
traitTarsusF:traitTarsusM.animal   0.1477  0.07651   0.2162     2000
traitTarsusM:traitTarsusF.animal   0.1477  0.07651   0.2162     2000
traitTarsusF:traitTarsusF.animal   0.2660  0.17994   0.3412     2000

            ~us(trait):Band_ID

                                      post.mean l-95% CI u-95% CI eff.samp
traitTarsusM:traitTarsusM.Band_ID  0.1225258  0.06856   0.17256    2000
traitTarsusF:traitTarsusM.Band_ID -0.0005377 -0.05460   0.05144    1838
traitTarsusM:traitTarsusF.Band_ID -0.0005377 -0.05460   0.05144    1838
traitTarsusF:traitTarsusF.Band_ID  0.1051469  0.05301   0.15493    2319

            ~us(trait):Observer

                                      post.mean l-95% CI u-95% CI eff.samp
traitTarsusM:traitTarsusM.Observer   0.11851  0.04362   0.2166     2000
traitTarsusF:traitTarsusM.Observer   0.02979 -0.03129   0.1145     1892
traitTarsusM:traitTarsusF.Observer   0.02979 -0.03129   0.1145     1892
traitTarsusF:traitTarsusF.Observer   0.12146  0.04647   0.2227     2000

            ~us(trait):NatalTerritory

                                           post.mean l-95% CI u-95% CI eff.samp
traitTarsusM:traitTarsusM.NatalTerritory   0.13044  0.06189   0.21712    1779
traitTarsusF:traitTarsusM.NatalTerritory   0.01066 -0.03492   0.06309    2000
traitTarsusM:traitTarsusF.NatalTerritory   0.01066 -0.03492   0.06309    2000
traitTarsusF:traitTarsusF.NatalTerritory   0.08852  0.04100   0.13860    2000

            ~us(trait):HatchYear

                                        post.mean l-95% CI u-95% CI eff.samp
traitTarsusM:traitTarsusM.HatchYear   0.133196  0.04268   0.25736    2000
traitTarsusF:traitTarsusM.HatchYear   0.008455 -0.06571   0.09527    2000
traitTarsusM:traitTarsusF.HatchYear   0.008455 -0.06571   0.09527    2000
traitTarsusF:traitTarsusF.HatchYear   0.115887  0.04270   0.22439    2000

 R-structure:  ~us(trait):units

                                     post.mean l-95% CI u-95% CI eff.samp
traitTarsusM:traitTarsusM.units   0.060013  0.05329   0.06680    2941
traitTarsusF:traitTarsusM.units   0.000378 -0.02212   0.02156    2000
traitTarsusM:traitTarsusF.units   0.000378 -0.02212   0.02156    2000
traitTarsusF:traitTarsusF.units   0.068955  0.05942   0.07812    2000

 Location effects: cbind(TarsusM, TarsusF) ~ trait - 1

           post.mean l-95% CI u-95% CI eff.samp    pMCMC
traitTarsusM    24.39    24.09    24.68     1841 <0.0005 ***
traitTarsusF    23.44    23.14    23.71     2000 <0.0005 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```