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Using different body size measures can lead to different conclusions about the effects of climate change

Running title: Weather effects differ with body size measure

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29 **Data availability:**

30 All data used in the manuscript are owned by the bird banders responsible for data collection.

31 Please contact Janet Gardner for data requests.

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39

Abstract:

Aim: Declining animal body size has been proposed as a general response to increasing global temperatures that should be observed across a broad biogeographical scale. However, published studies have shown large variation in both the magnitude and direction of body size trends. We aim to investigate how the way body size is measured (body mass, structural size, body condition) may contribute to differences in body size trends between studies.

Location: Semi-arid Australia.

Taxon: White-plumed honeyeater (*Ptilotula penicillatus*).

Methods: We studied two separate populations of *P. penicillatus* over 30 years to investigate the associations between weather and body size. We first investigated how body mass has been affected by weather conditions at each site and then determined how these same local weather conditions affected the constituent components of body mass (structural size and body condition).

Results: The magnitude and direction of weather effects differed with the measure of body size used. Average structural size (wing length) increased with increasing temperatures while average body condition decreased. As body mass is a composite of structural size and body condition, the magnitude and direction of body mass trends was affected by trends in these two other traits. For example, differences in temperature effects on structural size between our two sites led to clear differences in body mass trends.

Main conclusions: Trends in body size will be strongly affected by the choice of body size measure used in analyses. Change in body mass can be particularly difficult to interpret as it will be a composite of changes in both structural size and body condition. Our results indicate that it is difficult to compare studies using different measures of body size. Using consistent measures of body size will be important to better understand the general effects of climate change on body size.

Keywords: arid environment, Australia, Bergmann's rule, bird ringing, body condition, body mass, body size, climate change, honeyeater

69 **Introduction:**

70 With increasing global temperatures there has been a growing interest in identifying effects
71 of temperature change that are generalisable across a broad taxonomic and geographic range.
72 General effects have been identified in phenology and species range shifts (e.g., Parmesan,
73 2006), but more recently there has been an attempt to understand the impacts of increasing
74 temperatures on organismal body size (Yom-Tov, 2001; Meiri *et al.*, 2009; Gardner *et al.*,
75 2014). Decreasing body size may represent a common response to increasing global
76 temperatures (Daufresne *et al.*, 2009), a prediction based on Bergmann's Rule that describes
77 the tendency of animal species to be smaller in warmer, low latitude environments
78 (Bergmann, 1847). Yet considerable variation has been observed in both the direction and
79 magnitude of temporal trends in body size (Gardner *et al.*, 2011; Salewski *et al.*, 2014; Naya
80 *et al.*, 2017). Studies have reported body size declines (Yom-Tov, 2001), increases (Yom-
81 Tov & Yom-Tov, 2004; Gardner *et al.*, 2014), and lack of change altogether (Meiri *et al.*,
82 2009; Kruuk *et al.*, 2015) with increases in temperature. Understanding the causes of such
83 variation is important if we are to make general predictions about the effects of temperature
84 change on body size.

85 Body mass is commonly used as an index of overall body size (Inger *et al.*, 2014; Keinath *et*
86 *al.*, 2016), and has been proposed as a suitable metric for testing Bergmann's rule (Blackburn
87 *et al.*, 1999). However, body mass is ultimately determined by a combination of structural
88 size and body condition. These component traits may be affected differently by temperature
89 change (e.g., Canale *et al.*, 2016), making it difficult to draw conclusions on the relationship
90 between body size and temperature from analyses of body mass alone.

91 In organisms with determinant growth, early life conditions can affect growth rate with
92 consequences for adult structural size (Dubos *et al.*, 2019); however, structural size remains
93 fixed throughout adult life. Changes in the average value of adult structural size within a
94 population will therefore require a change in population composition (i.e. the ratio of small to
95 large individuals). Population composition might change via evolution across generations,
96 immigration or emigration, changes to age structure or sex ratio, or size-dependent mortality.
97 Size-dependent mortality has gained particular attention in the context of temperature change.
98 Temperature change may affect population composition if tolerance to thermal stress (either
99 hot or cold) is size-dependent. However, the expected direction of temperature effects on
100 structural size is not necessarily clear. Smaller individuals should be favoured in warmer

conditions, where a larger surface area to volume ratio increases the efficiency of heat dissipation (Mayr, 1956). However, for endotherms, the direction of size-dependent mortality may reverse as temperatures approach a species' upper thermal limits, where a larger surface area to volume ratio will lead to high rates of evaporative water loss and vulnerability to dehydration (McKechnie & Wolf, 2010).

Unlike structural size, body condition can vary within an individual over its lifetime. Changes in the average value of body condition in a population can therefore be driven by both population composition and within-individual plasticity. Like structural size, the effect of temperature change on body condition will be context dependent. In species inhabiting cold climates, warmer temperatures may alleviate energetic constraints leading to a positive relationship between temperature and body condition (Gardner *et al.*, 2018). Conversely, in species inhabiting environments closer to their upper thermal limits, warmer temperatures may cause heat stress and reduce body condition through effects on foraging, energy use, and water loss (du Plessis *et al.*, 2012; Gardner *et al.*, 2016; Smit *et al.*, 2016).

Some of the variation in body size trends reported in the literature can be attributed to true inter-specific differences, such as differences in ecological niches (Naya *et al.*, 2017); however, variation in the relationship between temperature and both structural size and body condition, and therefore also body mass, may also contribute to observed differences in body size trends. To understand this better there is a need to quantify how different body size traits may be differently affected by temperature change. To achieve this goal, it is useful to have morphometric information over a long time series so that a range of temperature conditions are encompassed and statistical power is high enough to detect small effects. Long-term bird ringing programs provide an excellent source of such data (Gardner *et al.*, 2011). In this study, we use long-term bird morphometric data to study the association between weather, body mass, and its individual components.

Climate change is predicted to increase the frequency and magnitude of temperature extremes (IPCC, 2013), which may be particularly detrimental for birds due to their relatively small body size, typically diurnal activity, and limited use of thermally buffered microsites (McKechnie & Wolf, 2010). Exposure to extreme high temperatures has been shown to cause immediate and widespread mortality (McKechnie *et al.*, 2012). However, exposure to less extreme temperatures, in the range of 30 – 40°C, can still have consequences for individual fitness even if immediate mortality is not observed (McKechnie *et al.*, 2012; Gardner *et al.*,

2014, 2016). Ambient temperatures above 35°C were associated with lower chick mass in the superb fairy-wren (*Malurus cyaneus*) (Kruuk *et al.*, 2015), while temperatures exceeding 35.5°C were linked to declines in body condition in adult southern pied babblers (*Turdoides bicolor*) (du Plessis *et al.*, 2012). Similarly, exposure to temperatures above 35°C was associated with declines in body condition of adult white-plumed honeyeaters (*Ptilotula penicillatus*) (Gardner *et al.*, 2016).

Effects of high temperatures may be ameliorated by rainfall, particularly in birds inhabiting environments where water is scarce. Birds predominantly use evaporative water loss to dissipate excess heat when ambient temperatures approach body temperature (Wolf & Walsberg, 1996), leading to a trade-off between water conservation and reliance on evaporative water loss to avoid hyperthermia (Smit & McKechnie, 2015; Smit *et al.*, 2016). In arid and semi-arid environments, rainfall may ameliorate the impacts of high temperatures by providing access to free-standing water and increasing food availability (Brown & Sherry, 2006; Gardner *et al.*, 2016). With global climate change expected to generate changes in precipitation patterns (Dore, 2005), it is important to understand how the impacts of high temperatures interact with those of rainfall.

Many previous studies of the effects of high temperature on birds have been restricted to single populations. However, studies of multiple populations will be important to account for intra-specific differences in responses to the same environmental conditions (McLean *et al.*, 2018), or spatial heterogeneity in climate change between sites (Ashcroft *et al.*, 2009). Differences in vegetation type (Martin *et al.*, 2015), the presence of cool microsites (McKechnie *et al.*, 2012), water and food availability (Smit & McKechnie, 2015; Gardner *et al.*, 2016), and topography (Suggitt *et al.*, 2017), and location within a species thermal range (Dubos *et al.*, 2019) can alter how high temperatures will affect individuals. Comparison between multiple populations will improve our understanding of how species will respond to a changing climate and provide an opportunity to identify patterns that may be generalised across populations.

This study first identifies associations between temperature, rainfall and body mass using two semi-arid populations of the white-plumed honeyeater (*Ptilotula penicillatus*; Gould, 1837), a small wide-spread passerine from the family Meliphagidae (Joseph *et al.*, 2014). We then investigate how the constituent components of body mass (structural size and body condition) are affected by the same temperature and rainfall variables to understand how changes in

these two components might explain observed body mass patterns. Our three key questions are therefore: What is the relationship between weather and *P. penicillatus* body mass (i), structural size (ii), and body condition (iii)?

We expect individual body condition to decline with increased exposure to high temperatures at both sites. At the same time, average structural size is expected to increase due to the loss of small individuals via size-dependent mortality. Given these contrasting expectations, the implications for body mass are unclear and will depend on the relative strength of body condition and structural size changes.

Materials and methods:

Here we provide a detailed overview of the methods used in our study, for a broad summary of the methods please see Appendix S1. All analyses were conducted using R (v 3.3.3; R Core Team, 2017).

Study sites

We studied two banded populations of *P. penicillatus* over a 30 year period (1986 – 2016) at The Charcoal Tank Nature Reserve (hereafter Charcoal Tank; -33.9831°S, 147.1575°E) and Weddin Mountains National Park (hereafter Weddin Mountains; -33.9386°S, 147.9872°E) in New South Wales in south-east Australia. The two study sites are 75 km apart within a fragmented agricultural landscape (Fig. 1). Despite their proximity, the sites have distinctly different characteristics. Charcoal Tank is small (86 ha) and generally flat with a combination of Mallee – Broombush shrubland (*Melaleuca uncinata*, *Eucalyptus viridis*, *E. polybractea*) and Mugga Ironbark – Grey Box woodland (*E. sideroxylon*, *E. microcarpa*). In contrast, Weddin Mountains is substantially larger (>8,000 ha) and shows topographic variation, rising 400m above the surrounding plains. It contains some Mugga ironbark forest (*E. sideroxylon*) as well as woodland communities of tumbledown gum (*E. dealbata*), kurrajong (*Brachychiton populneum*) and black cypress pine (*Callitris endlicheri*). Despite the topographic differences between sites, the elevation of ringing sites was similar at both locations.

Ptilotula penicillatus is largely sedentary, with 99.8% of ringed bird recoveries within 10km of the original ringing site (Higgins *et al.*, 2001) and no records of ringed birds moving between the two study sites over the 30 year study period. We therefore consider it unlikely that birds move to avoid harsh environmental conditions and are confident that conditions

recorded at each site reflect the environmental conditions experienced by individuals captured there.

Biological data collection

Both study sites were sampled 2-7 times annually (Gardner *et al.*, 2016). Data collection was overseen by authors Mark Clayton (Charcoal Tank) and Richard Allen (Weddin Mountains) ensuring consistency in methods. Our analysis included only adults (>12 months), classified based on plumage (Rogers *et al.*, 1990; Gardner *et al.*, 2016). We recorded mass using a Pesola balance (± 0.5 g). Wing length was measured as the length of the flattened wing chord from the carpal joint to the tip of the longest primary feather using a butt-ended ruler (± 1.0 mm). At each capture, all primaries were scored for moult. When moult status was not recorded, we estimated whether an individual was moulting based on the date of capture. Adult *P. penicillatus* are generally recorded moulting between December and March (Gardner *et al.*, 2014). We considered all individuals captured during this time as potentially moulting and all those outside these months to be non-moulting. Of the 3,036 unique captures used in this study, 16% had no recorded moulting information and were given a moult status based on the month of capture.

Wing length is considered the best single linear predictor of overall body size in passerines (Gosler *et al.*, 1998) and was used here as an index of structural size. However, measurement of wing length may be affected by bird age, due to feather wear, and sex, due to sexual dimorphism (Salewski *et al.*, 2014). A minimum age was calculated for all individuals. For birds caught in their first full year we could accurately calculate age in years at each subsequent recapture (Gardner *et al.*, 2014). Any bird first caught as an adult was given a minimum age at each subsequent recapture. Of the 2,008 unique individuals used in this study, the majority (93%) were first caught as adults and given a minimum age. As *P. penicillatus* shows no sexual dichromatism, sex could not be effectively determined using plumage. Some sexual dimorphism in wing length is observed in this species, but differences were not distinct enough to allow for reliable morphometric sexing (Fig. S1). Therefore, sex was not considered as a term in our analyses.

Accuracy of wing length measurements can be affected by feather wear between successive moults, which can influence results (Flinks & Salewski, 2012); therefore, we included an index of feather wear (months since last moult) in all statistical models with wing length as

the response variable (Gardner *et al.*, 2016). For individuals where timing of last moult was unknown, last moult was assumed to be in January, the peak month of moulting.

As we were interested in the effects of high temperatures, we include only captures from the hotter months of the year (October - March; Gardner *et al.*, 2016). We had 1,649 records at Charcoal Tank (1,041 individuals) and 1,387 records at Weddin Mountains (967 individuals). For the purpose of our analyses, all measurements were assigned to a bird 'breeding year' (July 1 – June 30; Gardner *et al.*, 2016).

Weather

We collated temperature data using meteorological station recordings from the Australian Bureau of Meteorology (www.bom.gov.au). Rainfall data were extracted from a gridded meteorological database (Hutchinson *et al.*, 2014). An overview of how weather data were collated, including interpolation of missing data, is provided in Appendix S2.

We tested for changes over time in mean annual rainfall, maximum daily temperature, and total number of days with maxima $>38^{\circ}\text{C}$ at both sites. The threshold of 38°C was based on sliding window analyses below and is similar to the threshold observed previously for the same species (Russell, 2012). All models were analysed using general(ised) linear mixed effects models with a Gaussian error distribution used for rainfall and maximum daily temperature, and a Poisson distribution (log link) used for days $>38^{\circ}\text{C}$. All models included calendar year, site and an interaction between the two, as well as a random intercept term for calendar year.

As the hotter and drier of the two sites (see Fig. 2), we expected stronger effects of climate on bird morphology in Charcoal Tank; however, this was not the case (see Results, Fig. 4).

Therefore, we carried out a post-hoc analysis to look at changes in maximum daily temperature over time within each month. We fitted general linear mixed effects models with a Gaussian error distribution and included a continuous year term and a categorical term for month, plus an interaction between the two. Calendar year was included as a random intercept term.

Sliding window analysis

We used a 'sliding window' analysis to determine the periods during which temperature and rainfall most strongly affected body mass using the R package 'climwin' (Bailey & van de

Pol, 2016; van de Pol *et al.*, 2016). We first identified a 'baseline' model to account for non-climatic effects on body mass (individual age, time of day, Julian date). Our choice of model was intended solely to optimise AICc and best account for variation in body mass due to non-weather variables (Table S1). We were not interested in making any biological conclusions from these fitted variables. We used this 'baseline' model as the basis for our sliding window analysis of maximum daily temperature, total daily rainfall, and temperature thresholds (i.e. temperature > x) over the year before capture (52 weeks) at each site. We considered 'relative' windows (days before individual measurement date) and 'absolute' windows (Julian calendar date) (Bailey & van de Pol, 2016; van de Pol *et al.*, 2016); however, as analyses using absolute windows returned no clear signals, we only consider relative windows henceforth.

At Charcoal Tank, we identified a clear relationship between body mass and our three weather variables; however, at Weddin Mountains there was no clear temperature signal. We identified a rainfall signal at Weddin Mountains which overlapped with that identified at Charcoal Tank (Weddin: 13 – 11 weeks prior to measurement; Charcoal: 29 – 2 weeks prior to measurement; Fig. S2). To allow for comparison between our two sites we therefore used the best windows found at Charcoal Tank in analyses of both sites.

Further details of the sliding window analysis can be found in Appendix S3.

Statistical models

All models were general linear mixed effects models with Gaussian error distributions and random intercepts for individual ID and 'breeding year'. Birds in moult will experience increased physiological costs (Hoye & Buttemer, 2011); therefore, we included a term for moult status (moulting or non-moulting) in all models. We created a subset of the data where both temperature and rainfall were available (1986 – 2014), leaving us with 1,483 records at Charcoal Tank (945 individuals) and 1,256 records from Weddin Mountains (883 individuals) for all further analyses.

We accounted for the effects of non-weather variables (age, Julian date, time of day), as described in Appendix S1, Step 4. We then considered effects of temperature (maximum daily temperature and days >38°C) and rainfall, plus an interaction between days >38°C and rainfall (Appendix S1, Step 5). All weather variables were mean centred.

We considered which combination of our three weather variables best explained variation in body mass, using AICc model selection (Appendix S1, Step 3).

After identifying the effects of temperature and rainfall on *P. penicilatus* body mass, we next wanted to understand the relative contribution of structural size and body condition towards observed body mass changes.

We considered the effect of temperature and rainfall on structural size (wing length) using the same windows identified as being important for body mass accounting for bird age and date in the season (Table S2). Birds moulting their longest primaries were excluded as wing length measurements of these individuals will be unreliable (24% of capture records).

To study body condition we fitted a model with body mass as the response variable but including a wing length term corrected for feather wear and age. We also accounted for effects of age, date in the season, and time of day on body mass (Table S3). This allowed us to test for changes in body mass after accounting for structural size (i.e. body condition). We excluded birds moulting their longest primaries. To test for size-dependent mortality we included an interaction between corrected wing length and each of our three weather variables.

To estimate the 95% confidence intervals for parameters in all mixed effects models we conducted parametric bootstrapping with 500 iterations. Marginal and conditional R^2 values were calculated for all models using methods described by Nakagawa & Schielzeth (2013).

Results:

Change in weather over time

Over the 30 years of study, maximum daily temperature increased at Charcoal Tank, but did not change at Weddin Mountains (Fig. 2a; Table S4). Number of days $>38^{\circ}\text{C}$ increased at both Charcoal Tank and Weddin Mountains, although this trend was weaker at Weddin Mountains (Fig. 2b; Table S4). Annual rainfall did not change over time at either site, but Charcoal Tank was consistently drier than Weddin Mountains (Fig. 2c; Table S4).

Maximum daily temperature at Charcoal Tank increased significantly over time in all months of the year except two (Fig. 3a; Fig. S3a). Weddin Mountains showed increases in temperature during the hotter months (Sep – Jan), but little or even *negative* trends in the colder months of the year (Fig. 3b; Fig. S3b).

Sliding window analyses

We identified climate windows at Charcoal Tank ($P_{AICc} < 0.05$) where maximum daily temperature, daily rainfall and days $>38^{\circ}\text{C}$ affected *P. penicillatus* body mass (Appendix S3). High temperatures (days $>38^{\circ}\text{C}$) negatively affected *P. penicillatus* body mass over a short period just prior to capture (~ 1 month; Fig. S2), representing the effect of high temperature exposure in the hotter months of the year. Rainfall (mm) positively affected *P. penicillatus* body mass 29 – 2 weeks prior to capture, effectively over the last 6 months (Fig. S2). This signal mostly encompasses rainfall over late winter and spring. Mean maximum daily temperature positively affected *P. penicillatus* body mass over a period 32 - 28 weeks before measurement. Because we are considering only birds measured in summer, this signal will reflect temperatures in late autumn/early winter, and we therefore refer to this metric as ‘Winter Temperature’ (Fig. S2).

Although the exact calendar dates at which temperature and rainfall were measured will vary between individuals, due to the use of ‘relative’ windows, we generally consider our temperature threshold window to represent conditions in the hotter months while our rainfall and maximum daily temperature windows represent conditions in the cooler months of the year.

The comparison of models with different windows are shown in Fig. S4 and S5.

Question 1: What is the relationship between weather and *P. penicillatus* body mass?

Effects of weather on *P. penicillatus* body mass differed between our two sites (Fig. 4a, d). At Charcoal Tank, there was a negative relationship between days $>38^{\circ}\text{C}$ and body mass in all top models ($\Delta AICc < 2$; Fig. 4a; Table S5). There was a positive relationship between maximum daily temperature in the colder months of the year and body mass (Table S5). The interaction between rainfall and days $>38^{\circ}\text{C}$ was included in the top model; however, 95% confidence intervals overlapped zero (Table S5).

At Weddin Mountains, there was no effect of any weather variables on body mass (Fig. 4d; Table S6).

Question 2: What is the relationship between weather and *P. penicillatus* structural size?

Effects of weather on wing length also differed between our two sites (Fig. 4b, e). At Charcoal Tank, there was no effect of any weather variables on wing length (Fig. 4b; Table S5).

At Weddin Mountains, there was a positive relationship between days $>38^{\circ}\text{C}$ and wing length (Fig. 4e; Table S6) and an interaction between days $>38^{\circ}\text{C}$ and rainfall in all top models ($\Delta\text{AICc} < 2$). The effect of days $>38^{\circ}\text{C}$ was more strongly *positive* following wetter conditions (Fig. 4e).

Question 3: What is the relationship between weather and P. penicillatus body condition?

Effects of weather on body condition were similar between the two study sites (Fig. 4c, f). At Charcoal Tank, there was a positive relationship between maximum daily temperature in the colder months of the year and body condition (Table S5). There was an interaction between days $>38^{\circ}\text{C}$ and rainfall in all top models ($\Delta\text{AICc} < 2$; Table S5). There was a slight negative association between body condition and days $>38^{\circ}\text{C}$ in mean rainfall conditions which became more strongly negative in wetter years (Fig. 4c).

At Weddin Mountains, there was also an interaction between days $>38^{\circ}\text{C}$ and rainfall in all top models ($\Delta\text{AICc} < 2$; Table S6). The effect of days $>38^{\circ}\text{C}$ was more strongly negative in wetter years, with a negative association between days $>38^{\circ}\text{C}$ and body condition during high rainfall periods (Fig. 4f).

There was no evidence for an interaction between structural size and any of our weather variables at either site (Table S5 - 6), suggesting that the relationship between body condition and weather variables was not dependent on the structural size of the individual.

Discussion:

We used long-term data from two populations of *Ptilotula penicillatus* to investigate how different weather variables affected body mass and its constituent components: structural size and body condition. Our analyses revealed differences both between body size metrics and between sites. While body condition was affected by days $>38^{\circ}\text{C}$ and rainfall, the two sites showed different changes in structural size and body mass. These results demonstrate how the choice of body size metric can affect biological conclusions, and, furthermore, demonstrate the potential for spatial heterogeneity in the effects of climate change on organismal morphology.

High temperatures ($>38^{\circ}\text{C}$) were associated with body mass decline at Charcoal Tank but not at Weddin Mountains (Fig. 4). An analysis of body mass alone would therefore suggest that *P. penicillatus* are more vulnerable to temperature change in Charcoal Tank; however, it is necessary to examine the relationship between weather and each component of body mass independently to properly assess differences between our two sites.

High temperatures (days $>38^{\circ}\text{C}$) were associated with an increase in *P. penicillatus* structural size (wing length) at Weddin Mountains but not at Charcoal Tank (Fig. 4). Structural size does not vary within the lifetime of an adult individual, so this association must be driven by changes in population composition, such as size-dependent mortality. In endotherms, small structural size is expected to be a disadvantage when environmental temperatures approach or exceed body temperature because a large surface area to volume ratio results in high rates of evaporative water loss and potential dehydration (McKechnie & Wolf, 2010). Size-dependent mortality at temperatures $>38^{\circ}\text{C}$ is consistent with our current knowledge of heat stress in arid and semi-arid birds. Inter-specific comparison of 30 arid zone birds in South Africa showed that at least 50% of observed individuals exhibited panting when temperatures exceeded 39.3°C (Smit *et al.*, 2016). For white-plumed honeyeaters in arid Western Australia this value was 37.3°C (Russell, 2012), similar to the 38°C threshold used here. Therefore, it seems likely that size-dependent mortality is one driver of the observed changes in structural size.

In addition to size-dependent mortality, structural size changes could also be a consequence of sex-dependent mortality. Higher temperatures may disproportionately impact females due to factors other than structural size (Gardner *et al.*, 2016), such as higher reproductive investment (Monaghan & Nager, 1997) or dominance related access to resources (Cunningham *et al.*, 2017). As the smaller of the two sexes, sex-specific temperature effects in *P. penicillatus* would increase average structural size; however, unlike size-dependent mortality, sex-dependent mortality will also affect sex-ratio. The weak nature of sexual dimorphism in *P. penicillatus* makes reliable sexing and analysis of sex-dependent mortality difficult; however, the use of genetic sexing or focus on more sexually dimorphic species could help disentangle size- and sex-dependent effects to provide a better understanding of the biological and demographic consequences of high temperature exposure.

The effect of days $>38^{\circ}\text{C}$ was greater following wet weather, with increased rainfall over the previous 6 months associated with greater increases in structural size. Cooler weather can

present an additional thermoregulatory challenge for endotherms (Williams *et al.*, 2015), which can be exacerbated by rainfall (e.g., Kennedy, 1970). In cold conditions, rainfall can reduce foraging success and increase heat loss by reducing the insulation capacity of feathers, leading to poorer survival, particularly for smaller individuals (Brown & Brown, 1998; Williams *et al.*, 2015). In a population of white-browed scrub-wrens (*Sericornis frontalis*), cold wet conditions in winter were directly associated with declines in survival (Gardner *et al.*, 2017), and our results appear to be consistent with these findings.

Unlike the differences between sites seen in structural size high temperatures ($>38^{\circ}\text{C}$) were associated with a decline in body condition at both sites (Fig. 4). Reduction in body condition (e.g. fat, water) may be a combination of increased energy use and water loss during evaporative cooling (Smit & McKechnie, 2015; Smit *et al.*, 2016) and reduced food intake (du Plessis *et al.*, 2012). This result builds on previous studies that have documented associations between high temperatures and loss of body condition in semi-arid species, including previous work with *P. penicillatus* (e.g., du Plessis *et al.*, 2012; Gardner *et al.*, 2016). This provides further support for consistent physiological drivers of body condition in semi-arid bird species exposed to high temperatures.

As with structural size, the association between high temperature and body condition was strengthened by rainfall, with wet conditions in winter and spring accentuating the effects of high temperatures. We expect that energetic constraints and cold stress during wet-cold winters will lead to a reduction in body condition, which in turn will impose carry-over costs on survival in summer such that birds are less able to cope with high temperatures (Brown & Sherry, 2006). Previous studies in other passerine species have shown that effects of weather on body condition in one season can have both direct and carry-over effects on survival (Gardner *et al.*, 2017, 2018). Furthermore, the temperature and rainfall conditions that were associated with reduced body condition at Weddin Mountains were also associated with larger average structural size, suggesting that declines in body condition are driving mortality in smaller individuals.

Although our results are broadly consistent with size-dependent mortality at Weddin Mountains, we failed to find direct evidence of size-dependent changes in body condition with high temperatures as might be expected if size-dependent mortality were occurring (Table S5 - 6). Therefore, we cannot discount the possibility that other factors underlie the size patterns we observed. Changes in net primary productivity (NPP) could be an alternative

driver of structural size patterns through effects on food availability, juvenile growth, and consequent adult structural size (Yom-Tov & Geffen, 2011). However, previous work on white-plumed honeyeaters at Charcoal Tank failed to find an association between adult body size and either annual NPP or that estimated over a 5-year period (Gardner *et al.*, 2014). It is also possible that larger individuals are simply more likely to be caught during periods of high temperature if they show different changes in foraging patterns or microhabitat use (Martin *et al.*, 2015; Smit *et al.*, 2016). However, without detailed individual level behavioural monitoring this possibility cannot yet be tested.

Although similar body condition patterns were observed at Charcoal Tank, there was no corresponding change in structural size, which suggests that abiotic or biotic differences between our two sites may mediate the impacts of temperature and rainfall. In their analysis of body condition in Dutch passerines, McLean *et al.* (2018) showed that population-level traits were more informative of responses to climatic variables than species-level traits. In our analysis, differing patterns of climate change between our two populations may help explain the observed differences in results. Winter conditions at Charcoal Tank, unlike those at Weddin Mountains, have become warmer over time (Fig. 3; Fig. S3). Relaxation in selective pressures during warmer winters can lead to improvement in body condition (e.g., Ozgul *et al.*, 2010), which would leave birds better able to cope with high temperatures. The difference in our results and those of McLean *et al.* (2018) provide a clear example of the spatial heterogeneity that complicates any study on the effects of climate change. Although incorporating multiple sites can be inhibitive when studying effects of climate change, our results provide an example that focussing on a single site will not fully reflect the potential impacts of climate change in other populations, even those of the same species. With only two study sites, our results provide a useful descriptive example of spatial heterogeneity in responses to climate change but are less applicable for identifying generalizable patterns. There is still a need for future studies that incorporate more study sites to help identify broad spatial patterns and quantify how particular physical and ecological conditions, such as vegetation type, elevation, or water availability, can ameliorate climate change effects.

Relationship between body mass, structural size and body condition

We provide a clear example of how different body size metrics can be affected by weather variables in different ways, demonstrating that the choice of metric used to represent body size (body mass, structural size, body condition) has the potential to affect conclusions about

the impacts of climate change on morphology. Body mass alone does not provide mechanistic insights as any changes in body mass may be the result of changes in either structural size, body condition, or both. This issue of interpretation can in turn lead to spurious conclusions. In our example, analysis of body mass would suggest that *P. penicillatus* at Weddin Mountains are unaffected by high temperatures; however, once body mass is decomposed into measures of structural size and body condition this conclusion is no longer supported.

The complexities associated with measuring body size are not unique to birds. Canale et al. (2016) reach similar conclusions in marmots when studying changes in body mass and structural size. Indeed, the composite nature of body mass is an inherent characteristic of this body size measure regardless of the taxonomic group being studied. With this in mind, studies using different metrics to represent body size will not be directly comparable, and this may explain some of the inconsistency in reported body size trends as a correlate of climate change. Using consistent measures of body size should be a goal for future studies as it will remove potential confounding effects of measurement method and allow studies to be more easily compared. Reliable comparisons between studies will be vital to draw any conclusion about decreasing body size as a common response to increasing global temperature. Furthermore, it will more easily allow for the identification of differences between species and taxonomic groups that will affect the relationship between body size and increasing global temperatures, which will provide us with a greater ability to predict the impacts of climate change on natural systems.

Figures:

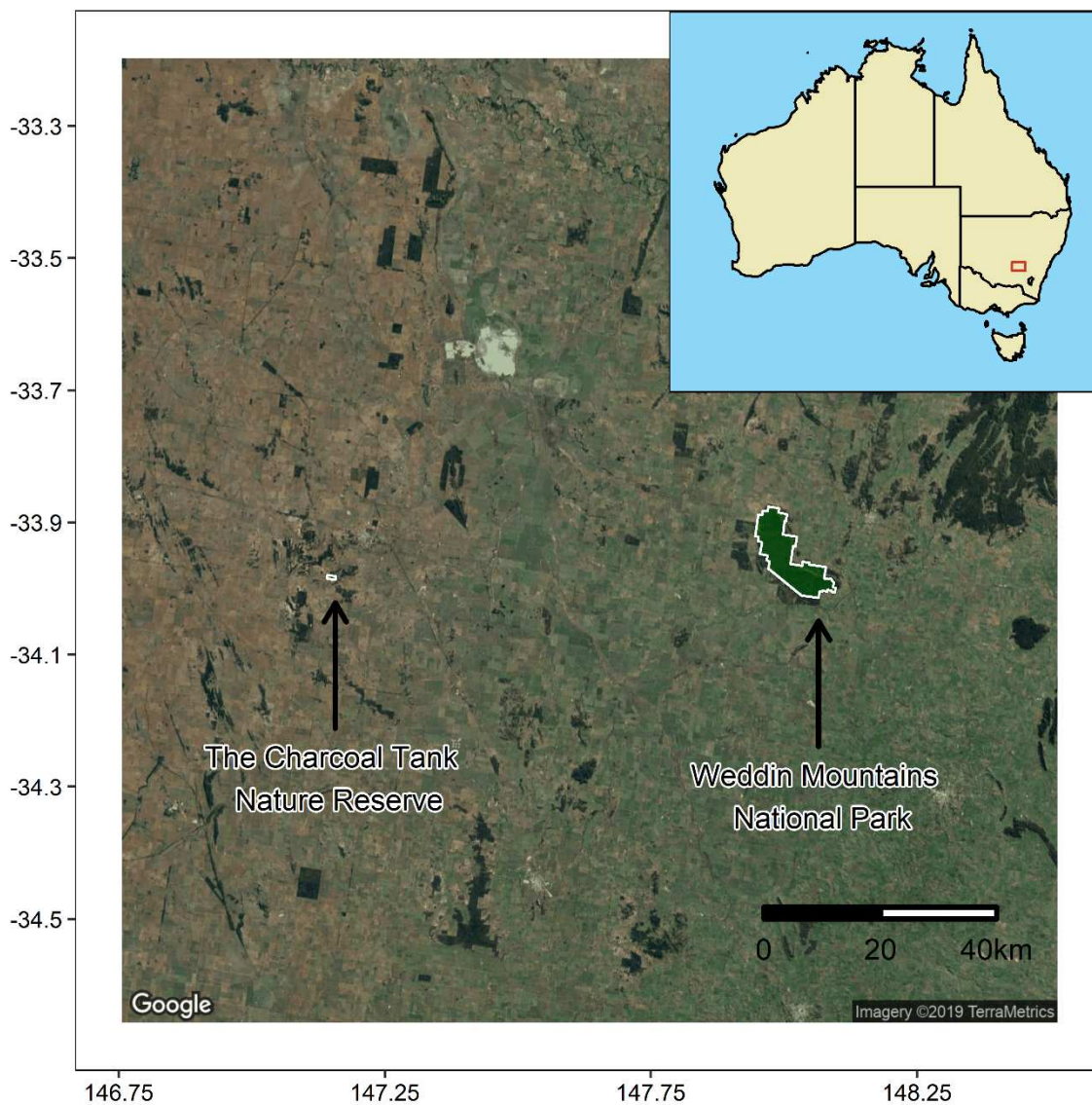
Figure 1: Map showing the location of the two study sites, Charcoal Tank and Weddin Mountains, in south-east Australia. Location within Australia can be seen in the inset. The two sites are 75 km apart. Weddin Mountains is substantially larger than Charcoal Tank (86 ha and >8,000 ha respectively).

Figure 2. Change in a) mean maximum daily temperature (°C), b) total days >38 °C and c) mean annual rainfall (mm) at Charcoal Tank (grey) and Weddin Mountains (black) in semi-arid south-east Australia. Maximum daily temperature and total days >38°C increased strongly at Charcoal Tank, more strongly than at Weddin Mountains. No change was observed over time in annual rainfall. Charcoal Tank is drier than Weddin Mountains.

Figure 3: Change in temperature (°C) over time within each month at a) Charcoal Tank and b) Weddin Mountains in semi-arid south-east Australia. Charcoal Tank has experienced temperature increases in all months of the year. In Weddin Mountains, temperatures have increased in warmer months (e.g. October – November), but have remained unchanged in colder months (e.g. June – August).

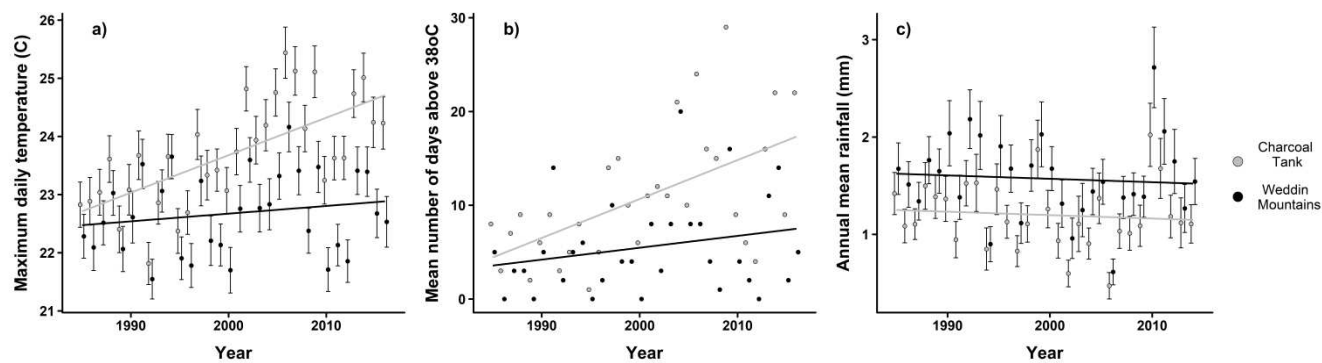
Figure 4: Association between high temperatures (days >38°C) and body mass (a, d), wing length (b, e) and body condition (c, f) of white-plumed honeyeaters (*Ptilotula penicillatus*) at Charcoal Tank (a – c) and Weddin Mountains (d – f) in semi-arid south-east Australia. Lines represent model estimates from the top model that included a term for days >38°C. Model estimates are calculated at low rainfall (25% quantile of rainfall; red) and high rainfall (75% quantile of rainfall; blue). Note that where bands overlap (e.g. a, b, d) bands will be purple. Bands around lines represent standard errors. We observe a negative relationship between high temperatures and body mass at Charcoal Tank (a) which was mirrored by a similar negative relationship between high temperatures and body condition (c). At Weddin Mountains, there was also a negative relationship between high temperatures and body condition (f); however, this did not translate into a negative relationship with body mass (d) due to counter-acting changes observed in wing length (e).

521 **Figure 1:**

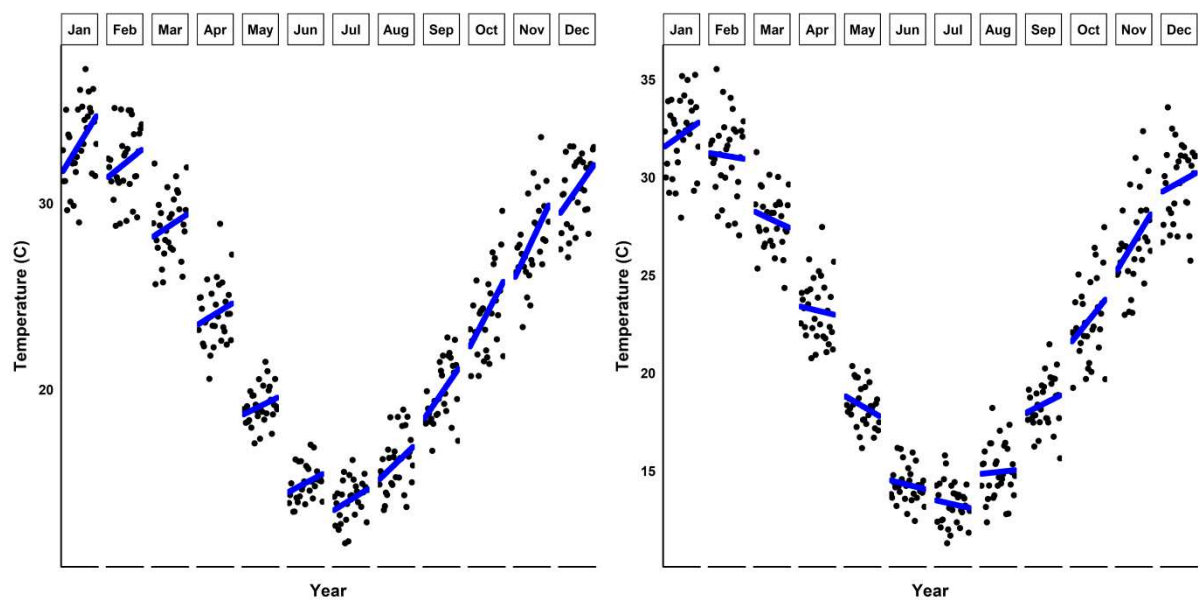


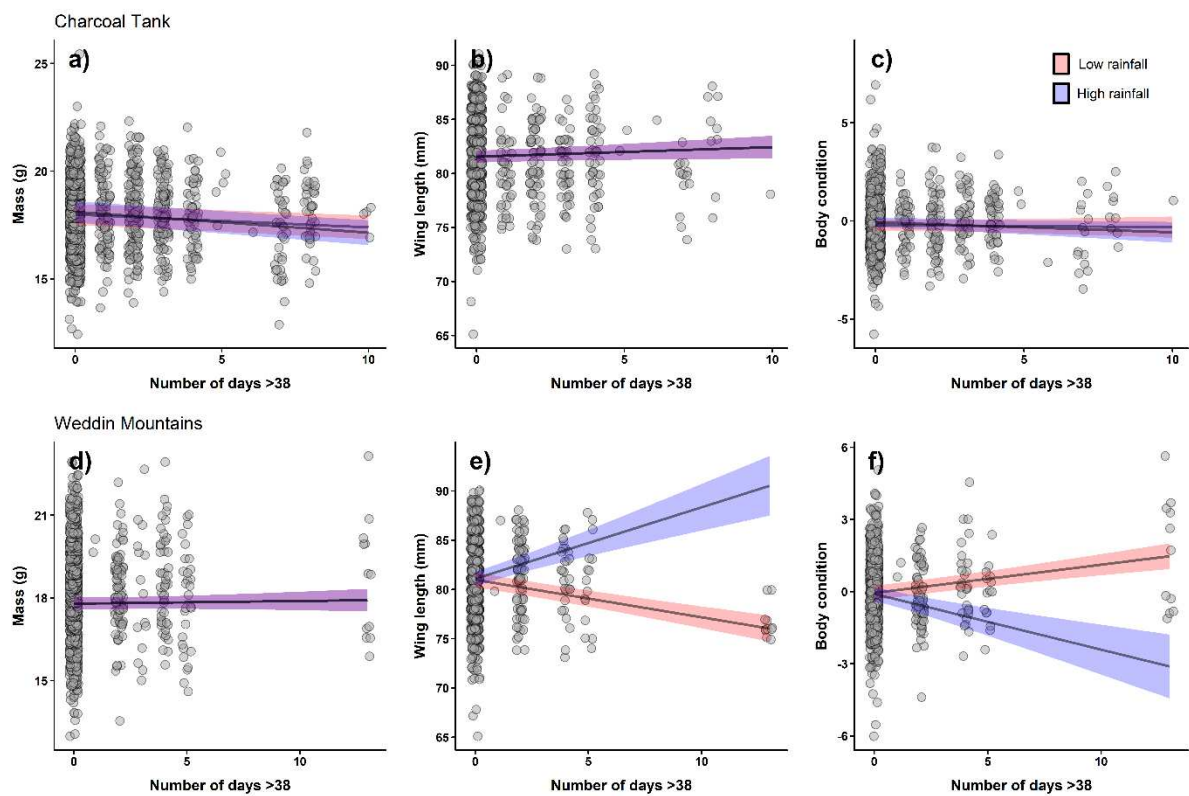
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523 **Figure 2:**



524





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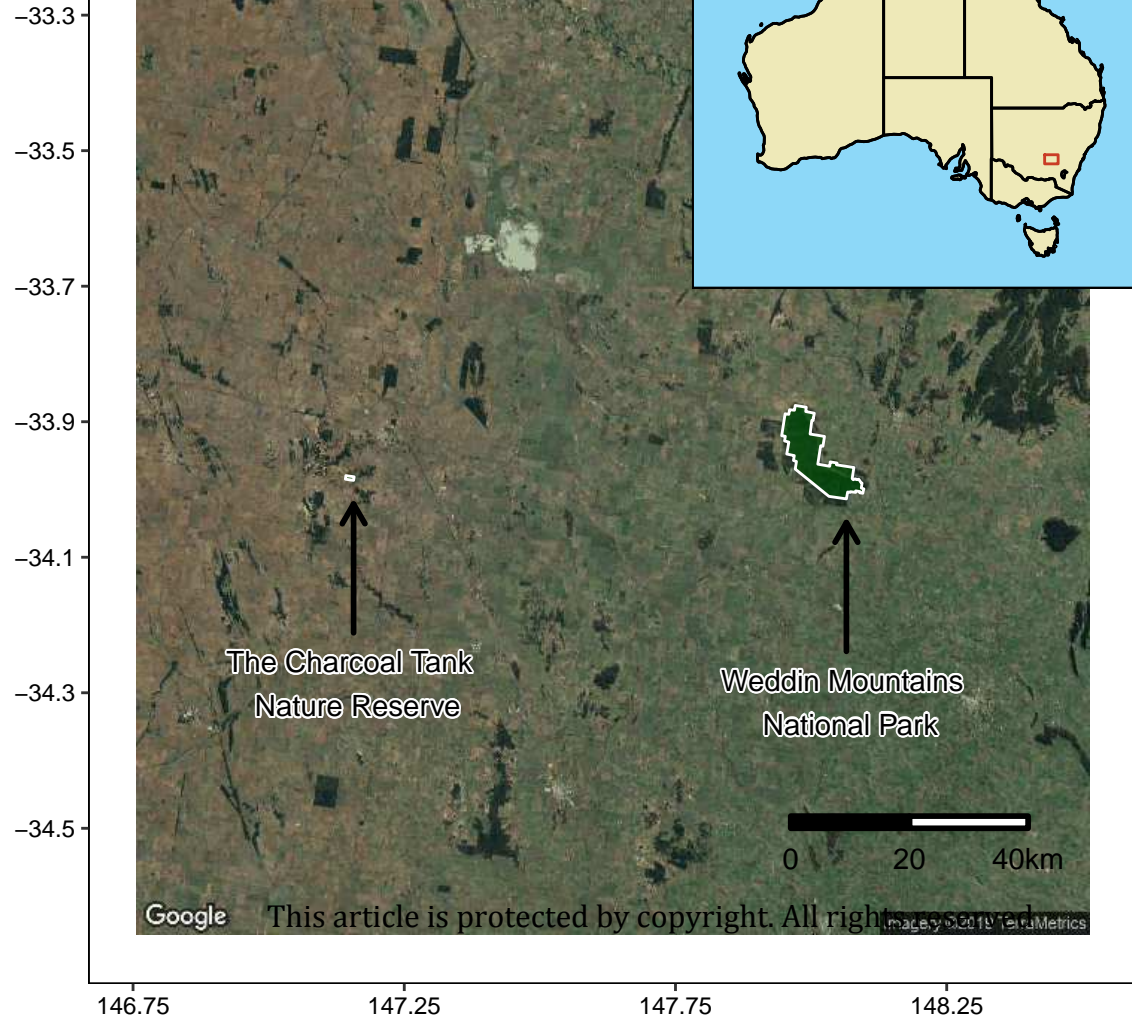
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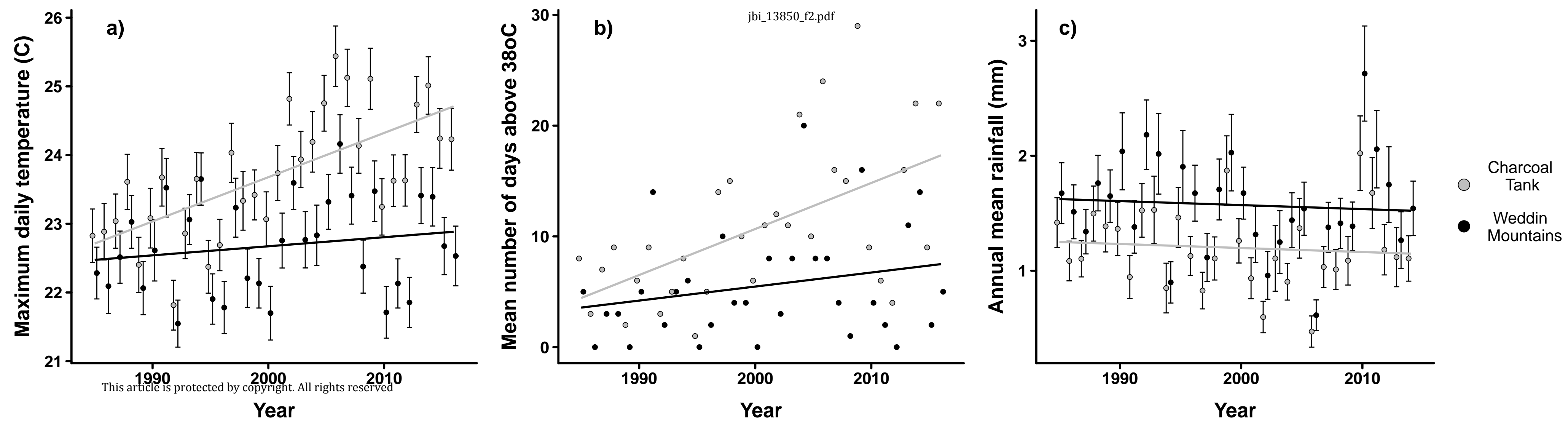
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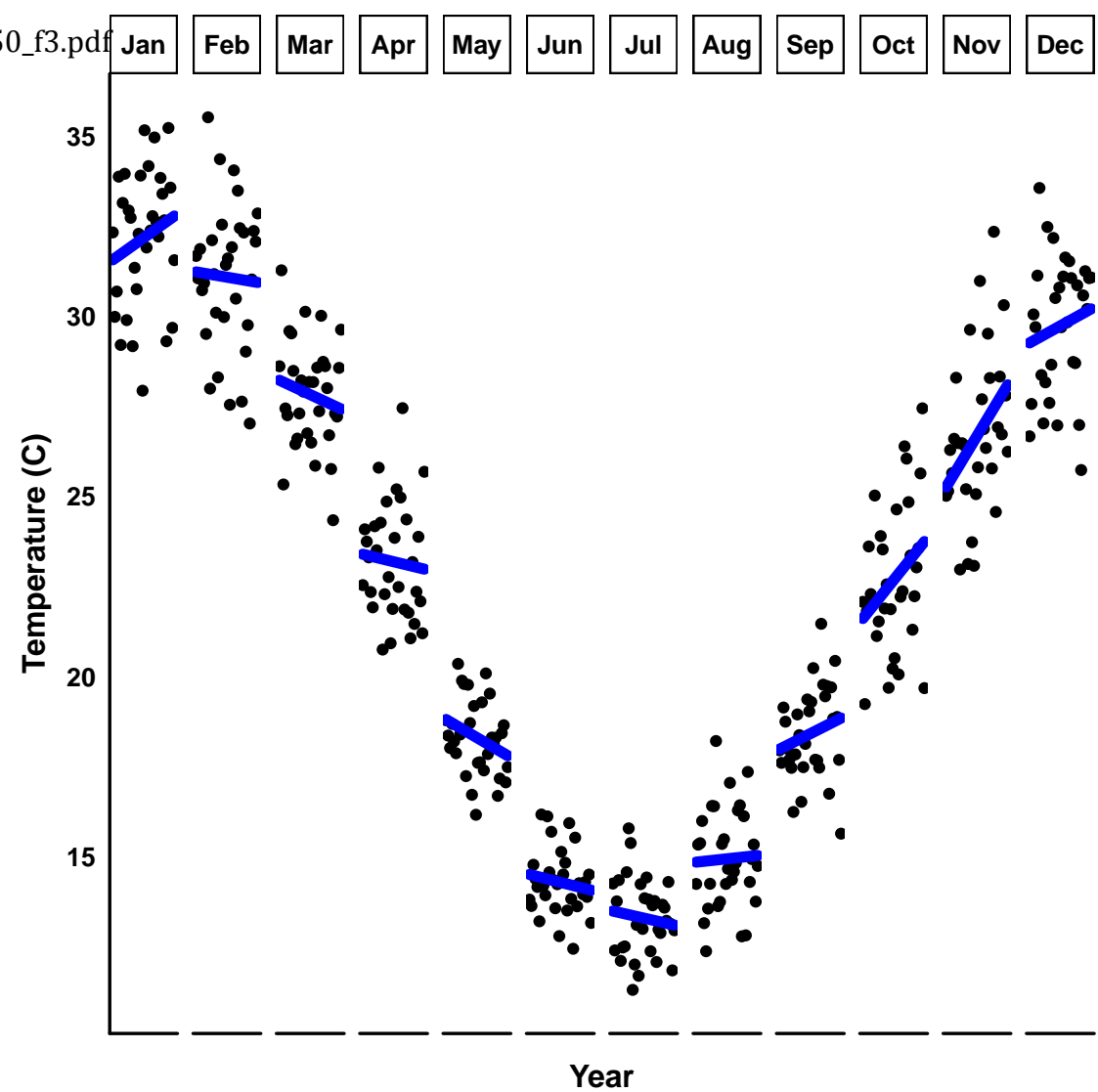
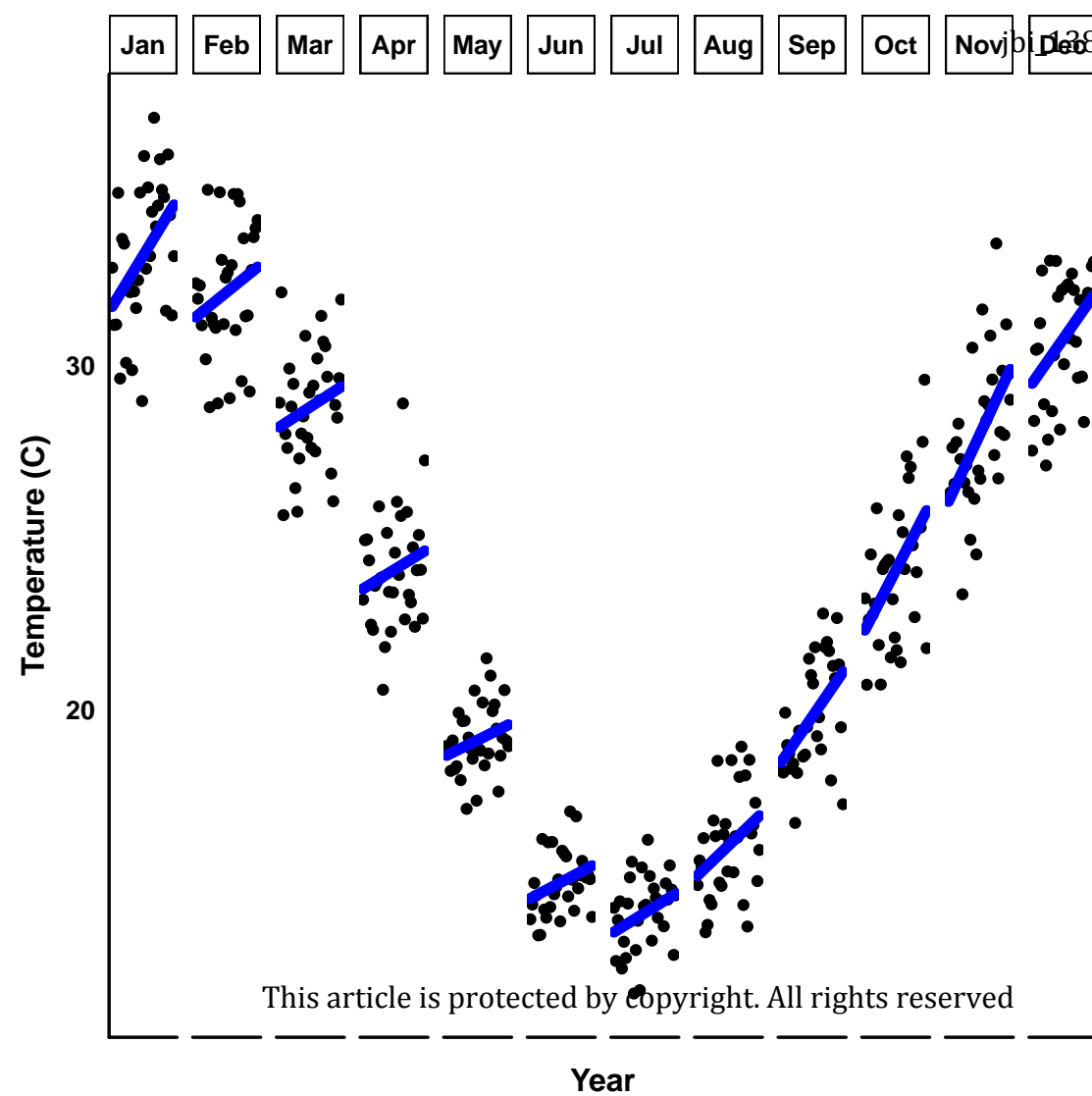
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Biosketch:

665 LDB is interested in understanding the effects of environmental change on complex
666 ecosystems, with a particular focus on climate change. His work has encompassed
667 observational fieldwork, experimental ecology and computational methods, including a
668 published R package (see liamdbailey.com). JLG conceived of the ideas and with LBD and
669 LEK developed the methods. RA, MC, and JS collected the data; LDB analysed the data and
670 led the writing.

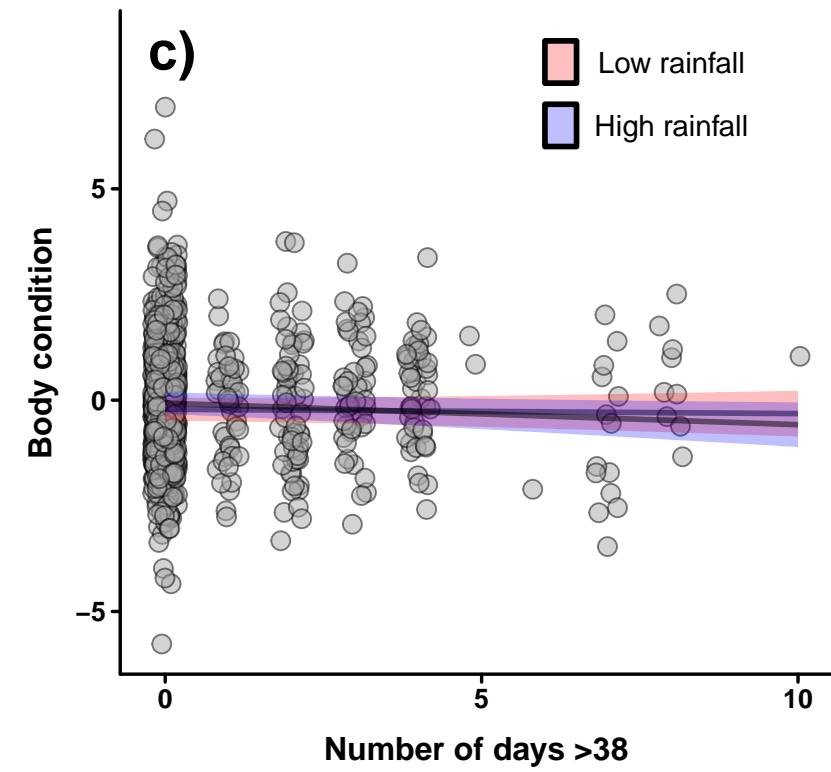
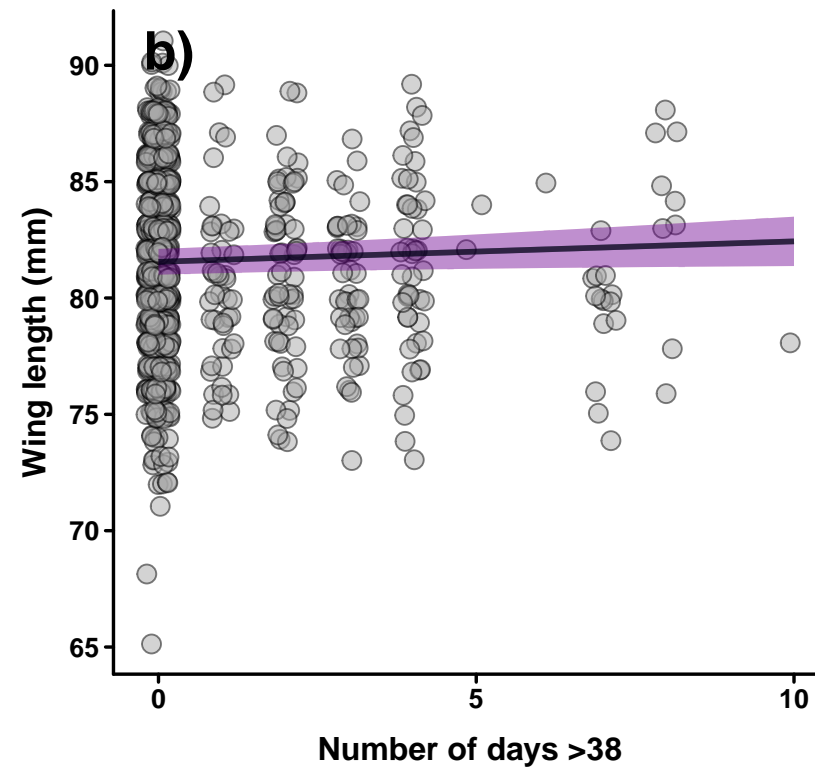
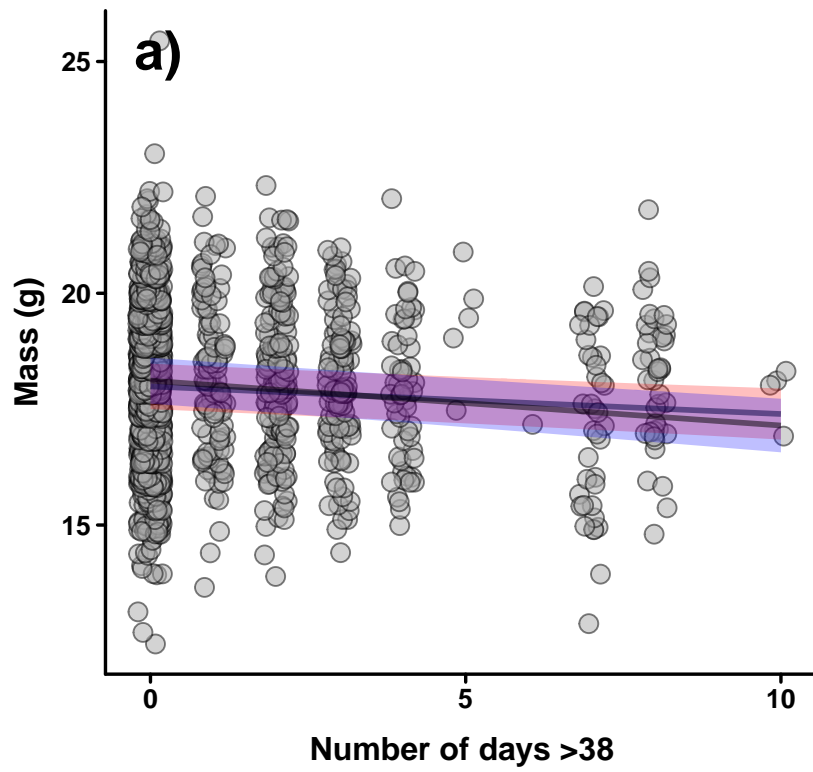






Charcoal Tank

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Weddin Mountains

