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Article

Weighing the cost: the impact of serial heatwaves on body mass in a small Australian passerine

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Rising temperatures pose a grave risk to arid zone birds because they are already living close to their physiological limits and must balance water conservation against the need for evaporative cooling. We assess how extreme temperatures affect a wild population of small passerines by monitoring daily mass change in individual jacky winters *Microeca fascians* (a small Australasian robin) across a series of severe heatwaves that afflicted southern Australia in the summer of 2018–2019. Daily maximum temperature and duration of heat exposure were negatively related to the birds' ability to maintain body mass. At maximum temperatures $\geq 42^{\circ}\text{C}$, birds lost 2.0% of their body mass daily and at $\geq 45^{\circ}\text{C}$, 2.6%. Apparent mortality increased almost three-fold, and all breeding birds abandoned their nests. Nevertheless, net daily mass loss was less than might be expected from laboratory-based findings, presumably because wild jacky winters undertook behavioural thermoregulation. The birds also regained some mass between heatwave events and suffered no long-term reduction in body condition.

Keywords: Australian passerine, body condition, evaporative water loss, heatwave, heat stress, thermoregulation

Introduction

Climate change is having a profound effect on wildlife populations (Hoffmann et al. 2019). Arid zone birds are particularly vulnerable to rising temperatures because they live close to their physiological limits (Iknayan and Beissinger 2018). Whenever ambient temperature rises above body temperature, birds must use evaporative cooling to avoid lethal hyperthermia (Boyles et al. 2011). Balancing the need for cooling against conserving water is particularly difficult for desert-dwelling species. If heat exposure is too great, or too prolonged, birds succumb to lethal dehydration or hyperthermia, and mass die-offs have already been observed (Saunders et al. 2011, McKechnie et al. 2012). Under global warming, heatwaves are expected to increase in intensity, frequency and duration, placing great pressure on arid zone species (McKechnie et al. 2012).

Even when birds survive heatwaves, they may suffer adverse consequences, both chronic and acute. High temperatures are associated with significant reductions in food intake due to changes in foraging patterns and microhabitat use, and because

heat dissipation behaviours (e.g. panting or wing-spreading) impair foraging efficiency (du Plessis et al. 2012, Edwards et al. 2015, Funghi et al. 2019). Southern pied babblers *Turdoides bicolor*, for example, are unable to maintain body condition on days when air temperature exceeds 35.5°C (du Plessis et al. 2012). Similarly, white-plumed honeyeaters *Ptilotula penicillatus* captured within seven days of exposure to multiple days with a maximum temperature > 35°C were significantly lighter than those not exposed (Gardner et al. 2016). Because body condition is linked to reproductive success and survival (Monaghan 2008), heat-induced loss of condition could jeopardise arid-zone populations.

In an effort to predict how rising temperatures and intensifying heatwaves will impact upon arid zone birds, researchers have developed models based on the physiological responses of captive birds to high temperatures (McKechnie and Wolf 2010, McKechnie et al. 2012, Albright et al. 2017). These models predict that catastrophic mortality events will become increasingly frequent under future climate scenarios, particularly within Australia and the south-western deserts of North America (McKechnie and Wolf 2010, Albright et al. 2017). However, it remains unclear whether laboratory-based findings can be extrapolated to wild populations. There is an urgent need to quantify the costs of heat exposure in natural populations.

Our study is the first to monitor daily mass change in a wild bird across a series of severe heatwaves. In December 2018–January 2019, southern Australia experienced a succession of extreme heat events; in fact, January 2019 was the hottest month ever recorded in Australia’s history (Bureau of Meteorology, <www.bom.gov.au>, <www.climatechangein-australia.gov.au>). At our site, in South Australia’s semi-arid zone, January’s mean daily maximum temperature was 4.2°C above average (Bureau of Meteorology); the same temperature increase predicted for the region in 2090 (RCP8.5) (Bureau of Meteorology). Throughout the two-month heat-wave period, we monitored body mass change in known individuals in a wild population of small passerine, the jacky winter *Microeca fascians*, an Australasian robin (Petroicidae). We predicted that maximum daily temperature and duration

of heat exposure would be negatively related to the birds’ ability to maintain body mass, and that exposure to serial heatwaves would lead to long-term reductions in body condition and increased mortality.

Material and methods

Study site and species

The study was undertaken in semi-arid mallee woodland at Calperum Station, South Australia (34°03’S 140°38’E) between May 2018 and February 2019. The vegetation at the study site is comprised of low, mallee eucalypts (*Eucalyptus oleosa*, *E. dumosa*, *E. incrassata*, *E. socialis*) and sugarwood *Myoporum platycarpum* above a sparse understorey of *Senna* and *Acacia* shrubs, between dunes, and porcupine grass *Triodia scariosa*, on the dune crests. Mean annual rainfall is 251 mm, distributed irregularly across the year (Bureau of Meteorology).

We monitored 37 breeding groups of jacky winters. This species normally breeds in pairs that are territorial year-round. They are ‘perch and pounce’ insectivores, feeding on small aerial and surface-dwelling arthropods (Higgins and Peter 2002). This small passerine (15 g) relies on dietary water, and surface water was unavailable to the study population during the data collection period. In hot weather, jacky winters employ heat dissipation behaviours: wing-spreading and ‘wind-surfing’ (using a head wind to lift the wings into flying position, while perched; Fig. 1b) which facilitate convective heat loss when environmental temperatures are lower than body temperature, and panting for evaporative cooling.

During May–August, the birds were captured in mist nets and fitted with two coloured, metal leg-bands for visual identification. Over subsequent months, nine breeding groups (25 individuals) were habituated to the presence of an observer walking within 5 m, and trained to perch on a portable electronic balance (Ohaus Scout STX; 600 g; 0.1 g; Ohaus Corporation; Parsippany, New Jersey) for a small food reward (1 × 0.2 g mealworm) (Fig. 1a).

Figure 1. A wild jacky winter (a) perched on a balance for weighing, (b) ‘wind-surfing’ to dissipate heat convectively and (c) exhibiting symptoms of dehydration after a heatwave.

Data collection

From September 2018 to February 2019, we weighed individuals as soon as they became active after sunrise, collecting 1022 measurements of body mass. All individuals within the habituated groups readily perched on the scales at every weighing session, so our weight data was not biased by level of hunger. To ensure accurate measurements, we excluded balance-readings that did not remain stable for > 1.5 s and we did not weigh when wind speeds exceeded 10 km h^{-1} . The balance was calibrated (using span calibration and a 300 g weight) prior to weighing sessions. We expressed daily mass change (the difference in mass from one morning to the next) as a percentage of the first morning's mass. We obtained 233 mass-change measures for 25 adults (nine groups). To assess inter-heatwave recovery, we used mass-change records from December to January only (172; 20 adults; eight groups). We used paired t-tests to compare an individual's mass immediately before and after the two-month heatwave period, for 15 individuals (eight groups).

To monitor survival, we visited every group at least weekly throughout the study period, and within two days after each heatwave event. Adults that disappeared from their territory and remained unsighted for the next six months were assumed to have died. Although some of these missing individuals may have dispersed, we normally sighted dispersers in nearby territories. For example, of the 11 birds that disappeared from their territory after the loss of their mate, all but one remained within our study population. We used Pearson's Chi-squared test to compare adult mortality during the 10-week period prior to the heatwaves (15 September–30 November) with the 10-weeks during (and immediately after) the heatwave period (1 December–14 February).

The weather data used in the analyses were derived from a Davis Vantage Pro 2 (Davis Instruments, California, USA) weather station, located at the study site, installed as per manufacturer instructions and checked against an OzFlux tower (Terrestrial Ecosystem Research Network (TERN) SuperSite), located within 5 km of the study site. Maximum and minimum temperature readings were taken every 15 min and rainfall daily. To facilitate discussion, we arbitrarily defined a heatwave event as two or more consecutive days with maximum temperatures $> 40^\circ\text{C}$, a definition used in previous studies of Australian arid-zone passerines (Gardner et al. 2016). Defining extreme weather events is fraught with difficulty and inconsistencies (Bailey and van de Pol 2016) and we chose a biologically meaningful definition: 40°C is the average daytime body temperature of birds (when they are not heat or cold stressed) (Boyles et al. 2011) and air temperatures above this level necessitate a thermoregulatory response.

Statistical models

To investigate the effect of high temperatures on adult body mass, we constructed linear mixed models using R ver. 3.3.2 (R Development Core Team). Models were fitted with

Table 1. Model selection results investigating daily percentage mass change in jacky winters, September 2018–January 2019. Shown are top models with $\text{AIC} < 2$ and standardized coefficients ($\pm \text{SE}$); important variables in top model (95% CIs of estimated coefficients that do not overlap zero) in bold.

Model	Intercept	Group status	Julian days	Sex	Mins between weighing	Mins post sunrise	No. consec days $\geq 40^\circ\text{C}$	T_{max} ($^\circ\text{C}$) (linear)	T_{max}^2 ($^\circ\text{C}$) (non-linear)	No. consec days $\geq 40^\circ\text{C} \times T_{\text{max}}$	df	Delta AIC	Weight
1	0.012 ± 0.162	NA	NA	NA	0.84 ± 0.17	NA	-0.35 ± 0.23	5.73 ± 0.15	-6.02 ± 0.16	NA	8	0.00	0.15
2	0.012	NA	-0.22	NA	0.85	NA	NA	6.72	-7.21	NA	7	0.13	0.14
3	0.481	NA	NA	NA	0.87	NA	0.60	4.86	-5.50	-0.81	9	0.99	0.09
4	0.012	NA	NA	NA	0.82	NA	-0.34	6.62	-6.71	NA	9	1.34	0.08
5	0.012	NA	NA	NA	0.82	NA	NA	7.64	-7.93	NA	8	1.35	0.08

Table 2. Summary of model selection results investigating the effects of days with $T_{\max}$ (a) $\geq 42^{\circ}\text{C}$ and (b) $\geq 45^{\circ}\text{C}$ on daily percentage mass change for jacky winters during the heatwave period (December 2018–January 2019). Standardized coefficients ($\pm\text{SE}$) shown for variables included in the top models with $\Delta\text{AICc} < 2$ following model selection based on AICc. Variables identified as important in the top model have 95% CIs of estimated coefficients that do not overlap zero and are shown in bold.

Model (A)	Intercept	Group status	Julian days	Sex	Mins between weighing	Mins post sunrise	$T_{\max} \geq 42^{\circ}\text{C}$	df	AICc	Delta	Weight
1	0.50 ± 0.19	NA	NA	NA	0.91 ± 0.17	NA	-2.04 ± 0.39	6	960.30	0.00	0.34
2	0.55	NA	0.20	NA	0.91	NA	-2.22	7	961.15	0.85	0.22
3	0.50	NA	NA	NA	0.94	-0.09	-2.04	7	962.21	1.92	0.13
Model (B)	Intercept	Group status	Julian days	Sex	Mins between weighing	Mins post sunrise	$T_{\max} \geq 45^{\circ}\text{C}$	df	AICc	Delta	Weight
1	0.36 ± 0.18	NA	NA	NA	0.98 ± 0.17	NA	-2.60 ± 0.49	6	959.77	0.00	0.41
2	0.37	NA	NA	NA	1.03	-0.11	-2.26	7	961.55	1.77	0.17
3	0.37	NA	0.06	NA	0.99	NA	-2.65	7	961.76	1.99	0.15

maximum likelihood (rather than REML) using the package lme4 (Bates et al. 2012), and model selection was conducted using the package MuMIn (Bartoń 2016). Daily percentage mass change was the response variable and weather variables, the predictors. We first fitted maximum daily temperature ($T_{\max}$) as both linear and non-linear terms, number of successive days recording $T_{\max} \geq 40^{\circ}\text{C}$ and their interaction to identify temperatures at which changes in body condition were observed. We then ran separate models to test for the specific effects of: days with $T_{\max} \geq 42^{\circ}\text{C}$ and $T_{\max} \geq 45^{\circ}\text{C}$; minutes of heat exposure per day when $T_{\max}$ was ≥ 40 , 42 and 44°C ; and recovery of mass between heatwave events ($T_{\max}$ 34– 40°C). In all models we controlled for sex, day of season (Julian day), time of day and difference in minutes between time of weighing on successive days. We fitted individual and group identity as random terms to account for repeated sampling.

In our data set, overnight minimum temperatures ($T_{\min}$) were highly correlated ($r > 0.8$) with daily maximum temperature ($T_{\max}$) and could thus potentially account for the body mass changes we observed. We therefore re-ran our main model (Table 1), replacing $T_{\max}$ with $T_{\min}$, and compared AICc values. Using $T_{\min}$ resulted in less well-fitting models and an increase in AICc ($\Delta\text{AICc} = 7.5$), indicating that the effect of $T_{\max}$ on body mass was stronger than that of $T_{\min}$. All subsequent models included $T_{\max}$ rather than $T_{\min}$ as an explanatory variable.

In our main model (Table 1) we included the number of successive days recording $T_{\max} \geq 40^{\circ}\text{C}$ as an explanatory variable because rates of evaporative water loss and energy use – which can affect body mass – increase when environmental temperature exceeds body temperature (approx. 40°C for birds). For subsequent models, that tested for specific effects of high temperature (40– 47.6°C) on body mass (Table 2–4), we restricted our analyses to weight measurements collected during the hottest months (December–January) to exclude the effects of $T_{\max} < 25^{\circ}\text{C}$ (recorded in the months September–November). In addition, because there was only one rainfall event during the study period, we did not include rainfall as a predictor in any model.

To account for model selection uncertainty, we adopted a multi-model inference approach based on the Akaike

information criteria (Burnham and Anderson 2002). We used AIC, corrected for small sample size (AICc) to select the most parsimonious model; models with lower AIC values are better supported by the data. To avoid multicollinearity among explanatory variables, we first estimated pair-wise Pearson's correlation coefficients and confirmed that correlations were low for all combinations ($r < 0.7$). We generated a candidate set of models with all possible parameter subsets, which were then fitted to the data and ranked by ΔAICc values (the difference between each model's AICc and AICcmin, that of the 'best' model). We report only top models within ΔAICc of two units of the best supported model. Confidence intervals of individual predictor variables were used as indicators of parameter importance (Galipaud et al. 2014).

Results

A series of five heatwave events (consecutive days $\geq 40^{\circ}\text{C}$) occurred at the study site during December 2018 and January 2019 (Fig. 2). Mean maximum daily temperature was 32.5°C in December (compared with a 45-year mean of 30.3°C) and a record-breaking 37.5°C in January (mean 33.3°C) (Bureau of Meteorology). The study site experienced seven days with $T_{\max} \geq 45^{\circ}\text{C}$ and the highest recorded temperature was 47.6°C .

The change in body mass of individuals, from one morning to the next, was significantly related to $T_{\max}$ on the intervening day (Table 1). Jacky winters lost mass when $T_{\max}$ was $\geq 42^{\circ}\text{C}$ or $< 26^{\circ}\text{C}$ (Fig. 3). On average, birds lost 2.0% of body mass over the 24 h period when $T_{\max}$ was $\geq 42^{\circ}\text{C}$ and 2.6% when $T_{\max}$ exceeded 45°C (Table 2a–b). Rate of mass loss did not accelerate after exposure to consecutive days of $T_{\max} \geq 40^{\circ}\text{C}$ (Table 1) but duration of heat exposure within a day was positively related to mass loss. Over a 24-h period, birds lost mass if exposed to approximately > 140 min of $\geq 40^{\circ}\text{C}$, > 70 min $\geq 42^{\circ}\text{C}$ or > 25 min $\geq 44^{\circ}\text{C}$ (Fig. 4, Table 3).

Birds regained mass on the 4–6 d between heatwave events, increasing, on average, 1.4% of body mass per day ($T_{\max}$ 34– 40°C) (Fig. 2, Table 4). After the two-month heatwave period, birds were significantly lighter than at the start

Table 3. Summary of model selection results investigating association between exposure (mins) to daily maximum temperatures ($T_{\max}$) (a) $\geq 40^{\circ}\text{C}$; (b) $\geq 42^{\circ}\text{C}$; (c) $\geq 44^{\circ}\text{C}$ and daily percentage mass change in jacky winters during the heatwave period (December 2018–January 2019). Standardized coefficients ($\pm$ SE) are shown for variables included in the top models with $\Delta\text{AICc} < 2$ following model selection based on AICc. Variables identified as important in the top model have 95% CIs of estimated coefficients that do not overlap zero and are shown in bold.

Model (A)	Intercept	Group status	Julian days	Sex	Mins between weighing	Mins post sunrise	Mins $\geq 40^{\circ}\text{C}$	$T_{\max}$ ($^{\circ}\text{C}$)	$T_{\max}^2$ ($^{\circ}\text{C}$)	Mins $\geq 40^{\circ}\text{C} \times T_{\max}$	df	AICc	Delta	Weight
1	0.85 ± 0.51	NA	NA	NA	0.73 ± 0.20	NA	0.10 ± 0.79	-0.82 ± 0.70	NA	-1.21 ± 0.53	8	685.30	0.00	0.16
2	0.87	NA	-0.22	NA	0.76	NA	0.12	-0.91	NA	-1.23	9	686.38	1.09	0.09
3	1.18	NA	NA	NA	0.75	NA	0.07	-5.62	4.86	-1.59	9	687.07	1.77	0.07
4	-0.21	NA	NA	NA	0.69	NA	-1.02	NA	NA	NA	6	687.11	1.81	0.07
Model (B)	Intercept	Group status	Julian days	Sex	Mins between weighing	Mins post sunrise	Mins $\geq 42^{\circ}\text{C}$	$T_{\max}$ ($^{\circ}\text{C}$)	$T_{\max}^2$ ($^{\circ}\text{C}$)	Mins $\geq 42^{\circ}\text{C} \times T_{\max}$	df	AICc	Delta	Weight
1	-0.21 ± 0.20	NA	NA	NA	0.73 ± 0.20	NA	-1.13 ± 0.20	NA	NA	NA	6	681.59	0.00	0.17
2	-0.21	NA	0.219	NA	0.76	NA	-1.18	NA	NA	NA	7	682.62	1.02	0.10
3	0.77	NA	NA	NA	0.76	NA	0.34	-0.79	NA	-1.29	8	683.33	1.74	0.07
Model (C)	Intercept	Group status	Julian days	Sex	Mins between weighing	Mins post sunrise	Mins $\geq 44^{\circ}\text{C}$	$T_{\max}$ ($^{\circ}\text{C}$)	$T_{\max}^2$ ($^{\circ}\text{C}$)	Mins $\geq 44^{\circ}\text{C} \times T_{\max}$	df	AICc	Delta	Weight
1	-0.21 ± 0.20	NA	NA	NA	0.76 ± 0.20	NA	-1.17 ± 0.20	NA	NA	NA	7	679.29	0.00	0.21
2	-0.21	NA	NA	NA	0.76	NA	-1.06	NA	-0.17	NA	6	829.25	1.76	0.09
3	-0.21	NA	NA	NA	0.76	NA	-1.07	-0.16	NA	NA	7	830.45	1.78	0.09
4	-0.21	NA	0.11	NA	0.77	NA	-1.19	NA	NA	NA	7	830.70	1.87	0.08

(paired t-test: $t_{14} = 2.3$, $p = 0.038$). However, this difference in body mass disappeared within two-weeks of the last heatwave event ($t_{13} = 0.6$, $p = 0.534$; Fig. 5).

Apparent mortality increased significantly during the heatwave period, with 20.0% of adults (16 of 80 individuals) lost, as compared with 7.1% (6 of 85) during an equivalent period prior to the heatwaves (Pearson's $\chi^2 = 6.641$, $df = 1$, $p = 0.01$). All nesting pairs ($n = 6$) abandoned their eggs when exposed to temperatures $> 40^{\circ}\text{C}$. No nest abandonments occurred prior to the heatwave period ($n = 73$ incubation attempts).

Discussion

The heatwave conditions had a substantial impact upon the study population. Individuals lost 2.0% of their body mass each day that temperatures rose above 42°C and were in significantly poorer condition at the end of the two-month heatwave period than at the beginning. Apparent mortality in adults increased almost three-fold and breeding ceased, with all nesting pairs abandoning their eggs.

During heatwaves, a jacky winter's daily mass loss was positively related to both maximum air temperature (Fig. 3) and duration of heat exposure (Fig. 4) suggesting that evaporative water loss formed a major component of the birds' net mass loss. When air temperature exceeds body temperature, birds must use evaporative cooling (e.g. panting) to avoid lethal hyperthermia (Boyles et al. 2011), resulting in steep increases in evaporative water loss with increasing air temperature. For example, captive yellow-plumed honeyeaters *Ptilotula ornatus* lose six times as much water at 46°C compared with 37.5°C (McKechnie et al. 2017). To minimize heat loads and water loss rates, birds retreat to cool, shaded microsites and remain largely inactive during the heat of the day (Wolf 2000, Pattinson and Smit 2017, Funghi et al. 2019). This behaviour suggests that foraging in the heat produces greater water deficits than remaining inactive in a cooler microsite. At 40°C , for example, a small passerine perched in the shade increases its evaporative water loss five-fold simply by moving into a sunlit area (Wolf and Walsberg 1996). Limits of survival are thus defined by water loss rates, duration of heat exposure and dehydration tolerance.

On the hottest days, the jacky winters at our site were exposed to air temperatures $\geq 40^{\circ}\text{C}$ for up to 10 h. They had no access to surface water and were never observed foraging, provisioning nestlings or incubating (Bayter 2019) at air temperatures $> 38^{\circ}\text{C}$. Based on rates of evaporative water loss shown by similar-sized passerines in the laboratory (Wolf and Walsberg 1996, McKechnie et al. 2017), we would expect jacky winters to lose approximately 20% of their body mass (via evaporative water loss) on an average day $\geq 45^{\circ}\text{C}$ (i.e. after 5.8 h of 40 – 44°C and 2.3 h of $\geq 45^{\circ}\text{C}$; $n = 7$ d). This level of water loss is above the estimated lethal limit (11–18% of body mass; Arad et al. 1989, Wolf and Walsberg 1996, Albright et al. 2017). However, contrary to these expectations, we recorded a net mass loss of 2.6% after a day $\geq 45^{\circ}\text{C}$. This net mass change, measured over 24 h, provides a good

Table 4. Summary of model selection results investigating recovery of body weight (daily percentage mass change) on days when $T_{\max}$ was 34–40°C for jacky winters during the heatwave period (December 2018–January 2019). Standardized coefficients ($\pm$ SE) shown for variables included in the top models with $\Delta\text{AICc} < 2$ following model selection based on AICc. Variables identified as important in the top model have 95% CIs of estimated coefficients that do not overlap zero and are shown in bold.

Model	Intercept	Group status	Julian days	Sex	Mins between weighing	Mins post sunrise	$T_{\max} < 40^\circ\text{C}$	df	AICc	Delta	Weight
1	-0.85 ± 0.28	NA	NA	NA	0.86 ± 0.17	NA	1.36 ± 0.35	6	971.85	0.00	0.34
2	-0.10	NA	0.23	NA	0.86	NA	1.60	7	972.61	0.76	0.23
3	-0.85	NA	NA	NA	0.90	-0.08	1.36	7	973.83	1.98	0.13

measure of the overall cost to the bird, but does not allow us to explicitly quantify evaporative water loss. Net mass change includes mass lost through energy use and the catabolism of tissue, and mass gained from food, not just lost body water. Nevertheless a loss of 2.6% seems low, given that, for days with $T_{\max} \geq 45^\circ\text{C}$, the birds had only a small window of foraging time prior to heat exposure and little opportunity to forage after exposure (because temperatures remained in the high 30°C until sunset).

The jacky winter's water loss may have been less than expected for a number of reasons. Taxa vary in their thermal sensitivity (Boyles et al. 2011) and species that rely on dietary water (such as jacky winters) may have less capacity for evaporative cooling than species with access to water

(McKechnie et al. 2017). Humidity and wind speed also influence rates of evaporative water loss (Wolf and Walsberg 1996). Most importantly, wild birds – unlike their captive counterparts – can employ behavioural thermoregulation, selecting sites that facilitate convective cooling (e.g. elevated perches that catch the wind for ‘wind-surfing’; Fig. 1b) and exploit cooler microhabitats to avoid the worst temperatures. For example, during extreme heat, the trunk bases of thin-barked trees can be up to 8.9°C cooler than air temperature (Briscoe et al. 2014) and we observed jacky winters resting against the base of tree trunks on several occasions. Water loss in captive birds confined to a metabolic chamber could also be exacerbated by the chamber's high air flow rates (Whitfield et al. 2015) or by stress. It is notable that

Figure 2. A wild jacky winter's body mass and maximum air temperature ($^\circ\text{C}$) on the preceding day, during the two-month heatwave period. Heat waves defined as consecutive days $> 40^\circ\text{C}$. Daily maxima $> 42.6^\circ\text{C}$ in the 95% percentile for this period, 1995–2018 (Renmark data; 12).

Figure 3. Model-predicted association between daily percentage mass change and maximum temperature (°C) on the preceding day (Table 1).

our findings are roughly comparable to predictions of net daily mass loss for other wild birds: i.e. 4% in southern pied babblers on days $> 38.5^{\circ}\text{C}$ (du Plessis et al. 2012), 4% for breeding male southern yellow-billed hornbills *Tockus leucomelas* on days $> 37.9^{\circ}\text{C}$ (van de Ven 2017) and 3% for white-plumed honeyeaters on days $> 35.0^{\circ}\text{C}$ (Gardner et al. 2016).

Figure 4. Association between daily percentage mass change and minutes exposed to temperatures ≥ 40 , ≥ 42 and $\geq 44^{\circ}\text{C}$, showing regression lines for each temperature (Table 3).

Figure 5. Mean body mass ($\pm$ SE) of jacky winters before and after the two-month heatwave period ($n = 14$ adults).

The most surprising of our findings was the resilience of the jacky winters, with heat-exposed birds able to regain lost mass during the 4–6 cooler days between heatwave events; albeit not a full recovery (Fig. 2). Although our sample is small, deaths were not associated with a cumulative reduction in body mass across heatwave events. Although many of the jacky winters exhibited signs of dehydration after exposure to heatwave conditions (i.e. sunken eyes, lethargy (Rupley 1998); Fig. 1c), birds that died showed no greater daily mass loss, before their disappearance, than birds that survived. This suggests that mortality may have been due to acute hyperthermia or predation (of birds made sluggish by dehydration or driven to risk-taking by their need to forage). It is possible that individual differences in body condition contributed to such a pattern of mortality. When fasting, birds catabolise body fat which generates small quantities of water. Recent work has shown that dehydrated zebra finches *Taeniopygia guttata* resort to catabolising fat for this purpose (Rutkowska et al. 2016). Although the water gains are small (compared to levels of evaporative water loss), jacky winters with larger fat reserves may have been able to escape lethal dehydration (despite exhibiting relatively high mass loss), while birds without fat stores would show lower mass loss and yet succumb to dehydration.

Contrary to our prediction, the jacky winters suffered no long-term reduction in body condition as a result of their heat exposure. Despite the severity of the heatwaves, and a concurrent drought (Bureau of Meteorology), the birds re-attained their pre-heatwave body mass within two-weeks of the final heatwave event (Fig. 5). However, we have not yet evaluated possible carry-over effects on survival and reproduction (Harrison et al. 2011), which may appear in subsequent seasons. For example, exposure to temperatures $> 35^{\circ}\text{C}$, when coupled with low rainfall, are associated with reduced winter

survival in white-plumed honeyeaters (Gardner et al. 2016). Additionally, it is important to note that our study focuses on a single arid-adapted population of jacky winters, and further work is needed to assess the generality of body mass responses to heatwaves. In particular, quantifying responses to heatwaves in sites that differ in habitat quality, and comparing arid-adapted individuals with those from mesic populations who may show differences in their capacity for coping with heat stress, would be valuable.

It is clear from our findings that maximum temperature is not the only factor that will impact upon the ability of wild avian populations to survive heatwave events. Temporal parameters are also critically important, both the duration of heatwave events and their frequency, given that this determines how much time individuals have to recover. The timing of a heatwave will also alter its potency; high temperatures in late spring/early summer – or after rain in desert communities – are likely to impact breeding (Cunningham et al. 2013, Wiley and Ridley 2016, van de Ven 2017) with long-term consequences for population survival.

Attempts to predict how intensifying heatwaves will affect future bird populations have drawn primarily on findings from laboratory-based research (McKechnie et al. 2012, Albright et al. 2017). Although captive studies provide invaluable information on avian thermal tolerance and critical threshold temperatures, it remains unclear whether their findings can be applied to natural populations.

Although our study documents the effects of serial heatwaves on just one population of a single species, our results suggest that wild birds may be less severely affected, and more able to recuperate, than anticipated. This suggests that behavioural thermoregulation may be critical in determining vulnerability to heatwaves and underscores the need for further research into the response of wild birds to extreme heat.

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.866t1g1m1>> (Sharpe et al. 2019).

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Author contributions – LS designed the methodology, habituated the birds, collected the data and wrote the manuscript; BC banded the study population, monitored the unhabituated groups and critiqued the manuscript; JG conceived and coordinated the research, secured funding, conducted the statistical modelling and critiqued the manuscript.

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