Maximum movement performance, not activity levels or thermoregulatory indices, affects survival in a free-ranging ectotherm

Kristoffer H. Wild[1,2*], John H. Roe[3], Jonathan Curran[1], Phillip R. Pearson[1], Lisa Schwanz[4], Arthur Georges[1] & Stephen D. Sarre[1]

[1] Centre for Conservation Ecology and Genomics, Institute for Applied Ecology, University of Canberra, Canberra, ACT, Australia
[2] Current Address: School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia
[3] Department of Biology, University of North Carolina Pembroke, Pembroke, North Carolina, USA
[4] Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia
* Corresponding author: K.H. Wild kristofferw@unimelb.edu.au

Key Words: Ectotherm, Thermoregulation, Performance, Survival

Abstract

1. Temperature profoundly influences the distribution and diversity of ectotherms, yet in natural settings, the trade-offs between environmental temperatures, behaviour, physiological function, and how they drive individual survival, remain poorly understood.
2. To address these gaps, we generated field-based thermal performance curves, using temperature-sensitive radio transmitters and accelerometers, to examine the links between thermal biology and survival in a widely distributed, well-studied, lizard: the Australian central bearded dragon (*Pogona vitticeps*). Using this approach, we were able to link the accuracy and effectiveness of thermoregulation in the wild to address if seasonal trade-offs of thermoregulatory behaviours affect individual performance and ultimately test if thermal performance and thermoregulatory behaviours predict survival.
3. Lizards adjusted their behaviour to maintain optimal body temperature with higher thermoregulatory precision when environmental costs to maintain body temperature were low, during spring and summer, but decreased that precision during winter when the costs of active thermoregulation were high.
4. Maximum movement performance in the field was a strong predictor of individual survival, regardless of sex, even though survival probabilities were higher in males than females. Specifically, higher maximum movement performance increased predation and, as a result, mortality risk. Conversely, survival was not related to activity levels or thermoregulatory indices.
5. These findings highlight the complex trade-offs that ectotherms must navigate to balance behavioural thermoregulation and survival, emphasising the importance of seasonal and sex-specific differences in making those trade-offs. Connecting accelerometer data to energy expenditure and to specific behaviours is a promising avenue for research into thermal ecology. Such data provides critical insights into how ectotherms can respond to climate warming.

1. Introduction

In meeting the competing demands on their time, animals must balance the costs and benefits of their behaviours where these decisions have an influence on their survival and reproductive success, that is, their fitness (Huey & Slatkin, 1976). The energy expended in undertaking those behaviours needs to be weighed against energetic costs and fitness gain. Trade-offs are inevitable, and manifest in such contexts as optimal foraging behaviour, investment in mating displays and territorial defence and in migration. This intricate balance is underpinned by a rich and diverse body of literature that spans decades and species (Boyd & Hoelzel, 2002; Brown et al., 2018; Campos-Candela, 2018; Huey & Slatkin, 1976). Understanding these trade-offs reveals the evolutionary forces that shape behaviour, especially as animals navigate their environments to maximise fitness.

Ectotherms, those animals that maintain body temperatures within narrow limits while active by drawing upon external thermal sources and sinks, have a unique set of trade-offs in order to maximise fitness (Huey, 1982; Huey & Slatkin, 1976). Trade-offs that involve when and when not to be active, shuttling between sun and shade, which compromises the ability to forage or find mates, exposure to heat sources, but also predation risk are all optimised within a narrow range of body temperatures (Angilletta et al., 2002; Porter et al., 1973; Van Damme et al., 1991). However, these trade-offs can be energetically costly or increase predation risk depending on the environment (Herczeg et al., 2008; Kearney et al., 2009; Sears & Angilletta, 2015). What remains unclear is how these decisions affect individual survival under natural conditions. Ectotherms thus provide unique opportunities to examine the relationship between animals and their environment in balancing the competing demands of survival and reproduction to maximise their fitness.

Presumed links between body temperature and survival underpin the study of thermal ecology in ectotherms. In particular, behavioural thermoregulation is assumed to enable individuals to achieve optimal body temperature and hence maximise their physiological performance (Angilletta, 2009). This, in turn, can provide performance advantages, such as enhanced digestion efficiency or increased sprint speed, that may influence individual fitness (Angilletta et al., 2002; Pearson & Warner, 2018). However, the benefits of maintaining optimal body temperatures carry trade-offs (Huey & Slatkin, 1976). Direct costs, like increased energy expenditure from active thermoregulation (Orrell et al., 2004), or indirect costs, such as heightened predation risk (Herczeg et al., 2008; Skelly 1994), are likely to increase as individuals seek micro-habitats to achieve optimal temperatures. According to the cost-benefit model of thermoregulation (Huey & Slatkin, 1976), these trade-offs influence the extent to which ectotherms thermoregulate. For example, thermoregulation should be more precise when the environmental costs are low and the benefits of maintaining optimal body temperatures are high (Vickers et al., 2011). This balance between the costs and benefits shapes ectotherms' responses to their thermal environments (Sears et. al., 2016; Chan et al. 2024). Understanding these trade-offs is therefore crucial for predicting how animals optimise body temperatures while minimising predation risks or additional environmental costs, and how these adjustments correspond to fitness-related traits such as growth, reproduction, and survival.

Variation in environmental conditions, particularly seasonal fluctuations, drive the thermoregulatory decisions that ectotherms must navigate to obtain and maintain optimal body temperatures in the wild (Giacometti et al., 2024). These fluctuations include not only temperature changes but also shifts in water balance, food availability, predation pressures, and interactions with conspecifics (Huey & Pianka, 1977; Leith et al., 2024). Seasonal shifts change the physical and thermal landscape, altering the availability of suitable microhabitats and thermal refuges in positive or negative ways (Sears & Angilletta, 2015). For example, in high-cost environments where ectotherms must expend more time and energy moving between microhabitats to optimise body temperature, individuals may grow more slowly due to energy diverted to thermoregulation (Brewster et al., 2013) or increase predation risk due to conspicuous behaviours to increase body temperature (Basson et al., 2016). The behavioural responses to environmental fluctuations, therefore, can help determine the physiological trade-offs that may influence survival (Chan et al., 2024).

Heliothermic lizards thermoregulate through behavioural means by seeking or avoiding heat sources, adjusting posture, and changing activity levels (Huey, 1982; Porter et al., 1973). Key components of thermoregulation include the range of individual thermal preferences available in the environment and the effectiveness of maintaining body temperature through behavioural means. Physiological responses to thermoregulation can be illustrated through a thermal performance curve (TPC), which depicts the relationship between body temperature and performance (Angilletta, 2009; Taylor et al., 2021). Using this curve the thermal optimum and maximum performance are identified, and are traits often indirectly related to individual survival (Gilbert & Miles, 2017; Pearson & Warner, 2018). However, TPC relationships are typically measured under controlled laboratory conditions, where stochastic environmental factors (temperature fluctuations, predation pressures, and food availability) are minimised or eliminated (Angilletta et al., 2002; Albuquerque et al., 2023; Wild & Gienger, 2018). While such studies provide valuable insights, they often fail to account for the complexities and variability experienced by ectotherms in natural environments (Childress & Letcher, 2017). This disconnect creates a significant knowledge gap, as it is unclear how laboratory-derived metrics translate to true ecological relevance for individuals in the wild. It is usually challenging to accurately measure individual survival in field settings due to the small size of these animals or the rarity of capturing predation events. For example, survival estimations are often limited to recapture events between sampling years (Gilbert & Miles, 2017; Husak, 2006), which may not be an accurate assessment of individual survival over shorter (i.e., seasonal) time frames. To gain a realistic understanding of the strategies employed by ectotherms to maintain optimal body temperatures and the performance benefits within their thermal performance curves, it is essential to conduct more field-based research.

Here, we examine in a field setting the links between survival and common metrics of thermal biology, specifically thermoregulatory behaviour and thermal performance curves, in the Australian central bearded dragon (*Pogona vitticeps*). In addition, we provide new insight into seasonal patterns of thermal ecology. Previous laboratory work with *P. vitticeps* has shown their thermoregulatory behaviours in the lab align with the cost-benefit model of thermoregulation (Cadena & Tattersall, 2009), yet it is unknown how these changes in precision relate to their behaviour in nature. We use temperature-sensitive radio transmitters equipped with accelerometers to quantify activity and body temperature in the wild (Fig. 1), allowing us to generate field-based thermal performance curves. In addition, by combining body temperatures with recordings of the thermal landscape, we estimate seasonal thermoregulatory behaviour (Fig. 1D). This approach enables us to examine how aspects of thermal performance curves and thermoregulatory behaviours relate to individual survival (Fig. 1E) during the reproductive season (spring) when this species experiences its highest predation pressures (Wild et al., 2022). We predict that thermoregulation will vary according to seasonal environmental costs (Huey & Slatkin, 1976). However, because of the lack of studies that account for sex differences in thermoregulation (Christian & Weavers, 1996; Vickers et al., 2011), we predict limited differences in body temperatures between sex. Finally, we predict individuals with high maximum performance will have a higher likelihood of survival compared to those with low maximal performance (Christian & Tracy, 1981; Gilbert & Miles, 2017). To date, no studies have continuously collected seasonal data on individuals to investigate the impact of thermoregulation on performance and how these trade-offs relate to survival in natural settings.

2. Materials and methods

2.1 Preferred body temperature estimation (T_{set}) and body temperature calibration

Preferred body temperature (T_{set}) trials were conducted on adult *P. vitticeps* that were either captured from the study site or captive-bred descendants of wild-caught lizards from the study region (*see* section 2.2 for region description). Trials were conducted in a temperature-controlled (20 °C) room where internal body temperatures were measured using surgically-implanted temperature loggers (Thermochron iButton, recording every 2min) as lizards moved along a laboratory thermal gradient that ranged from 20°C to 40°C (Fig. 1A; *see* SI for details on gradient and surgical protocols). Animals remained in the thermal gradient for a minimum of 12h. Preferred body temperature was defined as the bounds of the central 50% (i.e., the 25th and 75th quartiles) of body temperature in the thermal gradient (Hertz et al., 1993). Linear models were used to determine differences in T_{set} bounds between sex.

To predict internal body temperature using external body temperatures ('surface temperatures') in field settings, we examined the relationship between body temperature and surface temperature in a subset of captive animals measured in the indoor thermal gradient ($T_{b,\ Predict}$; Fig. 1A,B). This subset was equipped with a Pinpoint Beacon 250 (Lotek Ltd., Havelock North, NZ) that was placed in a custom-fit backpack harness (Wild et al., 2022). Each unit housed a temperature data logger that recorded surface temperature every 2s, which was averaged every 2min to pair with body temperature with iButton. Gradient methods followed the same protocol described above. The relationship between body and surface temperature was estimated using linear regression and paired t-test (surface vs. internal temperature at each time point) to examine the degree to which surface temperature underestimated or overestimated body temperature. The equation from the linear regression between body and surface temperature was used for $T_{b,Predict}$ correction.

2.2 Field study area and radiotelemetry

Field work for this study was conducted in a 140km² nature reserve (Bowra Wildlife Sanctuary) near Cunnamulla Queensland, Australia. Adult *P. vitticeps* were captured opportunistically and tracked continuously between October 2018 to September 2019. Each lizard was fitted with a Pinpoint Beacon 250 using the same custom-fit backpack harness used in the $T_{b,Predict}$ experiment. Each unit housed a GPS logger, a single-stage VHF transmitter (150–151 Hz), a temperature data logger, and a 2-axis accelerometer. Phenotypic sex was determined using hemipenile eversion. For further information on lizard collection, site description, or radio telemetry, see Wild et al. (2022).

2.3 Field predicted body temperature, operative environmental temperature, and thermoregulatory strategy

Temperature dataloggers in the Pinpoint Beacon 250 measured the range of temperatures that lizards experience in the wild. Loggers recorded a surface temperature (°C) every 2s, and this was averaged over 1min. The surface and body temperature correction was applied (Fig. 1A) to estimate field body temperature ($T_{b,Predict}$). Final body temperatures ($T_{b,Predict}$) for each lizard were averaged for each hour between 0500-2100. Hourly core body temperatures ($T_{b,obs}$) in the field were recorded for a subset of individuals (n=8) using surgically implanted iButtons and showed a near one-to-one relationship between laboratory-adjusted ($T_{b,Predict}$) and observed field temperatures ($p<0.001$, *see* SI for results, Fig. S1).

Environmental temperatures available to animals within the landscape (T_e) were estimated using physical models (Bakken & Gates, 1975) that were the same length and width of an average lizard. Models were constructed of hollow copper pipes (4.0cmx25.0cm) with a iButton suspended in the centre (Fig. 1C). These models were validated by comparison with fresh lizard carcasses with implanted iButton dataloggers recording internal body temperature (*see* SI for calibration methods). Copper models were deployed from October 2018 to September 2019 and recorded environmental temperature (T_e) every 1h. Copper models were placed in five micro-habitat categories: full shade (n=10), partial shade (n=10), open (n=10), tree (n=12), and burrow (n = 8; *see* Table S1 for definitions of micro-habitat categories). Micro-habitats accessible to *P. vitticeps* were considered when positioning each model (see SI for model calibration and verification). Mean T_e measurements were calculated for each hour between 0500-2100 to obtain a measure of the operative temperature of the habitat available to *P. vitticeps* for any given hour during the study. We assumed males and females experienced the same distribution of thermal microhabitats. We compared our T_e estimates to those predicted using the NicheMapR biophysical modelling software (Kearney & Porter, 2017) and found a close and near one-to-one relationship between our T_e estimates and those predicted with NicheMapR ($p<0.001$, *see* SI for results, Fig. S2).

Metrics of thermoregulation were quantified using laboratory preference range (T_{set}) and hourly measurements of environmental (T_e) and body temperature ($T_{b,Predict}$) in the field. The accuracy of thermoregulation (d_b) was defined as the overall mean deviations of body temperatures from the thermal preference range (calculated using sex-specific T_{set} values). Similarly, the average thermal quality of the habitat (d_e) was assessed by estimating the overall mean deviations of environmental temperatures from the thermal preference range for each individual copper model in each habitat (Hertz et al., 1993). These metrics were calculated hourly between 0500-2100h across the year. The hourly effectiveness of thermoregulation (E) for each individual lizard was then calculated using d_b and d_e with the following equation:

$$E = 1 - (\overline{d}_b) \,/\, \overline{d}_e$$

where E is expressed as a ratio generally ranging from 0 to 1, and over bars indicate mean deviations of body and environmental temperature. An E of 1 reflects perfect thermoregulation, where body temperature falls within the thermal preference range. An E of 0 is indicative of an animal not thermoregulating (Hertz et al., 1993). It is possible for E to be negative in situations where an individual actively avoids the thermal preference range even though T_e allows the opportunity for thermoregulation within the thermal preference range. Low E values can occur when predators are abundant, food availability is scarce, or during interaction with conspecifics (Christian & Weavers, 1996). All metrics of thermoregulation ($T_{b,Predict}$, d_b, d_e, and E) were averaged for each individual over the course of each season prior to analysis. For each metric, a linear mixed-effects model was used to test the effect of season, sex, and their interactions, with season and sex as fixed effects and either lizard ID (or model ID) as a random effect.

2.4 Activity and thermal performance curves

Activity (min/h) and field thermal performance curves (TPC) were estimated using the accelerometry and temperature data provided by the Pinpoint Beacon 250. Accelerometers recorded acceleration on two axes corresponding to X-heave and Y-surge at a rate of 6Hz. Acceleration values were averaged for each axis (1min) between 0500-2100h for each season (spring, summer, autumn, winter). Each axis of acceleration was transformed to resultant acceleration (hereafter acceleration, ms^{-2}) following manufacturer protocols (*see* SI for transformation details). Activity was defined as any change in acceleration from the previous value between samples taken with the accelerometer and calculated as the minutes moved for each hour (min/h). For analysis purposes activity was log-transformed (log(x+1)) to deal with the abundant sedentary periods in which individuals did not move (i.e., no changes in acceleration).

Thermal performance curves were constructed using $T_{b,Predict}$ and acceleration (ms^{-2}) values from accelerometers. Body temperatures ($T_{b,Predict}$) were averaged for each 1min to match the averaged timescale of acceleration data. General additive mixed-models (GAMM) were used with $T_{b,Predict}$ as the predictor and acceleration (i.e., performance) as the response variable. Performance for TPC was defined as the 95th percentile of acceleration at each 1°C. This allowed the ability to characterise the upper capacity for movement while avoiding the influence of outliers resulting from the many sedentary periods. The package mgcv was used for cubic spline rolling average regression for all GAMM (Wood, 2017). Model selection, fitting, and validation followed Zurr et al. (2009). The most inclusive GAMM included (in addition to temperature) season, sex, and their interaction as fixed effects, and individual as a random effect [modelled as a smoothed cubic spline]. The maximum predicted acceleration (ms^{-2}) from GAMM fit was defined as P_{max} and the temperature associated with P_{max} was defined as T_{opt} (Angilletta, 2009). For each TPC metric (P_{max} and T_{opt}) a linear mixed-effects model was used to test the effect of season, sex, and their interactions, with season and sex as fixed effects and lizard id random (repeated) effect. The *gam.check()* function from the package mgcv was used to examine model convergence, gradient range, Hessian matrix characteristics, and basis dimension checking results.

2.5 Estimating survival

Maximum likelihood survival probabilities were estimated using known fate models (White & Burnham, 1999). Parameter estimates derived from known fate models were used to determine the extent to which thermal or performance estimates could predict an individual's survivorship in the field (Fig. 1E). Survival was determined from daily telemetry surveys from Spring 2018, where deaths of individuals were documented when bodies were recovered. Spring was used for this analysis because movement and mortality rates are elevated during this period relative to other seasons (Wild et al., 2022), allowing the best chance to link variation in thermal and performance estimates with survival outcomes. AICc was used to correct for small sample sizes when estimating survivorship using known fate models during the spring season, and models with ΔAICc of < 2.0 were considered to have support. The analysis started with a fully saturated model in which survival probability during the spring was dependent on movement (min/h), accuracy of thermoregulation (d_b), effectiveness of thermoregulation (E), and maximum performance (P_{max}) as covariates, then a series of reduced-parameter models were fitted where sex was included (or removed) as an interaction.

2.6 Statistical analysis

Statistical analyses were performed using the R environment ver. 4.1.0 and survivorship estimates using the program MARK (White & Burnham, 1999). All analyses were tested for normality. If data did not fit normality assumptions, the appropriate transformation was applied to achieve normality. Seasonal periods were spring, summer, autumn, and winter for all analyses. Statistical significance was accepted at the $p<0.05$, and if results were significant, they were followed with the appropriate post-hoc test.

3. Results

3.1 Preferred body temperature estimation (T_{set}) and body temperature calibration

Preferred body temperature was determined for 20 lizards (male: n=10; female: n=10). Females consistently had higher estimates than males. This was observed in the 75% quantile measurements, with females at 33.8±0.92°C and males at 29.0±0.92°C ($F_{1,18}=4.78$; $p<0.05$). Similarly, in the 25% quantile measurements, females had estimates of 27.0±0.46°C, while males had 25.5±0.46°C ($F_{1,18}=4.77$; $p<0.05$).

There was a strong relationship between laboratory body temperature and surface temperature. (16,938 paired measurements were recorded for 10 individuals; $R^2=0.94$; $F_{1,16937}=2,469,723$; $p<0.01$). Surface temperature slightly overestimated body temperature by 0.12 ± 0.01°C (paired t =12.21; df =16,938; $p<0.01$), so body temperature estimates ($T_{b,predict}$)were corrected from surface temperatures using the linear regression results:

$$T_{b,Predict}=1.770+ (T_{surf} \cdot 1.058)$$

3.2 Thermoregulation in the field

Thermal-sensitive accelerometers were placed on 40 individual *P. vitticeps* (male: n=32; female: n=8) that were tracked between Spring 2018 and Winter 2019. There were differences in seasonal body temperatures ($T_{b,Predict}$) ($p<0.01$) and differences between the season × sex interaction ($p<0.01$; Table S2), but for sex alone there were no differences ($p=0.40$). Least squares estimates indicated significant seasonal differences in $T_{b,Predict}$ (Table S3), with the highest values in summer (33.4±0.25°C), followed by spring (29.2±0.27°C), autumn (26.5±0.25°C), and winter (20.8±0.25°C). Least squares estimates for the interaction suggested that differences in $T_{b,Predict}$ between the sexes were only observable during the summer (Fig. 2A,B), where females selected higher body temperatures than males. There were no detectable differences in $T_{b,Predict}$ during other seasons (Table S4).

Mean T_e was different across all seasons ($F_{3,329321}=371.03$; $p<0.01$), with higher temperatures observed in spring and summer, and lower temperatures in autumn and winter (Fig. 2A,B). Season and the interaction between sex and season had an effect on the accuracy of thermoregulation (d_b), but there was no overall effect of sex on d_b estimates (Table S2). Males thermoregulated more accurately (i.e. low d_b) than females during spring, and there were no differences during the other seasons (Fig. 2C; $p<0.05$). Season, sex, and the interaction had an overall effect on the thermal quality of the habitat (d_e , Table S2). Thermal environment was more favourable (i.e. lower de) for females than males during the summer (Fig. 2D; $p<0.05$) because females had a higher T_{pref} range than males.

The effectiveness of thermoregulation (E) was influenced by season, but the effect of season was different between sexes (Table S2 & Fig. 3). In the spring season, thermoconforming behaviours (i.e. low E) were exhibited by females, while males displayed thermoregulating behaviours (i.e. high E). Both male and female lizards engaged in thermoregulating behaviours during the summer (Fig. 3). However, in the autumn and winter, lizards of both sex were less effective thermoregulators, approaching thermoconformity to their environment (Fig. 3). Overall, the effectiveness of thermoregulation (E) was higher (Table S2; $p=0.05$) in males (0.48) than in females (0.29).

3.3 Seasonal activity and thermal performance curves

A total of 6,858,857 raw acceleration data points were collected on male (n=32) and female (n=8) *P. vitticeps*. . Average movement varied across the season ($F_{3,81}$=9.25; p<0.01), but there were no differences between sexes ($F_{1,68}$=0.23; p=0.63) or the interaction ($F_{3,81}$=0.29; p=0.83). Overall activity was highest in the summer and lowest in the winter (Fig. 4; Table S4).

The top candidate GAMM model for field thermal performance curves (ΔAIC score = 0.00) accounted for season, sex and their interaction allowing for random intercept and smoothed spline per individual and explained 71% of the total deviance (Fig. 5; *see* S5 for other model comparisons). Season ($F_{3,88}$=190.62; p<0.01) and the interaction between sex and season ($F_{3,88}$=143.08; p<0.01) had an overall effect on the maximum performance, but there was no effect on sex alone ($F_{1,90}$=0.34; p=0.56). Maximum movement performance (P_{max}) was highest in spring, whereas winter had the lowest values of other seasons (p<0.05; Table S6). Females exhibited higher P_{max} values in autumn and winter than in other seasons, and males demonstrated higher values in spring and summer than in other seasons (Table S7). The average thermal optimum (T_{opt}) temperature (mean±SE) was 36.6±0.24°C. There were no differences in T_{opt} across seasons ($F_{3,88}$=0.24; p=0.63), between sex ($F_{1,90}$=0.57; p=0.64), or their interaction ($F_{3,88}$=1.79; p=0.64).

3.4 Applying metrics of thermoregulation, activity, and performance to survival

Twenty-seven lizards were tracked during the spring, eight of which died during this period. Survival probabilities (mean±SE) were higher for males (0.75±0.08) than females (0.33±0.20). The top competing model accounted for sex and maximum performance (Fig. 6; Table S8). There was a distinct pattern between performance and survival for both sexes, where individuals with lower maximum performance had higher survival rates compared to those with higher performance. This decline happened at lower levels of P_{max} in females than in males, such that a given P_{max} was associated with lower survival in females than males (Fig. 6).

4. Discussion

In the context of the cost-benefit model of thermoregulation (Huey & Slatkin, 1976), our study provides unprecedented insights into the trade-offs between thermoregulation and survival in ectotherms. For the first time, we demonstrate that maximum movement performance in the field is a strong predictor of individual survival, highlighting the nuanced relationship between thermal biology and fitness outcomes. Using telemetry and temperature-sensitive accelerometry, we generated the first in situ thermal performance curves for an ectotherm, providing a rare examination of field-based thermoregulatory strategies and their associated seasonal trade-offs. Notably, our findings reveal that high maximum performance, often associated with optimal thermoregulation, correlates with an increased frequency of predation for both males and females, with this effect being more pronounced in females. This suggests a negative relationship between maximum movement performance and survival, challenging the traditional view that higher performance within the thermal optimum invariably enhances fitness. Our results underscore the critical role of individual behavioural variation and sex in determining survival, and imply that seasonal shifts in thermoregulatory behaviour and performance are key drivers of variation in field body temperatures, thermoregulatory effectiveness, overall activity, and maximum performance observed in natural settings (Angilletta et al., 2002; Husak & Fox, 2006; Sears et al., 2011).

Contrary to previous studies, which have linked maximum movement performance—often measured as sprint speed under controlled laboratory conditions—to increased survival (Gilbert & Miles, 2017; Pearson & Warner, 2018), we found that higher maximum performance was associated with decreased survival in the wild. Our field-based findings suggest that high-performing individuals may be more prone to engaging in conspicuous or risky behaviours (Horváth et al., 2024), which could elevate their mortality rates due to increased visibility, risk-taking, or age-related factors (Sergio et al., 2014; Stamps, 2007; Ward-Fear et al., 2018). It is likely that individuals with greater acceleration that we followed were engaging in more conspicuous activities, making them more susceptible to predation (Skelly, 1994). Bolder lizards, which may exhibit high-performance traits (Albuquerque et al., 2023), often have more extensive core home ranges and spend more time in predator-abundant areas, increasing predation risk (Ward-Fear et al., 2018).

Outside of the reproductive season for females, we found that activity metrics of thermoregulation and maximum performance followed general predictions of the cost-benefit model of thermoregulation (Huey & Slatkin, 1976). Predictions from this model postulate that ectotherms should prioritise thermoregulation when environmental costs are low and the benefits of maintaining optimal body temperatures are high, while reducing thermoregulatory efforts when costs outweigh the benefits. We observed that during winter, when thermoregulation is more challenging due to lower ambient temperatures and limited time to achieve thermal preference, there was a marked decline in both the accuracy and effectiveness of thermoregulation. These declines coincided with decreases in other physiological traits that are temperature-dependent, such as maximum movement performance (ms^{-2}) and fine-scale activity (min/h). Conversely, during the summer the accuracy and effectiveness of thermoregulation were high, which corresponded with increased activity levels and maximum movement performance. These seasonal trade-offs demonstrate the dynamic balance that lizards must maintain while accounting for the energetic costs and benefits of thermoregulation (Angilletta & Sears, 2016; Vickers et al., 2011) and emphasise how seasonal thermoregulatory strategies influence activity levels and performance, with direct implications for growth, survival, and reproductive success.

Although the accuracy or effectiveness of thermoregulation was not critical for survival in our study, such strategies of thermoregulation can play a significant role in other aspects of lizard fitness, such as growth and maintenance (Brewster et al., 2013) or preventing overheating (Huey & Slatkin, 1976; Kearney et al., 2009). Our results further emphasise the seasonal dynamics of thermal biology, highlighting that maximising physiological performance through active thermoregulation is a high priority. This is particularly true for heliothermic lizards, which rely heavily on behavioural thermoregulation and demonstrate the ability to adjust their thermoregulatory accuracy in response to varying environmental costs (Sears et al., 2011).

Sex differences in thermal ecology in ectotherms have often been overlooked (Bodensteiner et al., 2021; Huey & Pianka, 2007; Pottier et al., 2021) mostly because of difficulties in studying the reproductive complexities of females. For example, females often alter their behaviour and physiology during gestation, incurring additional costs not experienced by males (Miles et al., 2000; Shine, 1980). For *P. vitticeps*, these trade-offs likely contribute to the observed increases in daily movements and the reductions in body condition during the reproductive season (Wild et al., 2022), as well as the overall higher energy demands that females experience (Wild et al., 2023). These increased energetic pressures associated with reproduction may drive the observed sex differences in the effectiveness of thermoregulation during spring (Angilletta & Sears, 2000; Congdon, 1989). Although fine-scale activity did not differ between sexes, males and females may allocate activity time differently (Orrell et al., 2004), allowing males to benefit more from thermoregulation, while females focus on reproduction or predator evasion (Herczeg et al., 2006; Gilbert et al., 2023). Differences in habitat use could explain differences in sex-specific thermal efficiency due to varying microclimates (Logan et al., 2021). To our knowledge, the present study is the first to account for sex when investigating the efficiency of thermoregulation in natural settings for any ectotherm (*see* Herczeg et al., 2006 for lab example). Comparing habitat use patterns or field metabolic rates between sexes could help determine seasonal sex strategies of thermoregulation.

Laboratory results in other ectothermic vertebrates suggest a limited plasticity in optimal temperatures (MacLean et al., 2019; Pottier et al., 2022; Zhang et al., 2023). Our field findings corroborate this, indicating that the field optimal temperature of 36.6±0.24°C—where movement intensity was maximised—remained consistent across sexes and seasons. A constrained thermal optimum suggests that energetically expensive behaviours, like thermoregulation, are necessary to maintain optimal temperatures throughout the year, regardless of environmental changes (Huey et al., 2012; Kearney et al., 2009). This requirement becomes particularly challenging during energetically demanding periods like spring and summer when heliothermic lizards divert surplus energy reserves toward reproduction (Nagy, 1983). Maintaining a static thermal optimum appears to be crucial for performance, despite the costs of thermoregulation (Herczeg et al., 2008; Huey & Slatkin, 1976). These findings highlight the trade-offs involved in maintaining optimal body temperatures, as the energetic costs of thermoregulation must be balanced against other physiological needs (Blouin-Demers & Nadeau, 2005; Vickers et al., 2011).

The methods used to quantify ectotherm responses to temperature gradients in the laboratory are well-established (Angilletta, 2009; Huey, 1982; Taylor et al., 2021). However, replicating laboratory methods in natural environments is challenging due to the extensive data needed to link temperature fluctuations with behaviour and physiology, yet understanding these interactions is crucial for insights into organism-temperature relationships and selection processes (Angilletta, 2009; Christian & Tracy, 1981; Seebacher & Franklin, 2005). For the first time in any lizard species, we have shown that temperature-sensitive accelerometers can estimate thermal performance curves in a natural setting. We refined the method of measuring body temperatures by calibrating body surface temperatures, and our summer estimate (32.7±0.02°C) aligns well with the only documented field core body temperatures published for this species (34.3±3.75°C: Greer, 1989; 32.9±0.88°C: Melville & Schulte, 2001). New applications of accelerometers provide promising research avenues as their usage continues to rise across other vertebrate groups (Chakravarty et al., 2019; Garde et al., 2022; Pagano & Williams, 2019). Studies connecting data from accelerometers to estimates of energy expenditure or identifying specific behaviours provide promising avenues for future research regarding questions relating to thermal ecology.

We have shown that by combining basic physiological measurements with the technology of thermosensitive accelerometers, it is possible to test challenging ecological and physiological hypotheses regarding thermal ecology. Our approach allows the linking of seasonal variation in thermal performance to survival, highlighting its role as a key driver. Such analyses are crucial for predicting how species may respond to anthropogenic disturbance and climate warming, and how selection may act on ectotherms in these scenarios (Sinclair et al., 2016). Our data highlight the need to consider species-specific ecological contexts when interpreting physiological metrics like sprint speed or acceleration, as selection may act on ecological performance depending on how organisms utilise their maximal performance in nature. Further work is needed to understand this dynamic relationship within species and test how common physiological traits measured in the lab vary seasonally under field conditions in a warming and more variable climate.

Acknowledgements

We acknowledge the Kunja, people as the traditional custodians of the land where this study took place. The project was funded by a Discovery Grant from the Australian Research Council (DP170101147) awarded to A.G. (lead), Clare Holleley, Janine Deakin, Tariq Ezaz, S.D.S, L.S., Paul Waters and Jennifer Marshall Graves. The Ecological Society of Australia provided additional funds awarded to K.H.W. K.H.W was supported by a Commonwealth Research Scholarship and the Institute for Applied Ecology at the University of Canberra. We thank Australian Wildlife Conservancy (AWC) for access to study site and research facilities. We thank Mallory Strawn-Wild, K. Joyner, J. Soroka, & H. Warick for field help. We thank J. Richardson for animal husbandry and support for the captive animals at UC. Data collection for this project was performed under UC Animal Ethics approval AEC 17-13.

Conflict of interests

We declare we have no competing interests.

Author contributions

K.W organised the sampling design, collection materials, laboratory work, and figures with the support of J.R, J.C., P.P., L.S., A.G., and S.S. The first draft of the manuscript was written by K.W. Comments from J.R, J.C., P.P., L.S., A.G., and S.S. contributed to the final version. The project was funded by a Discovery Grant from the Australian Research Council (DP170101147) awarded to A.G. (lead), Clare Holleley, Janine Deakin, Tariq Ezaz, S.D.S, L.S., Paul Waters and Jennifer Marshall Graves. The Ecological Society of Australia provided additional funds awarded to K.H.W. K.H.W was supported by a Commonwealth Research Scholarship and the Institute for Applied Ecology at the University of Canberra. We acknowledge the Kunja people as the traditional custodians of the land where this study occurred.

Data accessibility

Data, code, and additional resources are available on GitHub: https://github.com/kris-wild/TPC_Survival.git

Literature cited

Albuquerque, R. L., Zani, P. A., & Garland, T. (2023). Lower-level predictors and behavioral correlates of maximal aerobic capacity and sprint speed among individual lizards. Journal of Experimental Biology, 226(5).

Angilletta, M. J. (2009). Thermal Adaptation (Vol. 53). Oxford University Press.

Angilletta, M. J., Hill, T., & Robson, M. A. (2002). Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*. Journal of Thermal Biology, 27(3), 199–204.

Angilletta, M. J., & Sears, M. W. (2000). The metabolic cost of reproduction in an oviparous lizard. Functional Ecology, 14(1), 39–45.

Bakken, G. S., & Gates, D. M. (1975). Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. In Perspectives of biophysical ecology (pp. 255–290).

Bodensteiner, B. L., Agudelo-Cantero, G. A., Arietta, A. Z. A., Gunderson, A. R., Muñoz, M. M., Refsnider, J. M., & Gangloff, E. J. (2021). Thermal adaptation revisited: How conserved are thermal traits of reptiles and amphibians? Journal of Experimental Zoology Part A: Ecological and Integrative Physiology, 335(1), 173–194.

Brown, J. H., Hall, C. A., & Sibly, R. M. (2018). Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nature Ecology & Evolution*, *2*(2), 262-268.

Boyd IL, Hoelzel A. 2002. Energetics: consequences for fitness. In Marine Mammal Biology: An Evolutionary Approach, ed. AR Hoelzel, pp. 247–77. Malden, MA: Blackwell.

Cadena, V., & Tattersall, G. J. (2009). The effect of thermal quality on the thermoregulatory behavior of the bearded dragon *Pogona vitticeps*: Influences of methodological assessment. Physiological and Biochemical Zoology, 82(3), 203–217.

Campos-Candela, A., Palmer, M., Balle, S., Álvarez, A., & Alós, J. (2019). A mechanistic theory of personality-dependent movement behaviour based on dynamic energy budgets. *Ecology letters*, *22*(2), 213-23.

Chakravarty, P., Cozzi, G., Ozgul, A., & Aminian, K. (2019). A novel biomechanical approach for animal behaviour recognition using accelerometers. Methods in Ecology and Evolution, 10(6), 802–814.

Chan, R. L., Hodgson, M., & Schwanz, L. E. (2024). The two environmental drivers of thermoregulatory costs: Interactions between thermal mean and heterogeneity influence thermoregulation. *Functional Ecology*.

Childress, E. S., & Letcher, B. H. (2017). Estimating thermal performance curves from repeated field observations. Ecology, 98(5), 1377–1387.

Christian, K. A., & Tracy, C. R. (1981). The effect of the thermal environment on the ability of hatchling Galapagos Land Iguanas to avoid predation during dispersal. Oecologia, 49(2), 218–223.

Christian, K. A., & Weavers, B. W. (1996). Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecological Monographs, 66(2), 139–157.

Congdon, J. D. (1989). Proximate and evolutionary constraints on energy relations of reptiles. Physiological Zoology, 62(2), 356–373.

Garde, B., Wilson, R. P., Fell, A., Cole, N., Tatayah, V., Holton, M. D., Rose, K. A. R., Metcalfe, R. S., Robotka, H., Wikelski, M., Tremblay, F., Whelan, S., Elliott, K. H., & Shepard, E. L. C. (2022). Ecological inference using data from accelerometers needs careful protocols. Methods in Ecology and Evolution, 13(4), 813–825.

Giacometti, D., Palaoro, A. V., Leal, L. C., & de Barros, F. C. (2024). How seasonality influences the thermal biology of lizards with different thermoregulatory strategies: a meta-analysis. Biological Reviews, 99(2), 409–429.

Gilbert, A. L., & Miles, D. B. (2017). Natural selection on thermal preference, critical thermal maxima and locomotor performance. Proceedings of the Royal Society B: Biological Sciences, 284(1860), 20170536.

Gilbert, A. L., Shine, R., & Warner, D. A. (2023). Carrying eggs uphill: are costs of reproduction stronger on steeper slopes? Biology Letters, 19(5).

Greer, A. E. (1989). The biology and evolution of Australian lizards. Surrey Beatty and Sons.

Herczeg, G., Herrero, A., Saarikivi, J., Gonda, A., Jäntti, M., & Merilä, J. (2008). Experimental support for the cost-benefit model of lizard thermoregulation: The effects of predation risk and food supply. Oecologia, 155(1), 1–10.

Hertz, P. E., Huey, R. B., & Stevenson, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. The American Naturalist, 142(5), 796–818.

Hodgson, M. J., & Schwanz, L. E. (2024). Best of both worlds: Acclimation to fluctuating environments confers advantages and minimizes costs of constant environments. *Functional Ecology*, *38*(4), 724-738.

Horváth, G., Sos, T., Bóné, G., Lőrincz, C. E., Pap, P. L., & Herczeg, G. (2024). Integrating behavioural thermoregulatory strategy into the animal personality framework using the common lizard, *Zootoca vivipara* as a model. Scientific Reports, 14(1).

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In Biology of the Reptilia.

Huey, R. B. (1991). Physiological consequences of habitat selection. The American Naturalist, 137, S91–S115.

Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society B: Biological Sciences, 367(1596), 1665–1679.

Huey, R. B., & Pianka, E. R. (1977). Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. Ecology, 58(5), 1066–1075.

Huey, R. B., & Pianka, E. R. (2007). Lizard thermal biology: Do genders differ? American Naturalist, 170(3), 473–478.

Huey, R. B., & Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. The Quarterly Review of Biology, 51(3), 363–384.

Husak, J. F. (2006). Does speed help you survive? A test with collared lizards of different ages. *Functional Ecology*, 174-179.

Husak, J. F., & Fox, S. F. (2006). Field use of maximal sprint speed by collard lizards (*Crotaphytus collaris*): compensation and sexual selection. Evolution, 60(9), 1888–1895.

Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proceedings of the National Academy of Sciences, 106(10), 3835–3840.

Leith, N. T., Miller, E. A., & Fowler-Finn, K. D. (2024). Thermoregulation enhances survival but not reproduction in a plant-feeding insect. Functional Ecology, 38(6), 1344–1356.

Logan, M. L., Neel, L. K., Nicholson, D. J., Stokes, A. J., Miller, C. L., Chung, A. K., Curlis, J. D., Keegan, K. M., Rosso, A. A., Maayan, I., Folfas, E., Williams, C. E., Casement, B., Koyner, M. A. G., Perez, D. J. P., Falvey, C. H., Alexander, S. M., Charles, K. L., Graham, Z. A., … Cox, C. L. (2021). Sex-specific microhabitat use is associated with sex-biased thermal physiology in Anolis lizards. Journal of Experimental Biology, 224(2).

MacLean, H. J., Sørensen, J. G., Kristensen, T. N., Loeschcke, V., Beedholm, K., Kellermann, V., & Overgaard, J. (2019). Evolution and plasticity of thermal performance: An analysis of variation in thermal tolerance and fitness in 22 Drosophila species. Philosophical Transactions of the Royal Society B: Biological Sciences, 374(1778).

Melville, J., & Schulte, J. A. (2001). Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. Austral Ecology, 26(6), 660–669.

Miles, D. B., Sinervo, B., & Frankino, W. A. (2000). Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. Evolution, 54(4), 1386–1395.

Nagy, K. A. (1983). Ecological energetics. In R. B. Huey, E. R. Pianka, & T. W. Schoener (Eds.), Lizard Ecology (II, pp. 24–54). Harvard University Press.

Orrell, K. S., Congdon, J. D., Jenssen, T. A., Michener, R. H., & Kunz, T. H. (2004). Intersexual differences in energy expenditure of Anolis carolinensis lizards during breeding and postbreeding seasons. Physiological and Biochemical Zoology, 77(1), 50–64.

Pagano, A. M., & Williams, T. M. (2019). Estimating the energy expenditure of free-ranging polar bears using tri-axial accelerometers: A validation with doubly labeled water. Ecology and Evolution, 9(7), 4210–4219.

Pearson, P. R., & Warner, D. A. (2018). Early hatching enhances survival despite beneficial phenotypic effects of lateseason developmental environments. Proceedings of the Royal Society B: Biological Sciences, 285(1874).

Porter, W. P., Mitchell, J. W., Beckman, W. A., & DeWitt, C. B. (1973). Behavioral implications of mechanistic ecology. Oecologia, 13(1), 1–54.

Pottier, P., Burke, S., Drobniak, S. M., Lagisz, M., & Nakagawa, S. (2021). Sexual (in)equality? A meta-analysis of sex differences in thermal acclimation capacity across ectotherms. Functional Ecology, 35(12), 2663–2678.

Pottier, P., Burke, S., Zhang, R. Y., Noble, D. W. A., Schwanz, L. E., Drobniak, S. M., & Nakagawa, S. (2022). Developmental plasticity in thermal tolerance: Ontogenetic variation, persistence, and future directions. Ecology Letters, 25(10), 2245–2268.

Sears, M. W., & Angilletta, M. J. (2015). Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. The American Naturalist, 185(4), E94–E102.

Sears, M.W., Angilletta Jr, M.J., Schuler, M.S., Borchert, J., Dilliplane, K.F., Stegman, M., Rusch, T.W. & Mitchell, W.A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences*, *113*(38), 10595-10600.

Seebacher, F., & Franklin, C. E. (2005). Physiological mechanisms of thermoregulation in reptiles: a review. Journal of Comparative Physiology B, 175(8), 533–541.

Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L. L., Blas, J., Tavecchia, G., Preatoni, D., & Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. Nature, 515(7527), 410–413.

Shine, R. (1980). “Costs” of reproduction in reptiles. Oecologia, 46(1), 92–100.

Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., Dong, Y., Harley, C. D. G., Marshall, D. J., Helmuth, B. S., & Huey, R. B. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures?. *Ecology letters*, *19*(11), 1372-1385.

Skelly, D. K. 1994. Activity level and the susceptibility of anuran larvae to predation. *Animal Behaviour*, 47, 465-468.

Stamps, J. A. (2007). Growth-mortality tradeoffs and “personality traits” in animals. rowth-mortality tradeoffs and ‘personality traits’ in animals. *Ecology letters*, *10*(5), 355-363.

Taylor, E. N., Diele-Viegas, L. M., Gangloff, E. J., Hall, J. M., Halpern, B., Massey, M. D., ... & Telemeco, R. S. (2021). The thermal ecology and physiology of reptiles and amphibians: A user's guide. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *335*(1), 13-44.

Van Damme, R., Bauwens, D., & Verheyen, R. F. (1991). The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara*. Functional Ecology, 507–517.

Vickers, M., Manicom, C., & Schwarzkopf, L. (2011). Extending the cost-benefit model of thermoregulation: High-temperature environments. American Naturalist, 177(4), 452–461.

Ward-Fear, G., Brown, G. P., Pearson, D. J., West, A., Rollins, L. A., & Shine, R. (2018). The ecological and life history correlates of boldness in free-ranging lizards. Ecosphere, 9(3).

Warner, D. A., & Andrews, R. M. (2002). Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. Biological Journal of the Linnean Society, 76(1), 105–124.

White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. Bird Study, 46, 120–139.

Wild, K. H., & Gienger, C. M. (2018). Fire-disturbed landscapes induce phenotypic plasticity in lizard locomotor performance. Journal of Zoology, 305(2), 96–105.

Wild, K. H., Roe, J. H., Schwanz, L., Georges, A., & Sarre, S. D. (2022). Evolutionary stability inferred for a free ranging lizard with sex-reversal. Molecular Ecology, 31(8), 2281–2292.

Wild, K. H., Roe, J. H., Schwanz, L., Rodgers, E., Dissanayake, D. S. B., Georges, A., Sarre, S. D., & Noble, D. W. A. (2023). Metabolic consequences of sex reversal in two lizard species: a test of the like-genotype and like-phenotype hypotheses. Journal of Experimental Biology, 226(13).

Wood, S. N. (2017). Generalized Additive Models. In Generalized Additive Models: An Introduction with R, Second Edition. Chapman and Hall/CRC.

Zhang, R. Y., Wild, K. H., Pottier, P., Carrasco, M. I., Nakagawa, S., & Noble, D. W. A. (2023). Developmental environments do not affect thermal physiological traits in reptiles: an experimental test and meta-analysis. Biology Letters, 19(5).

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed-effects modeling for ecology with R.

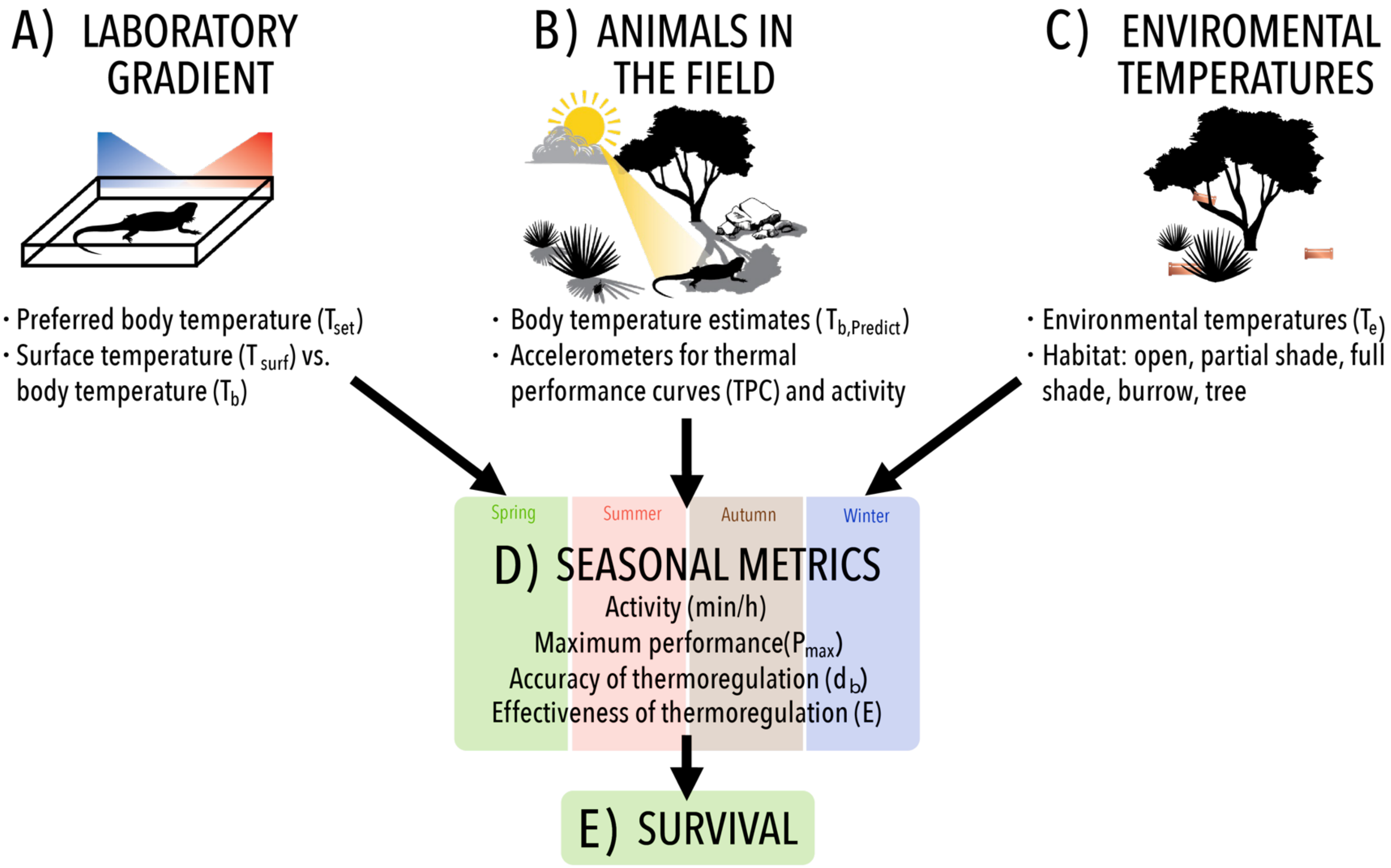

Figure 1. The comprehensive workflow of the experimental design aimed at identifying trade-offs in thermoregulation and their implications for survival. Laboratory thermal gradient experiments (A) were used to (1) measure the preferred body temperature (T_{set}) and (2) assess the relationship between surface temperatures (T_{surf}) recorded with accelerometers and internal body temperatures, enabling the prediction of body temperatures in the field ($T_{b,Predict}$). Seasonal thermoregulation and field performance metrics were evaluated using accelerometers (B). Copper pipes were placed in various microhabitats to characterise the thermal environment (T_e) available to lizards in the field (C). Metrics derived from experiments were then compared across seasons (D) and then used as covariates to understand their impact on survival during the spring season (E) when predation pressures are highest for this species.

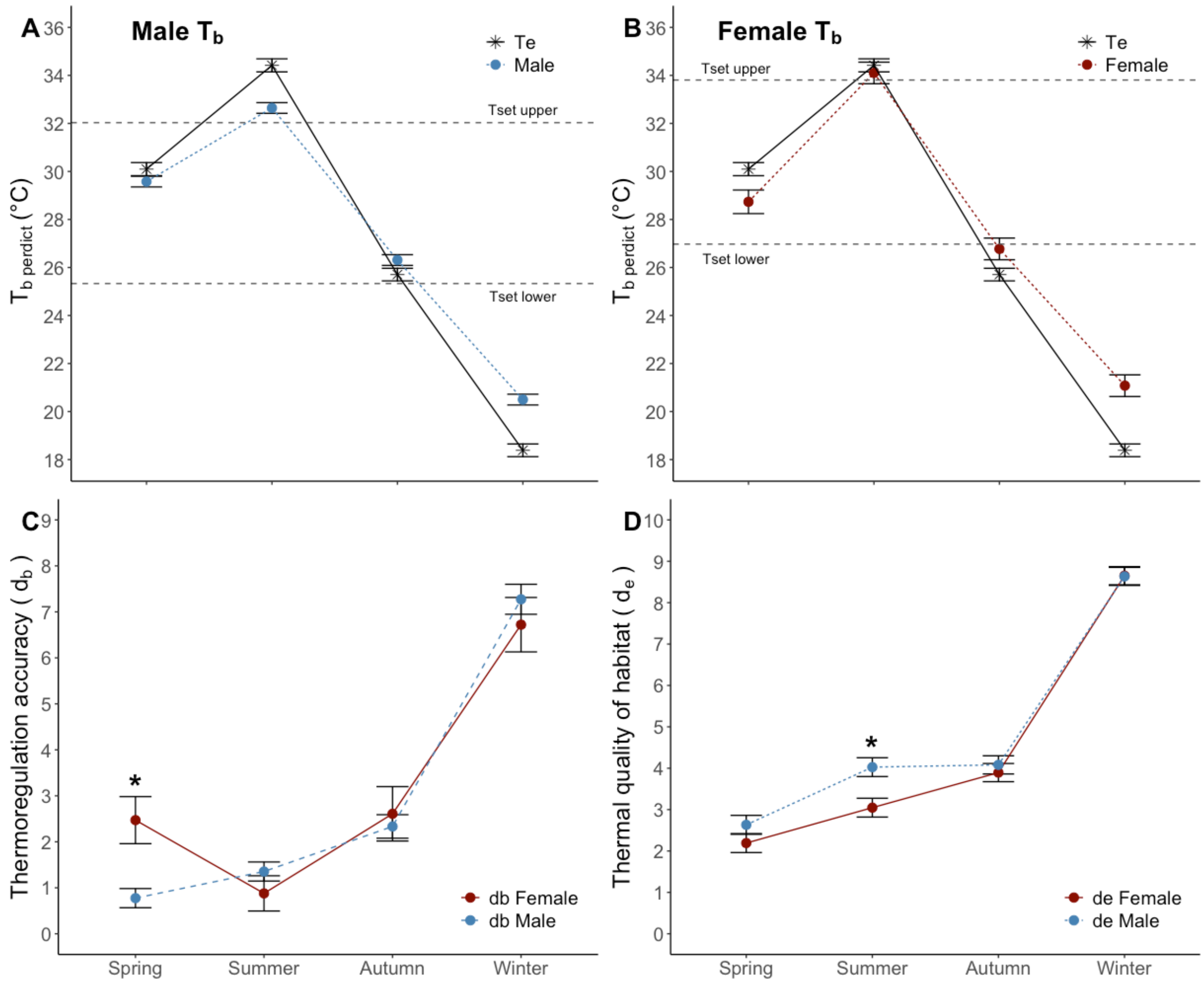

Figure 2. (A&B) Mean seasonal environmental temperature (T_e), thermal preference (T_{set}), and predicted body temperature ($T_{b,Predict}$) for male (A) and female (B) *Pogona vitticeps*. (C) Accuracy of thermoregulation (d_b) between sex, where low d_b denotes body temperature closer to thermal preference. (D) The thermal quality of habitat (d_e), measured with copper models, accounting for sex differences in thermal preference. Low d_e values indicate more environmental temperatures fell within T_{set} (i.e. favourable thermal environment). Error bars for all panels are ±1 standard error of the mean. The asterisk symbol indicates a significant difference ($p<0.01$) when comparing mean differences between sexes for that season.

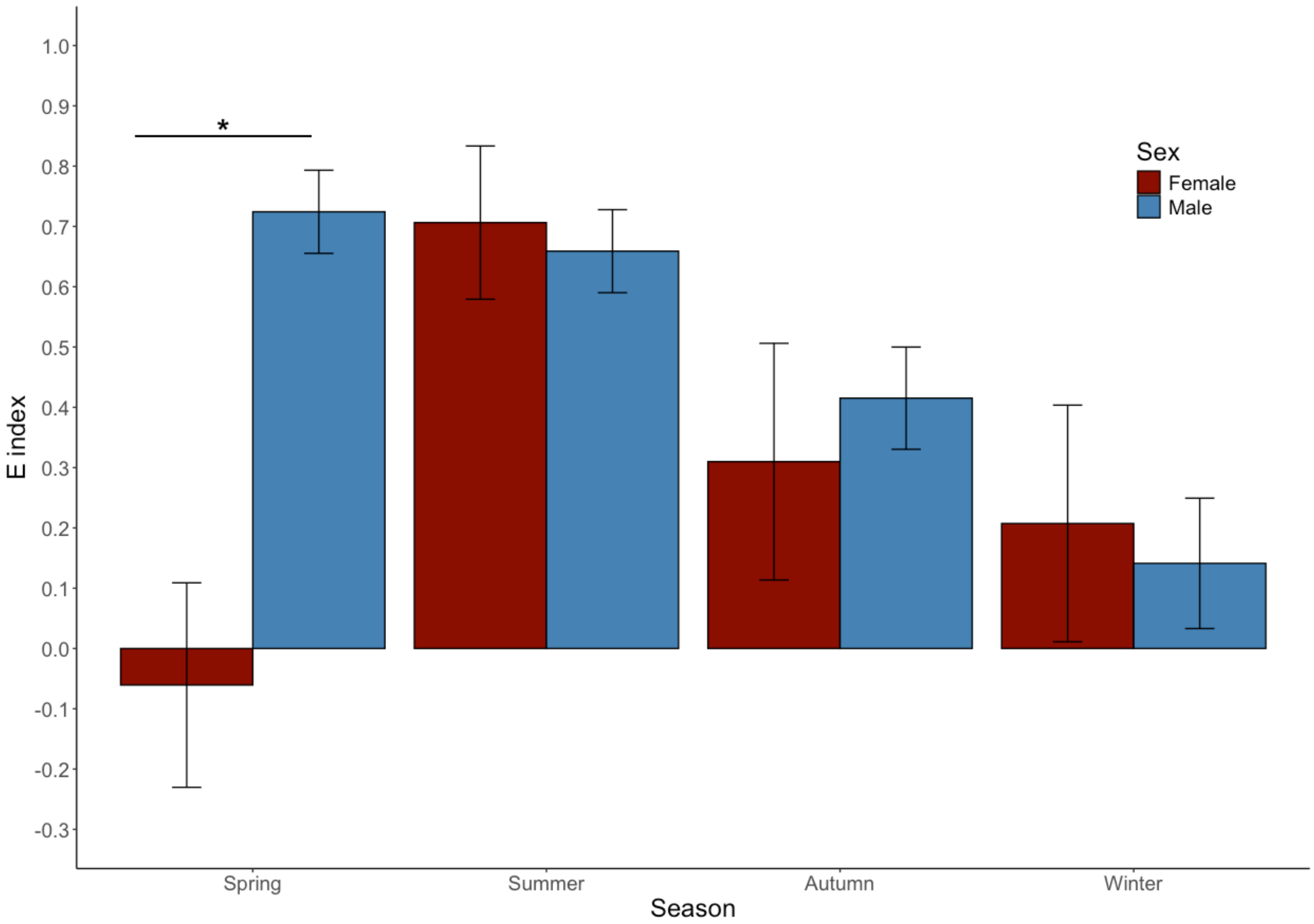

Figure 3. Effectiveness of thermoregulation (E index) by sex and season in *Pogona vitticeps*. E index values approaching 0 are indicative of conformity, and values approaching 1 are indicative of regulation. Values are means accounting for all individuals for each season. Error bars indicate ±1 standard error of the mean. The asterisk symbol denotes a significant difference ($p<0.01$) between sex when comparing mean differences for that season.

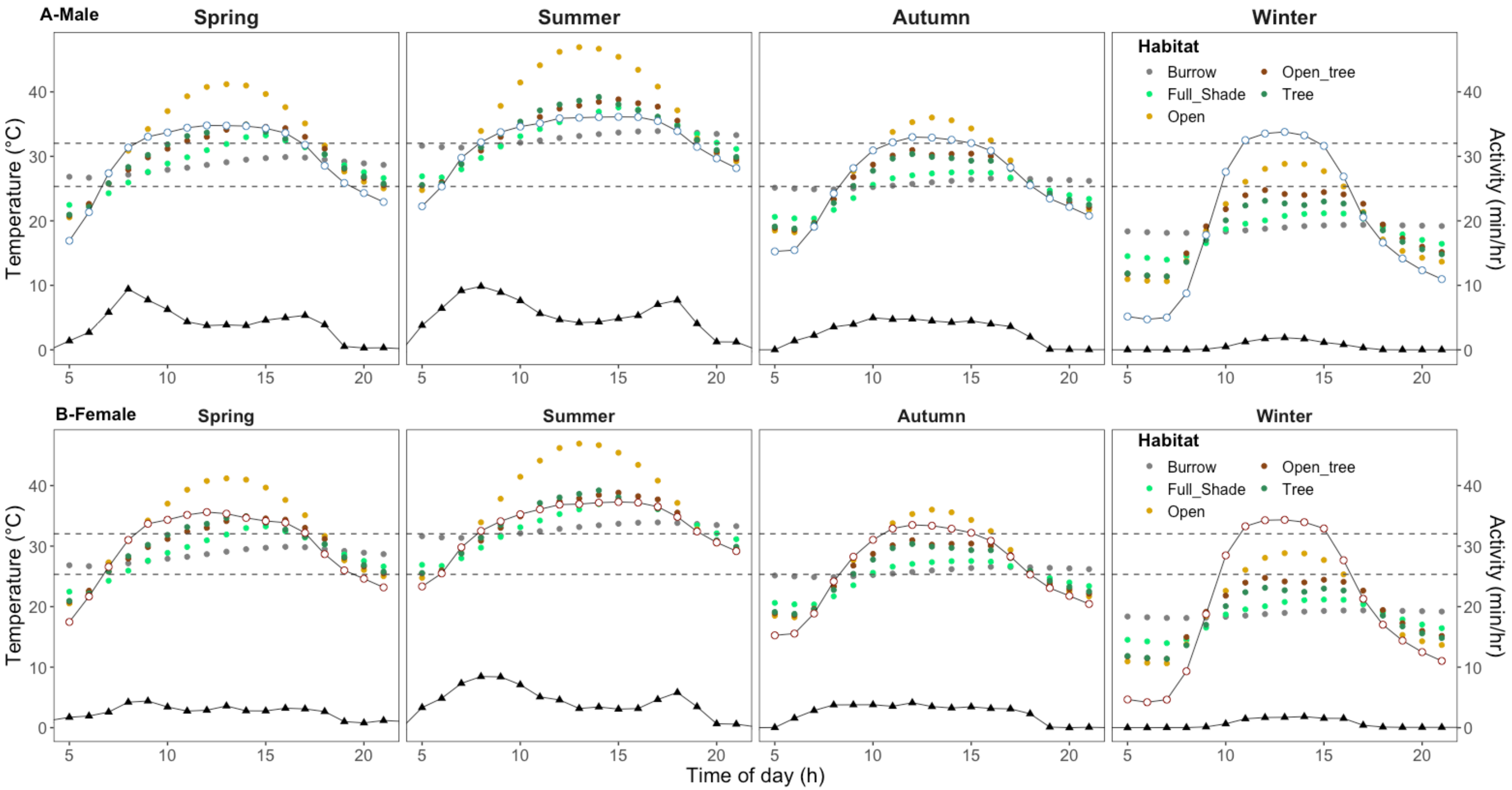

Figure 4. Mean predicted body temperatures (lines with circles) and activity levels (lines with triangles) for male (A) and female (B) *Pogona vitticeps* by season and time of day. The dashed line represents their preferred body temperature range. Coloured circles indicate mean environmental temperatures for different habitat types, measured using copper models.

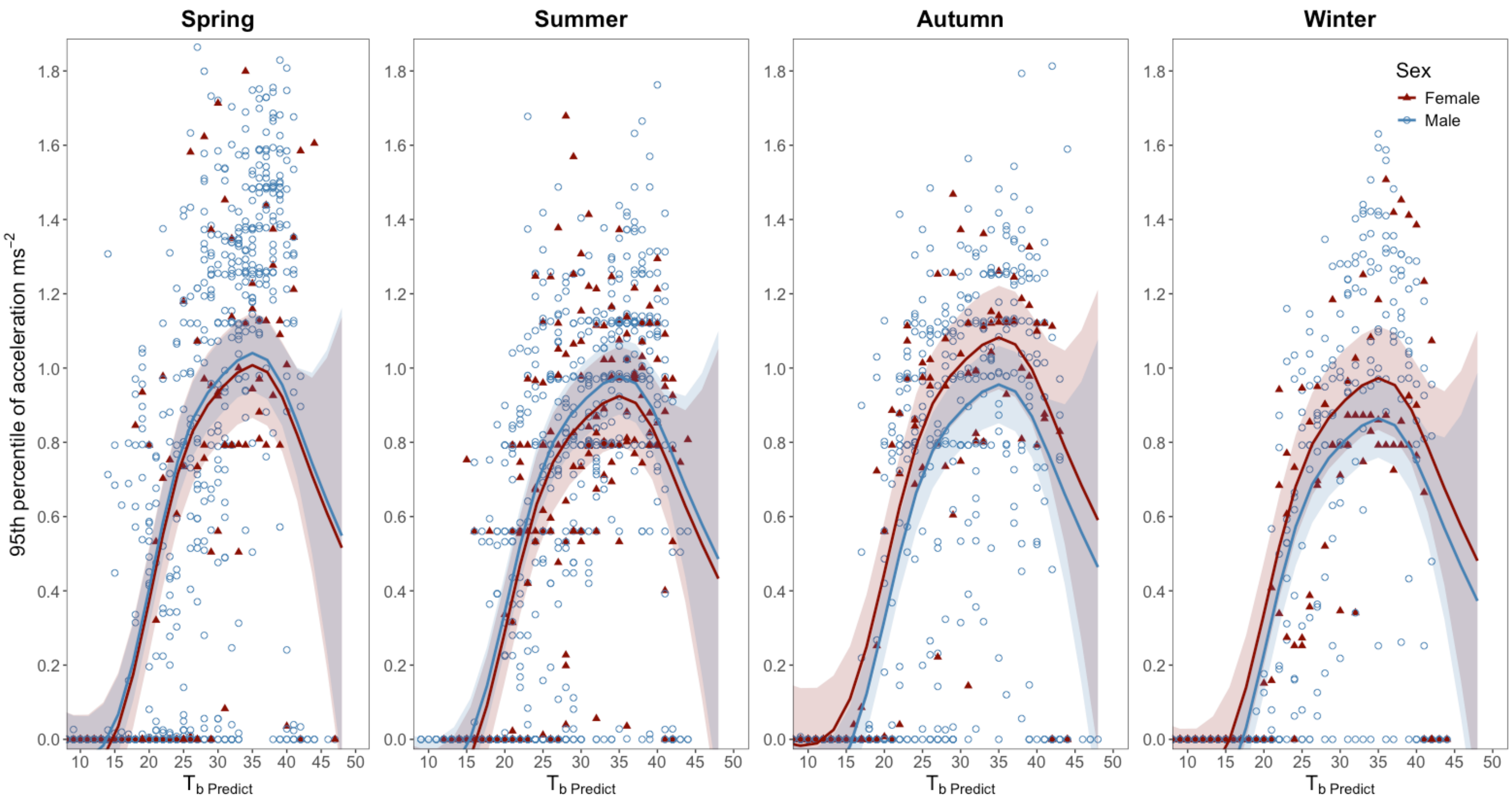

Figure 5. Thermal performance curves of free-ranging *Pogona vitticeps* across season and sex. The data were obtained from the top-performing Generalized Additive Mixed Models (GAMM) presented in Table S5. Each data point represents the average performance (95th percentile of acceleration) at a given temperature for all individuals in each season and sex. Bands around lines are 95%CI of model fit.

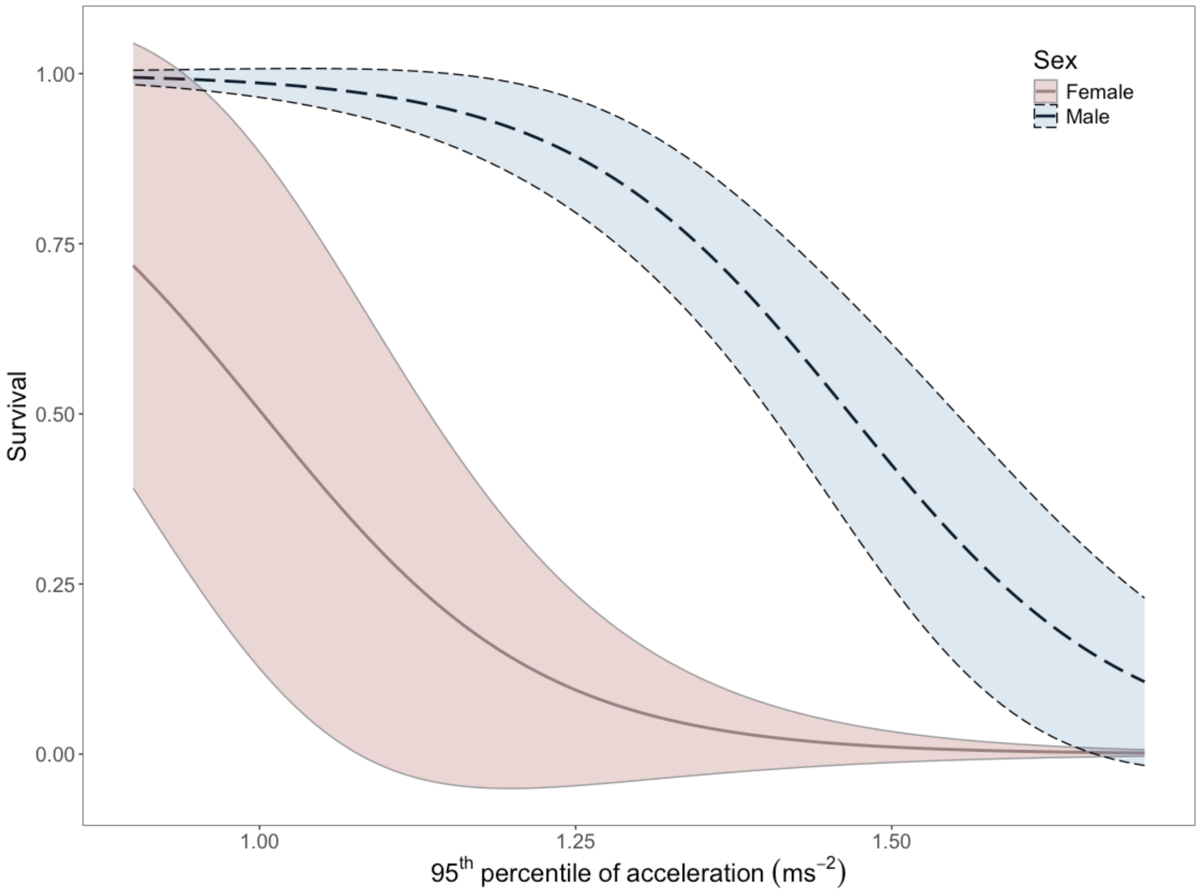

Figure 6. Survivorship as a function of the maximum performance (P_{max}) for free-ranging male and female *Pogona vitticeps* in spring (September -November). Data are extracted from the top-performing survival model in Program MARK that accounted for season and sex (Table S8). Lines represent the predicted mean survival for each sex, and bands indicate 95%CI.

Supplement Information

Thermal gradient and surgical protocols:

Thermal gradient: A series of ceramic heat lamps placed above the gradient (5.0m long × 1.0m high × 2.0m wide) achieved continuous temperatures that ranged from 20°C to 40°C. The gradient was arranged in lanes where each sex was randomly assigned a lane before each trial. The thermal gradient contained sand (15cm depth) and fluorescent lighting that was on a 12h on/off cycle

Surgical protocols: Internal body temperature (T_b) was measured with a surgically implanted Thermochron iButton. To accurately measure internal body temperature (T_b), a Thermochron iButton was surgically implanted following the surgical techniques outlined by(Koenig et al., 2001). Each lizard (male: n = 10; female: n = 10) was given an inhalant anaesthetic (isoflurane 3 – 5) until the surgical plane of anaesthesia was reached. All iButtons were inserted into the peritoneal cavities by a 2cm incision through the ventral abdominal wall. Following surgery, lizards were allowed 48h to recover from surgery procedures prior to being placed in the gradient and then were placed in the gradient. The first 12h were considered an acclimation period once lizards were placed in the gradients before iButtons began recording T_b every 10min.

Body temperature validation in the field

Field body temperature vs laboratory body temperature adjustment: A subset of individuals in the field (n = 8) had iButtons that were surgically implanted following the surgical protocols described above. iButtons recorded hourly core body temperatures ($T_{b,obs}$) from January to March 2019. Accelerometers that recorded temperature were placed on these animals so that the laboratory $T_{b,predict}$ adjustment from surface temperatures could be compared to observed field core body temperatures. Comparisons of our body temperature adjustment ($T_{b,predict}$) and body temperature ($T_{b,obs}$) measured with surgically implanted iButtons revealed a close and near one-to-one relationship (regression statistics ± 1 se: slope = 0.82 ± 0.004, intercept = 3.74 ± 0.140, $r^2 = 0.86$, N = 6,961, t = 203.87, $p < 0.001$). It appeared that ($T_{b,predict}$) slightly under predicted core body temperature (Fig S1).

Operative model calibration and verification:

Operative model calibration: Models were calibrated using a fresh carcasses of *P. vitticeps*, which were placed beside one of the copper models on the ground in partial shade during three sunny days in November 2018. Temperatures were recorded in the carcass and the model every 5min from dawn to dusk. We used a linear regression of the carcass temperature to the model temperature to subsequently correct all records from field-deployed copper models (T_e). \

Operative model verification: To further verify T_e values, we simulated operative temperatures of a non-thermoregulating animal in the open ($T_{e, predicted}$) using the package NicheMapR biophysical modelling software package (v.3.2.1) for the programming environment (4.2.2) to predict microclimates(Kearney & Porter, 2017). Historical weather data were obtained from the ERA5 reanalysis dataset (Klinges et al., 2022), a high-resolution (0.1° × 0.1°, hourly) reanalysis product converted to microclimate model input using the pipelines described in (REF). This simulated biophysical model was set during the duration of our study (2018-2019) and was set at the geographic location of our study site (DD:145.679184, -28.094142). Specifically, the ‘*micro_era5’* function was used to simulate microclimate, querying the soil grids database (soildgrids.org) for soil textural properties needed for soil moisture calculations, setting maximum shade to 80% and adjusting the local height for microclimatic estimates of air temperature, wind speed, and humidity to the body size of an adult *P. vitticeps*. The parameters of the model were based on the solar absorptivity documented in the field ($\alpha = 0.78$;Smith et al., 2016) and morphometric characteristics (mass:310g, SVL:25cm, and height:2.5cm) of an average adult *P.* vitticeps.

Comparisons of copper model T_e and $T_{e\ predicted}$ ranged in temperature from -4.1° to 64.0°c revealed a close and near one-to-one relationship (Figure S1; regression statistics ± 1 se: slope = 1.052 ± 0.001, intercept = 1.468 ± 0.105, $r^2 = 0.95$, N = 5533, t = 333, $p < 0.001$). Therefore, we are confident that our T_e correction applies to various microhabitat types (Fig S2).

Accelerometer protocol and TPC analysis:

Calculation of Resultant Acceleration: To calculate the resultant acceleration, we considered only the x and y axes due to the limited acceleration on the z-axis for lizards. Resultant acceleration was computed using the Euclidean norm as follows:

$$\text{Resulant acceleration} = \sqrt{a_x^2 + a_y^2 + a_z^2}$$

where a_x, a_y and a_z are the accelerations along the x, y, z axes, respectively. The z-axis was ignored due to limited acceleration on that plane for lizards. This resultant acceleration provides a measure of the overall intensity of movement, integrating the contributions from both axes. This method ensures a comprehensive representation of the lizard's activity based on changes in acceleration.

Model selection TPC: Other GAMMs in the series considered all reduced variants of this model. This approach allowed us to compare Akaike Information Criteria (AIC) changes among models and allowed us to determine whether a given model explains significantly different amounts of the deviance in the data (Vickers et al., 2017). All GAMM models were ranked using AIC scores and those with ΔAIC of < 2.0 from the best model were considered to have support (Burnham & Anderson, 2004). The *‘gam.check’* function was used to evaluate the adequacy of each model by examining model convergence, gradient range, Hessian matrix characteristics, and basis dimension checking results across multiple models. In general, TPC GAMM models showed a rise in the explanation of deviance when incorporating parameters that consider differences among individuals and season (Table S5).

Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference. *Sociological Methods & Research*, *33*(2), 261–304.

Kearney, M. R., & Porter, W. P. (2017). NicheMapR – an R package for biophysical modelling: the microclimate model. *Ecography*, *40*(5), 664–674.

Klinges, D. H., Duffy, J. P., Kearney, M. R., & Maclean, I. M. D. (2022). mcera5: Driving microclimate models with ERA5 global gridded climate data. *Methods in Ecology and Evolution*, *13*(7), 1402–1411.

Koenig, J., Shine, R., & Shea, G. (2001). The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia? *Wildlife Research*, *28*(3), 214–227.

Smith, K. R., Cadena, V., Endler, J. A., Porter, W. P., Kearney, M. R., & Stuart-Fox, D. (2016). Colour change on different body regions provides thermal and signalling advantages in bearded dragon lizards. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1832).

Vickers, M. J., Aubret, F., & Coulon, A. (2017). Using GAMM to examine inter-individual heterogeneity in thermal performance curves for Natrix natrix indicates bet hedging strategy by mothers. *Journal of Thermal Biology*, *63*, 16–23.

Supplementary figures & tables

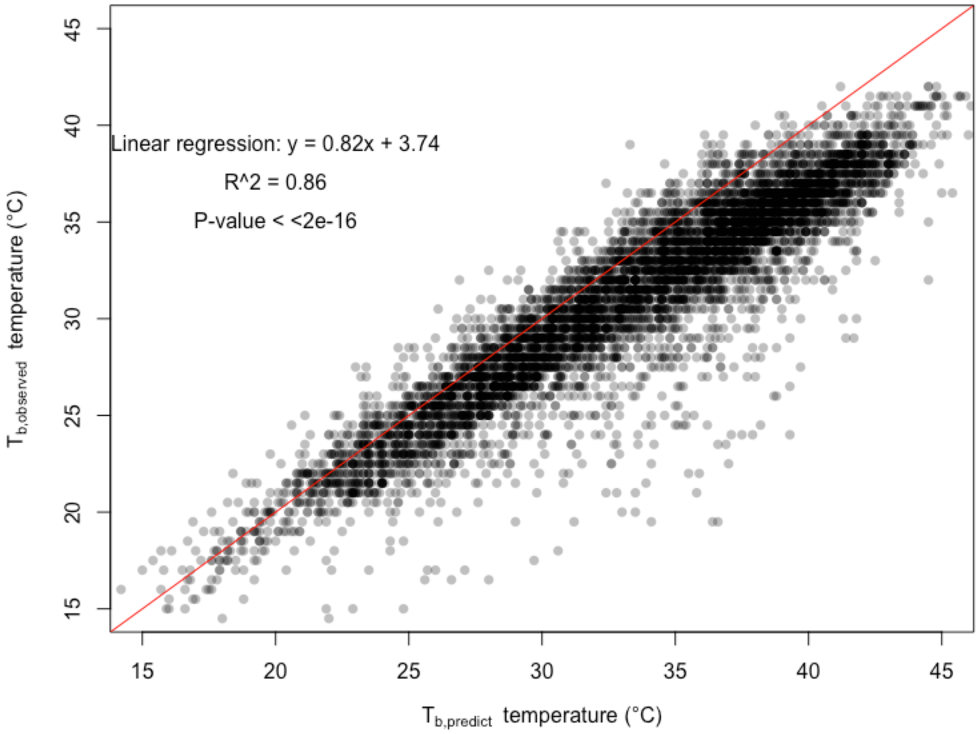

Figure S1. Comparison of predicted and core body temperatures of lizards in the field. Predicted body temperature ($T_{b,predict}$) was estimated through laboratory adjustments of surface temperature and core body temperature measured in a laboratory thermal gradient. Field core body temperature ($T_{b,observed}$) represents temperature recorded from implanted iButton in the field. The red line represents a perfect 1 to 1 relationship.

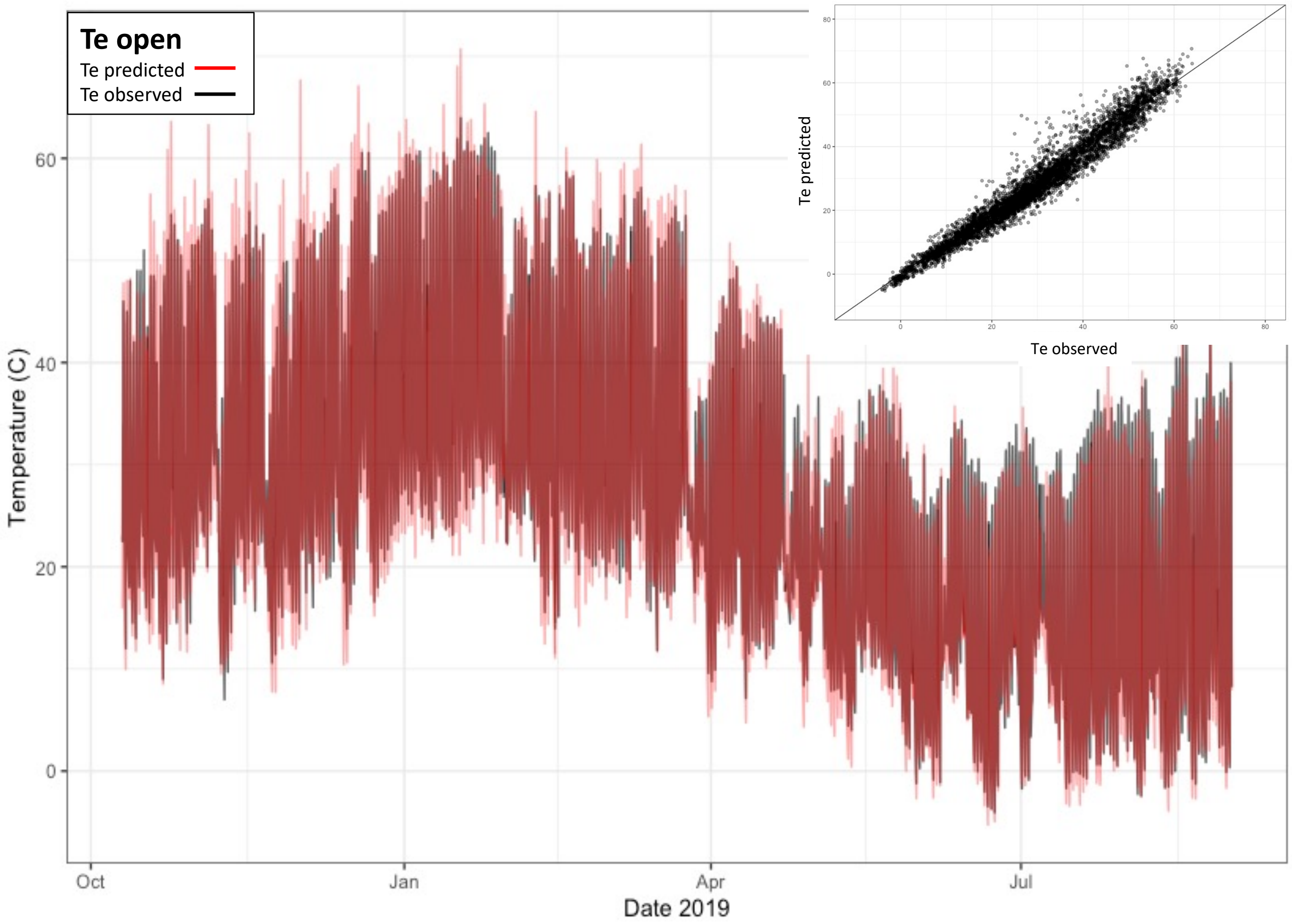

Figure S2. Hourly observations of lizard environmental temperatures measured with copper models T_e (black) and predicted T_e(red) across the entire study period from October 2018-September 2019. The panel in the top right indicate a 1:1 relationship between observed T_e and predicted T_e. Predicted T_e was estimated using the package NicheMapR (Kearney and Porter, 2017).

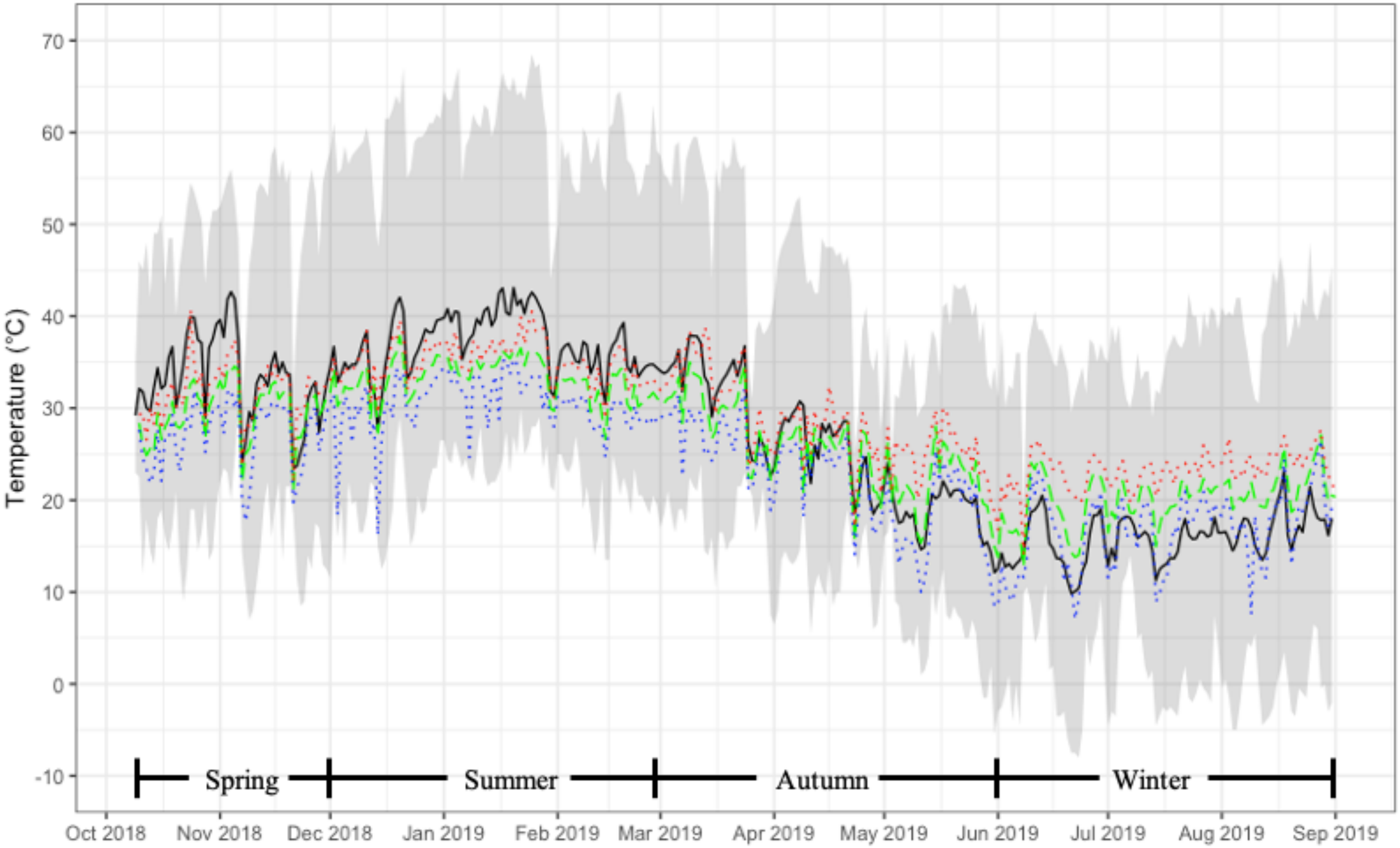

Figure S3. Environmental temperature range and how *Pogona vitticeps* thermoregulated during the duration of the study. Black solid lines represent the mean environmental temperatures of operative models (T_e) for each day, and grey bands represent the daily mean minimum and maximum of T_e. Coloured lines represent the daily mean (green), mean minimum (blue), and mean maximum (red) predicted body temperatures $T_{b\ Predict}$ for all lizards during the study.

Table S1. Microhabitat categories of sun exposure. At each micro-habitat category, copper pipes were placed at each cardinal direction. Sun% was calculated using a spherical densiometer.

Exposure category	n	Definition
Full shade	10	%Sun < 25% on ground
Partial shade	10	25% ≥ % Sun ≤ 50% on ground
Full sun	10	%Sun > 50% on ground
Burrow	8	1m within open lizard/rabbit burrow
Shade-tree at 2m	4	Within shaded tree with %Sun > 50%
Partial shade-tree at 2m	4	Within tree 25% ≥ % Sun ≤ 50%
Open-tree at 2m	4	On branches of dead tree %Sun > 50%

Table S2. ANOVA table for predicted body temperature ($T_{b\ Predict}$), accuracy of thermoregulation (d_b), thermal quality of habitat (d_e), and effectiveness of thermoregulation (E) for *Pogona vitticeps*. Each estimate is compared across the season, sex, and interaction. Individual lizard (or copper model ID) was treated as a repeated (random) variable. Bold values indicate significant differences.

Model Name	Effects	Sum Sq	Mean Sq	NumDF	DenDF	F value	p value
$T_{b\ Predict}$	Sex	9.80	9.80	1	37	0.70	0.41
	Season	**743,844.79**	**247,948.26**	**3**	**24,044**	**17,810.07**	**<0.01**
	Season x Sex	**1,814.79**	**604.93**	**3**	**24,044**	**43.45**	**<0.01**
d_b	Sex	5.66	5.66	1	33	0.73	0.4
	Season	**201,042.09**	**67,014.03**	**3**	**8,233**	**8,670.41**	**<0.01**
	Season x Sex	**816.86**	**272.29**	**3**	**8,233**	**35.23**	**<0.01**
d_e	**Sex**	**14.05**	**14.05**	**1**	**304.09**	**12.65**	**< 0.01**
	Season	**1983.80**	**661.27**	**3**	**306.74**	**595.59**	**< 0.01**
	Season x Sex	**12.36**	**4.12**	**3**	**304.09**	**3.71**	**0.01**
E	Sex	0.46	0.46	1	83	4.10	0.05
	Season	**2.14**	**0.71**	**3**	**83**	**6.34**	**<0.01**
	Season x Sex	**1.69**	**0.56**	**3**	**83**	**4.99**	**<0.01**

Table S3. Tukey-Kramer multiple comparisons from $T_{b,predict}$ model (Table 2). Contrasts were extracted from the overall seasonal effect on $T_{b,predict}$.

contrast	estimate	SE	df	t.ratio	p value
Autumn – Spring	**-2.61**	**0.15**	**10217.31**	**-18**	**<0.01**
Autumn - Summer	**-6.83**	**0.05**	**66587.12**	**-125.52**	**<0.01**
Autumn - Winter	**5.75**	**0.05**	**67846.58**	**125.52**	**<0.01**
Spring - Summer	**-4.22**	**0.14**	**9537.75**	**-29.2**	**<0.01**
Spring - Winter	**8.37**	**0.15**	**10266.14**	**57.53**	**<0.01**
Summer - Winter	**12.58**	**0.05**	**66582.53**	**229.03**	**<0.01**

Table S4. Tukey-Kramer multiple comparisons of overall seasonal activity rate (min/h). Activity rate was log (x+1) transformed.

contrast	estimate	SE	df	t.ratio	p value
Spring - Summer	-0.28	0.15	92	-1.86	0.25
Spring - Autumn	0.12	0.20	83	0.61	0.93
Spring - Winter	**0.80**	**0.21**	**83**	**3.89**	**<0.01**
Summer - Autumn	0.40	0.20	82	2.03	0.19
Summer - Winter	**1.08**	**0.21**	**82**	**5.23**	**<0.01**
Autumn - Winter	**0.68**	**0.23**	**69**	**3.01**	**0.02**

Table S5. General additive mixed-models for investigating how performance curves varied across season, sex and their interactions for *Pogona vitticeps*. a) accounted for all individuals in the study, b) accounted for smooth per individual, c) accounted for sex as a fixed factor, d) accounted for sex as a fixed factor and allowed for smooth per individual, e) accounted for season as a fixed factor, f) accounted for season as a fixed factor and allowed for smooth per individual, g) accounted for season and sex as a fixed factor, h) accounted for season and sex as a fixed factor and allowed for smooth per individual, i) accounted for season, sex, and the interaction as a fixed factor, and j) accounted for season, sex, and the interaction as a fixed factor and allowed for smooth per individual. Models b:j accounted for random intercept for individual lizard. Bold values indicate values were considered to have support (ΔAICc of < 2.0).

Model id	Model	Residual Df	Residual Deviance	DF	AIC	Delta AIC	Deviance Explained (%)
j	**Season + Sex + Season*Sex + s(Temperature, by = id) + (1|id)**	**2756.35**	**262.57**	**277.61**	**1688.84**	**0**	**70.57**
h	Season + Sex + s(Temperature, by = id) + (1|id)	2760.13	264.88	273.83	1707.66	18.82	70.31
f	Season + s(Temperature, by = id) + (1|id)	2760.12	264.93	273.84	1707.87	19.03	70.3
e	Season s(Temperature) + (1|id)	2967.9	299.67	66.06	1724.75	35.91	66.41
d	Sex + s(Temperature, by = id) + (1|id)	2766.84	270.68	267.12	1760.11	71.27	69.66
b	s(Temperature) + (1|id)	2766.56	270.73	267.4	1760.93	72.09	69.65
i	Season + Sex + Season*Sex + s(Temperature) + (1|id)	2989.09	315.19	44.87	1840.57	151.73	64.67
g	Season + Sex + s(Temperature) + (1|id)	2992.13	317.28	41.84	1854.36	165.52	64.43
c	Sex + s(Temperature) + (1|id)	2986.68	319.93	47.28	1888.45	199.61	64.14
a	s(Temperature)	3033.96	358.89	8.96	2152.09	463.25	59.77

Table S6. Tukey-Kramer multiple comparisons from the Pmax model that accounted for the season, sex and interaction. Contrasts were extracted from the seasonal effect.

Contrast	Estimate	SE	df	t Ratio	p value
Autumn - Spring	-0.01	0.01	45	-1.3	0.57
Autumn - Summer	**0.07**	**0.01**	**45**	**13.4**	**<0.01**
Autumn - Winter	**0.10**	**0.01**	**45**	**18.6**	**<0.01**
Spring - Summer	**0.08**	**0.00**	**45**	**15.1**	**<0.01**
Spring - Winter	**0.11**	**0.01**	**45**	**18.4**	**<0.01**
Summer - Winter	**0.03**	**0.01**	**45**	**6.1**	**<0.01**

Table S7. Tukey-Kramer multiple comparisons from the Pmax model that accounted for the season, sex and interaction. Contrasts were extracted from season and sex interaction.

Contrast	Season	Estimate	SE	df	t Ratio	p value
Female - Male	Autumn	0.03	0.1	39	0.34	0.74
Female - Male	Spring	-0.13	0.1	38	-1.33	0.19
Female - Male	Summer	-0.15	0.1	38	-1.49	0.14
Female - Male	Winter	0.01	0.1	39	0.14	0.89

Table S8. Model comparisons of spring survival probability (φ) for *Pogona vitticeps*, depending on sex, movement (min/h), accuracy of thermoregulation (d_b), effectiveness of thermoregulation (E), and maximum performance (P_{max}). Sex interactions for d_b and E were accounted for because of the differences between males and females during the spring (Table S2). Values within the brackets are nested variables, and variables outside of brackets are covariates. Bold values indicate values were considered to have support (ΔAICc of < 2.0).

Model	AICc	Δ AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance
φ(Sex)P_{max}	27.67	**0.00**	**0.79**	**1.00**	**3**	**20.63**
φ(.)P_{max}	31.47	3.80	0.12	0.15	2	26.97
φ(.)	34.99	7.30	0.02	0.03	1	32.82
φ(Sex)	35.31	7.64	0.02	0.01	2	30.81
φ(db)	36.52	8.84	0.01	0.01	2	32.02
φ(.)E	36.57	8.90	0.01	0.01	2	32.07
φ(.)T_{opt}	36.86	9.18	0.01	0.01	2	32.36
φ(Sex)d_b	37.02	9.35	0.01	0.01	3	29.98
φ(.)Activity	37.31	9.64	0.01	0.01	2	32.81
φ(Sex)T_{opt}	37.35	9.68	0.01	0.01	3	30.31
φ(Sex)E	37.36	9.68	0.01	0.01	3	30.31
φ(Sex)Activity	37.77	10.10	0.01	0.01	3	30.73