Thermal performance curves, activity and survival in a free-ranging ectotherm

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Abstract

1. Temperature profoundly influences the distribution and diversity of ectotherms, yet in natural settings, interactions between environmental temperatures, behaviour, physiological function and the influence of these factors on individual survival remain poorly understood. In particular, it is unclear as to how trade-offs between these factors are optimised in wild, free-ranging species.
2. We combined temperature-sensitive radio transmitters and accelerometers to measure *in situ* body temperatures and field-based thermal locomotor performance, estimating thermal optimum and maximum performance. This allowed us to quantify the effectiveness of thermoregulation in the wild and determine whether seasonal trade-offs in thermoregulatory behaviour shape thermal performance and influence survival in the Australian central bearded dragon (*Pogona vitticeps*)
3. Lizards adjusted their behaviour to maintain optimal body temperatures, achieving greater thermoregulatory precision in spring and summer when environmental costs of thermoregulation were low, but reducing that precision in winter when costs were higher. Activity time and maximum locomotor performance were higher during seasons when thermoregulatory precision was high.
4. Maximum locomotor performance in the field was a strong predictor of survival, regardless of sex, even though survival probabilities were higher in males than females. Specifically, higher locomotor performance was associated with increased mortality risk, but survival was not influenced by activity levels or thermoregulatory indices.
5. These findings highlight the complex trade-offs that ectotherms must navigate to balance behavioural thermoregulation and survival. Our data demonstrate the important influence of seasonal and sex-specific variation on behaviour and fitness-related outcomes. Interpreting field-derived thermal performance curves alongside laboratory measures is crucial for distinguishing 'true' physiological capacity from the integrated ecological contexts that shape performance and fitness in nature. Such insights are vital for predicting how ectotherms may respond to future climate warming.

1. Introduction

In meeting competing demands on their time, animals must balance the costs and benefits of various behaviour to maximise their fitness (Huey & Slatkin, 1976). Energy expended in undertaking those behaviours needs to be weighed against fitness gains, where trade-offs are inevitable and manifest in such contexts as optimal foraging behaviour, investment in mating displays, territorial defence, migration, and other allocations of time and energy ((Boyd & Hoelzel, 2002; Brown et al., 2018; Campos-Candela, 2018; Huey & Slatkin, 1976). A clear understanding of these trade-offs may reveal the evolutionary forces that shape various ecological strategies.

Ectotherms rely on external thermal sources to regulate their body temperature (Huey, 1982), a strategy that carries both benefits and constraints (Huey & Slatkin, 1976). Habitat variability often restricts many ectothermic species to narrow thermal margins, requiring behaviours such as shuttling between sun and shade (Huey, 1991). However, some ectotherms inhabit highly variable environments and maintain broader thermal ranges (Huey & Slatkin 1976; Woods et al., 2015). Although such behaviours help maintain optimal temperatures, they may divert time from mating, foraging, and other important activities (Angilletta et al., 2002; Porter et al., 1973; Van Damme et al., 1991). Further, the energy costs of active thermoregulation vary depending on environmental conditions, and costs can compromise fitness-related traits (Herczeg et al., 2008; Kearney et al., 2009; Sears & Angilletta, 2015). The presumed links between body temperature and fitness underpin much of thermal ecology, as accurate thermoregulation can confer performance advantages, including enhanced digestion and sprint speed (Angilletta, 2009; Angilletta et al., 2002; Pearson & Warner, 2018). However, when access to resources (e.g., food, water, mates) is time-limited, the benefits of maintaining optimal temperatures must be balanced against trade-offs such as increased predation risk and additional energy expenditure (Orrell et al., 2004; Skelly, 1994). According to the cost-benefit model of thermoregulation (Huey & Slatkin, 1976), thermoregulation should be more precise when benefits are high and costs are low. Understanding how ectotherms navigate these trade-offs is crucial for predicting how individuals balance predation risk, energy demands, and other constraints. Quantifying these trade-offs can provide valuable insights into the mechanisms that influence individual growth, reproduction, and survival (Sears et al., 2016; Chan et al., 2024).

Variation in environmental conditions, particularly seasonal fluctuations, drives 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 alter the physical and thermal landscape, affecting the availability of suitable microhabitats and thermal refuges in either 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 experience increased predation risk due to conspicuous behaviours to regulate body temperature (Basson et al., 2017). Quantifying the behavioural responses to environmental fluctuations can help determine the physiological trade-offs that may influence survival (Chan et al., 2024).

Life history theory for ectotherms explicitly predicts trade-offs between survival, growth, and reproduction, such that investment in one trait reduces the resources available for others, ultimately influencing fitness (Brown et al., 2018; Stearns, 1989; Roff & Fairbairn, 2007). Specifically, increased reproductive effort often incurs direct costs to individual

survival due to either heightened energy demands or increased predation risk (Roff, Heibo & Vøllestad, 2006; Stearns & Koella, 1986). Thermoregulatory behaviours can mediate these trade-offs by altering energy allocation strategies, as ectotherms facing seasonal environmental changes must carefully balance the energy costs of active thermoregulation against reproductive investment (Alujević et al., 2023; Calsbeek & Sinervo, 2007; Huey & Slatkin, 1976). Consequently, behavioural decisions around thermoregulation can directly influence the survival-reproduction dynamic and have implications for lifetime fitness (Roff, Mostowy & Fairbairn, 2002). These life history trade-offs are central to understanding how ectotherms optimise their physiological performance through thermoregulatory strategies.

Heliothermic lizards primarily use behavioural strategies, such as seeking heat and adjusting posture, but can also employ physiological mechanisms like vasoconstriction, panting, or colour change to thermoregulate (Smith et al., 2016; Huey, 1982; Porter et al., 1973). The physiological outcomes of these behaviours can be measured using thermal performance curves (TPCs) that assess how ectotherms perform across a range of environmental temperatures. Interpreting their parameters (critical limits, thermal optimum and maximum performance) in terms of fitness involves linking key curve parameters to survival, growth, and reproduction (Huey & Stevenson, 1979). The parameters commonly derived from thermal performance curves, such as thermal optimum and performance capacity at specific temperatures, are correlated to individual survival or other fitness proxies (Angilletta, 2009; Christian & Tracy, 1981; Gilbert & Miles, 2017; Pearson & Warner, 2018). However, TPCs are typically measured under controlled laboratory conditions where variability in temperature, predation and food availability are minimised or eliminated (Angilletta et al., 2002; Albuquerque et al., 2023; Wild & Gienger, 2018). This disconnect contributes to a broader knowledge gap regarding how laboratory-derived metrics translate into meaningful ecological outcomes for individuals in natural environments (Irshick & Losos, 1998; Husak & Fox, 2006; Warner & Andrews, 2006). Often, it is challenging to accurately measure individual survival in field settings owing to the small size of heliothermic lizards or the rarity of capturing predation events *in situ*. As a result, survival in lizards is typically inferred from coarse recapture intervals (Gilbert & Miles, 2017; Husak, 2006), which may miss fine-scale, seasonal mortality patterns. Field-based studies that continuously track individuals and directly link thermoregulatory behaviour or thermal performance to survival are essential for understanding whether and how laboratory-based metrics translate to fitness in natural environments.

Using field-based measurements, we examined how survival relates to common thermal biology metrics (thermoregulatory behaviour and thermal performance curves) in the Australian central bearded dragon *(Pogona vitticeps*). Previous laboratory work with *P. vitticeps* has shown their thermoregulatory behaviours align with the cost-benefit model of thermoregulation (Cadena & Tattersall, 2009). Yet, it is unknown how these behaviours manifest in nature, nor do we understand their fitness outcomes in the wild, free-ranging individuals. Here, we used 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. Unlike traditional laboratory thermal performance curves, which estimate the direct effects of body temperature on performance under controlled conditions, our field-based approach captures performance variability under realistic ecological conditions, accounting for additional factors that influence performance. We integrated body and environmental temperature measurements to estimate if changes in seasonal thermoregulatory behaviours aligned with predictions of the cost-benefit model of thermoregulation benefit (Fig. 1D). Together, these approaches enabled us to examine how

aspects of thermal performance curves and thermoregulatory behaviours influence survival (Fig. 1E) during the reproductive season (spring) when predation pressures are highest (Wild et al., 2022). Our goal is to understand how thermoregulatory behaviours and thermal performance curves influence survival in heliothermic lizards in situ, providing insight into the cost-benefit model of thermoregulation.

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* (n = 20; 10 male & 10 female; mean mass = 378.57g) 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 (iButton® model DS1921G; accuracy± 1°C) recording every 2 min while lizards moved along a laboratory thermal gradient (Fig. 1A). The thermal gradient (5.0 m L× 1.0 m H × 2.0 m W) was heated with a series ceramic heat lamps placed above the gradient and achieved continuous temperatures that ranged from 20°C to 40°C. The thermal gradient contained sand (15 cm depth) and fluorescent lighting that was on a 12 h on/off cycle. Implanted iButtons are a commonly used technique for larger-bodied reptiles and are considered a best practice for the continuous study of thermal biology of reptiles (Taylor et al., 2020). Postabsorptive lizards were then allowed to recover for a minimum of 48 h before being placed in the thermal gradient and given 12 h to acclimate before initiating measurements. Body temperature recordings used for analysis included only those after the acclimation period. The preferred body temperature was defined as the bounds of the interquartile range of body temperature in the thermal gradient (Hertz et al., 1993). Linear models were used to determine differences in T_{set} bounds between sexes.

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 transmitter (Lotek Ltd., Havelock North, NZ) that was placed in a custom-fit backpack harness (Wild et al., 2022). Each transmitter (Pinpoint Beacon 250) and ibutton (11g total) package weighed less than 5% of the mass of the lizard. Each Pinpoint Beacon 250 housed a temperature data logger that recorded surface temperature every 2 s, which was averaged every 2 min 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 140 km² 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. During the reproductive season (spring) females were

palpated bi-weekly when transmitters were replaced, and gravid females were excluded from all analyses. For further information on lizard collection, site description, or radio telemetry, see Wild et al. (2022).

2.3 Field predicted body temperature, 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 2 s, and this was averaged over 1 min. The surface and body temperature correction was applied (Fig. 1A) to estimate field body temperature ($T_{b,Predict}$).

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 (40.0 mm outside diameter, 1.22 mm wall thickness, 250 mm length) 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), but were not designed to estimate true operative temperatures based on instantaneous heat flux equilibrium (i.e. operative temperature). 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). Mean T_e measurements were calculated for each hour between 0500-2100 to obtain a measure of the environmental 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.

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 0500-2100 h 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 highly effective thermoregulation, meaning that an animal maintains body temperatures close to its preferred range despite thermal conditions. In contrast, an E of 0 indicates that an animal's body temperatures are no better than the surrounding environmental temperatures, consistent with thermoconformity (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 0500-2100 h for each season. 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^{o}C. This allowed for the characterisation of the upper capacity for movement while avoiding the influence of outliers resulting from the many sedentary periods. This also ensured that we captured the highest possible value, allowing for the closest comparison to laboratory TPCs. 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). Known-fate models assume perfect detection (sampling probability = 1), meaning that the fate (alive or dead) of each radio-tagged animal is known with certainty at each sampling occasion. Thus, survival is modelled using a product of binomial likelihoods, where animals not confirmed dead (i.e., carcasses not recovered) are treated as alive or censored (due to loss of telemetry gear or transmitter failure) but never assumed dead. Parameter estimates derived from known-fate models were then 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, during which deaths were recorded based on recovered carcasses. Animals were only classified as dead if carcasses were physically recovered. In cases where the cause of mortality could be inferred, depredated individuals exhibited extensive, fresh injuries to the body and transmitter, likely from a raptor or mammalian predator; individuals without clear signs of predation were noted separately. Spring was used for this analysis because movement

rates were elevated and most variable among individuals, and mortality rates were highest during this period (Wild et al., 2022), providing the best opportunity 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. Data collection for this project was performed under UC Animal Ethics approval AEC 17-13.

3. Results

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

Females consistently had higher preferred body temperatures 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. For a subset of these individuals (n = 8), we validated our $T_{b,predict}$ estimates by concurrently recording core body temperature with implanted iButtons and found they closely approximated actual core temperature (r^2 = 0.86, Fig. S1). There were differences in seasonal body temperatures ($T_{b,Predict}$) ($p<0.01$) and a 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, females were not effective thermoregulators (i.e. low E), whereas males were effective thermoregulators (i.e. high E). Both male and female lizards were effective thermoregulators during summer (Fig. 3). However, in the autumn and winter, males and females were less effective at thermoregulating (Fig. 3). Overall, males were more effective thermoregulators (0.48) than females (0.29; Table S2; $p=0.05$).

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 locomotor 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. Seven mortalities showed signs of predation, with extensive injuries consistent with raptor or mammalian predation. One individual showed no evidence of predation, as indicated by the absence of injuries or disturbance to the body. 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 important insights into the trade-offs between thermoregulation, locomotor performance, and survival in ectotherms. Previous studies have suggested that increased locomotor activity can elevate predation risk (Vitt & Congdon, 1978) and that individuals

with higher locomotor performance may incur greater costs associated with reproduction or survival (Vitt & Price, 1982; Vitt et al., 1990; Padilla-Pérez & Angilletta, 2022). Using telemetry and temperature-sensitive accelerometry, we generated the first in situ thermal performance curves for an ectotherm, providing a rare examination of thermoregulatory strategies and their associated seasonal trade-offs in the field. Notably, our findings reveal that maximum performance correlates positively with mortality risk for both males and females, with this effect being more pronounced in females during the reproductive season (spring). While survival during spring does not fully capture lifetime reproductive success, it remains a critical fitness-related trait, as individuals who die would have no further reproductive opportunities. Our field observations indicate that predation was likely the primary cause of death for lizards, consistent with predation observations documented in this same population (Wild et al., 2022). Regardless of the exact cause of death, maximum locomotor performance was strongly linked to mortality risk. These results challenge the traditional view that higher locomotor performance within the thermal optimum will enhance fitness outcomes in the field (Calsbeek & Sinervo, 2007; Christian & Tracy, 1981; Gilbert & Miles, 2017).

Interpreting the parameters of thermal performance curves (TPCs) derived from field data requires careful consideration of their conceptual differences from lab-based TPCs. Laboratory-based TPCs often isolate 'true' physiological performance metrics by directly stimulating animals to perform (e.g., forced running, biting) while controlling tightly for extrinsic environmental variables (Angilletta, 2009; Taylor et al., 2021). In contrast, field-based TPCs inherently capture the integrated ecological contexts – including predation risk, resource availability, and environmental variability – which shapes fitness-relevant behaviours and traits (Childress & Letcher, 2017; Nowakowski et al., 2020). For instance, optimal temperatures (T_{opt}) in field settings do not merely represent physiological peaks but correspond to conditions where animals maximise fitness components such as survival, growth, and reproduction (Kingsolver & Gomulkiewicz, 2003; Clusella-Trullas et al., 2011). Performance measured as maximum movement capacity in the field might reflect behavioural choices influenced by multiple ecological factors beyond temperature alone (Alujević et al. 2023; Childress & Letcher, 2017). Future studies could benefit from comparing field-derived thermal performance curves with laboratory-based estimates.

Contrary to previous studies that have linked maximum locomotor performance (e.g. sprint speed measured in controlled laboratory conditions) to increased survival in the wild (Christian & Tracy, 1981; Gilbert & Miles, 2017; Pearson & Warner, 2018), we found that higher maximum performance was associated with decreased survival in the wild. Our findings contrast with previous work, which demonstrates positive associations between thermoregulatory accuracy, the thermal quality of the environment, and fitness-related traits such as survival and reproductive success in the field (Alujević et al., 2023; Calsbeek & Sinervo, 2007). For instance, Calsbeek and Sinervo (2007) experimentally improved the thermal environment of territories and observed increased juvenile survival due to more efficient thermoregulation. Alujević et al. (2023) demonstrated that higher thermal quality of territories is associated with enhanced reproductive behaviours and greater reproductive success. Our field-based observations, in contrast, suggest that high-performing (P_{max}) individuals may engage in conspicuous or risky behaviours (Horváth et al., 2024), thereby increasing predation risk due to heightened visibility or expanded home ranges in predator-rich areas (Skelly, 1994; Ward-Fear et al., 2018). Our findings show that in natural settings, high P_{max} may not universally confer survival advantages

and, under certain ecological contexts, can be associated with elevated mortality risk. We acknowledge the limitations of our modest sample size for survival (n=27), but similar cohorts are not uncommon in field-based telemetry studies (e.g., McIntyre al. 2009, Golden Eagle[n=22]; Olson et al. 2013, Hellbenders[n=21]; Goetz et al., 2021, Brown Treesnake[n = 30]; Ferronato et al., 2016, Eastern Long-necked turtle[n = 46]). These data provide high-resolution ecological information despite increased uncertainty in parameter estimates.

Outside of the reproductive season for females, we found that activity patterns, thermoregulation metrics, and maximum performance followed general predictions of the cost-benefit model of thermoregulation (Huey & Slatkin, 1976). 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 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 locomotor 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 locomotor performance. These seasonal trade-offs demonstrate the dynamic balance that lizards must maintain while accounting for the energy trade-offs of thermoregulation (Angilletta & Sears, 2016; Sears et al., 2015; Vickers et al., 2011). Although the effectiveness of thermoregulation was not associated with survival in our study, this metric has been shown to have direct consequences for growth, reproductive success, and even survival in other lizards (Basson et al., 2017; Brewster et al., 2013; Sears et al., 2016).

Sex differences in ectotherm thermal biology, largely documented from laboratory data or short-term field manipulations, show that males and females can exhibit distinct thermoregulatory behaviours and thermal performance traits associated with different ecologies and reproductive strategies (Beal et al., 2014; Lailvaux et al., 2003; Ortega et al., 2016). However, translating the ecological significance of these results into natural systems remains challenging because continuous field observations are needed to track how seasonality, reproductive demands, and species interactions can shape thermoregulatory strategies in both sexes (Bodensteiner et al., 2021; Huey & Pianka, 2007; Pottier et al., 2021). There are examples where female lizards can exhibit altered thermoregulatory behaviours during reproductive periods, leading to trade-offs between optimal body temperature maintenance and reproductive or predator-avoidance strategies (Logan et al., 2021; Ortega et al., 2016). In *P. vitticeps*, females exhibit overall higher energy demands (Wild et al., 2023) and poor body condition during the reproductive season (Wild et al., 2022), which may contribute to the sex-specific differences in survival. While existing literature emphasises behavioural or physiological distinctions between sexes, few studies have directly linked these thermal strategies to explicit fitness outcomes, such as survival under natural conditions.

Laboratory results in other ectothermic vertebrates suggest limited plasticity in optimal temperatures (MacLean et al., 2019; Pottier et al., 2022; Zhang et al., 2023). Our findings support this pattern, where the field optimal temperature (36.6 ± 0.24°C) remained consistent across sexes and seasons. 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; Wild et al., 2025). This requirement becomes particularly challenging during energetically demanding periods, such as spring and summer, when heliothermic lizards divert surplus energy reserves towards reproduction (Nagy, 1983). Maintaining a static thermal optimum appears to be crucial for optimal performance, despite the costs associated with thermoregulation (Herczeg et al., 2008; Huey & Slatkin, 1976). These findings demonstrate the trade-offs involved in

maintaining optimal body temperatures, as the energy costs of thermoregulation must be balanced against other physiological needs (Blouin-Demers & Nadeau, 2005; Vickers et al., 2011).

By using temperature-sensitive accelerometers in conjunction with surface calibration**s**, we derived predicted body temperature estimates ($T_{b,predict}$: 32.7 ± 0.02 °C) that closely matched previously published core field body temperatures for this species (34.3±3.75°C: Greer, 1989; 32.9±0.88°C: Melville & Schulte, 2001). However, future studies might benefit from improved operative modelling techniques, such as copper electroforming or 3D printing, which have shown greater accuracy, reproducibility, and cost-effectiveness for quantifying operative temperatures in terrestrial thermal environments (Alujević et al., 2024). Combining basic physiological measurements with thermosensitive accelerometers offers a powerful approach for testing challenging ecological and physiological hypotheses in thermal ecology. New applications of accelerometers, including linking movement data to field energy expenditure (doubly labelled water) and identifying specific behaviours with raw acceleration, provide promising avenues for future research across diverse vertebrate groups (Chakravarty et al., 2019; Garde et al., 2022; Pagano & Williams, 2019). Such approaches will be crucial for understanding how physiological traits vary under field conditions in a warming and increasingly variable climate.

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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 and Zenodo: 10.5072/zenodo.268672

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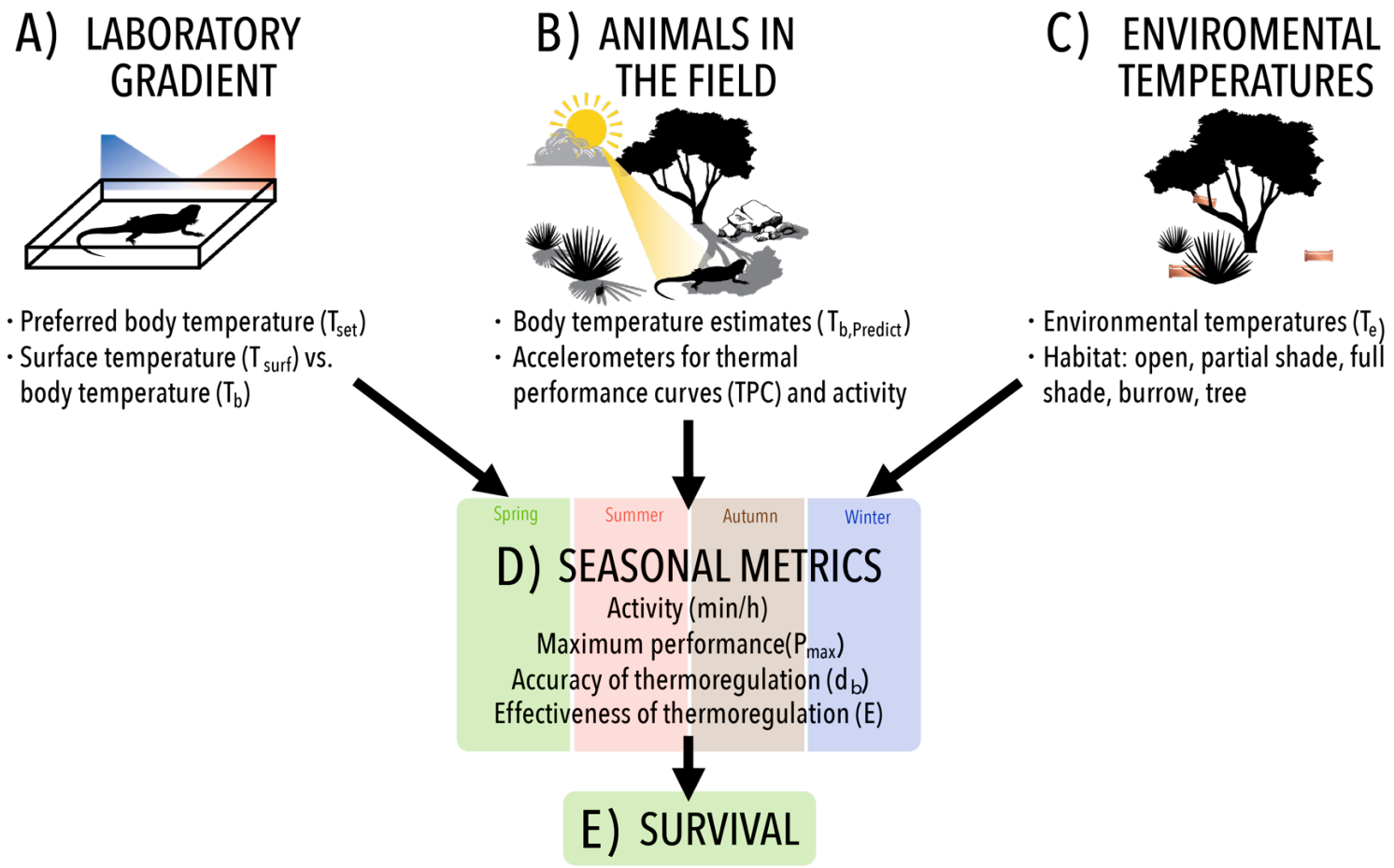

Figure 1. The comprehensive workflow of the experimental design aimed at identifying trade-offs in thermoregulation and their implications for survival. Laboratory thermal gradient experiments (A) were used to measure the preferred body temperature (T_{set}) and assess the relationship between surface 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 (estimated with known-fate models) during the spring season (E) when predation pressures are highest for this species.

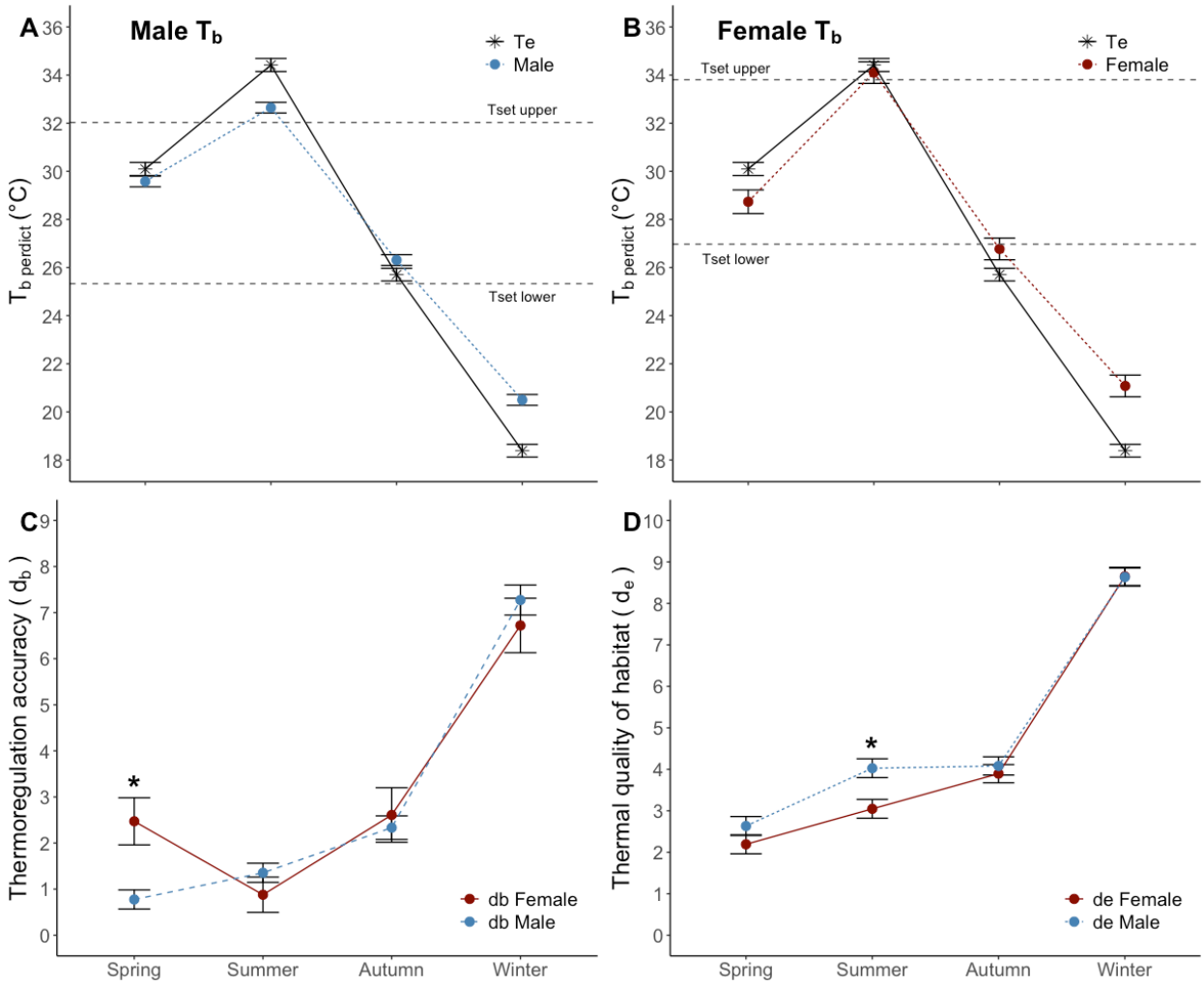

Figure 2. Mean seasonal environmental temperature (T_e), thermal preference (T_{set}), and predicted body temperature ($T_{b,Predict}$) for male (A) and female (B) *Pogona vitticeps*. Accuracy of thermoregulation (d_b) between sex (C), where low d_b denotes body temperature closer to thermal preference. The thermal quality of habitat (d_e), measured with copper models, accounting for sex differences in thermal preference (D). 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.

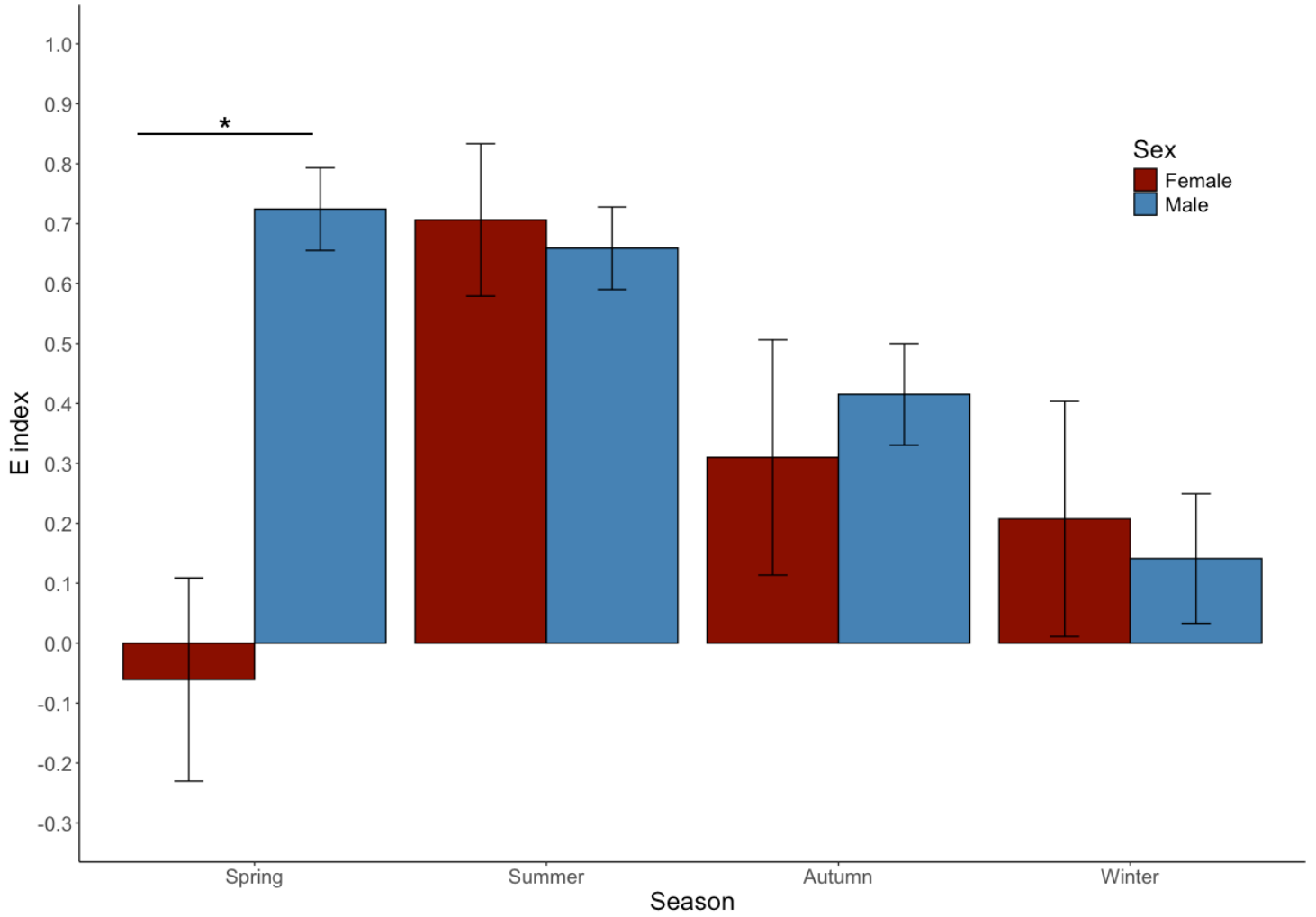

Figure 3. Effectiveness of thermoregulation (E index) by sex and season in *Pogona vitticeps*. E values approaching 0 indicate thermoconformity (body temperatures closely track environmental temperatures), while values approaching 1 indicate highly effective thermoregulation (body temperatures maintained near preferred values despite environmental variation). Data 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.

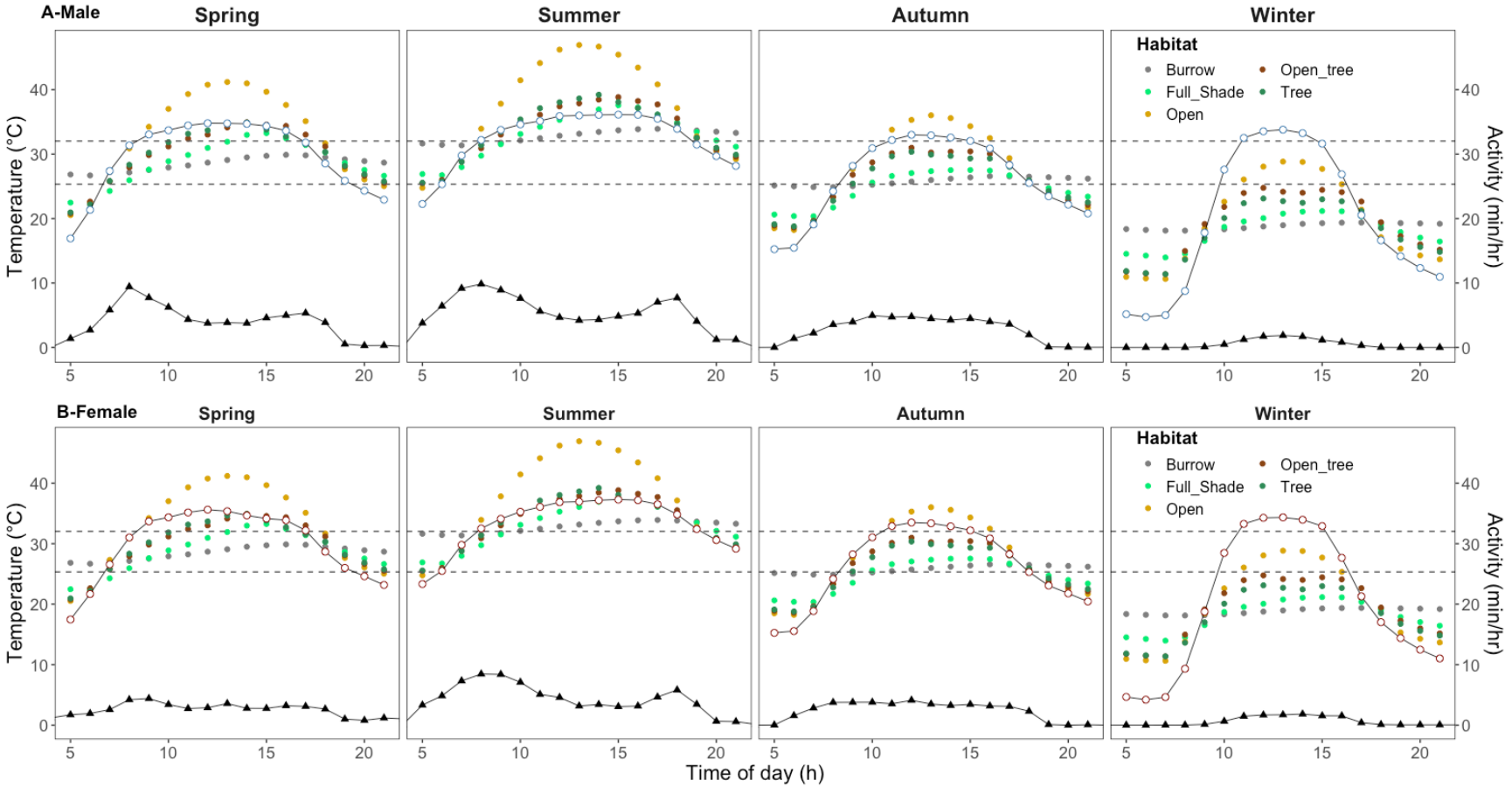

Figure 4. Mean predicted body temperatures (lines with circles) and activity levels (lines with triangles) for male (A) and female (B) *Pogona vitticeps* by season and time of day. The dashed line represents their preferred body temperature range. Coloured circles indicate mean environmental temperatures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

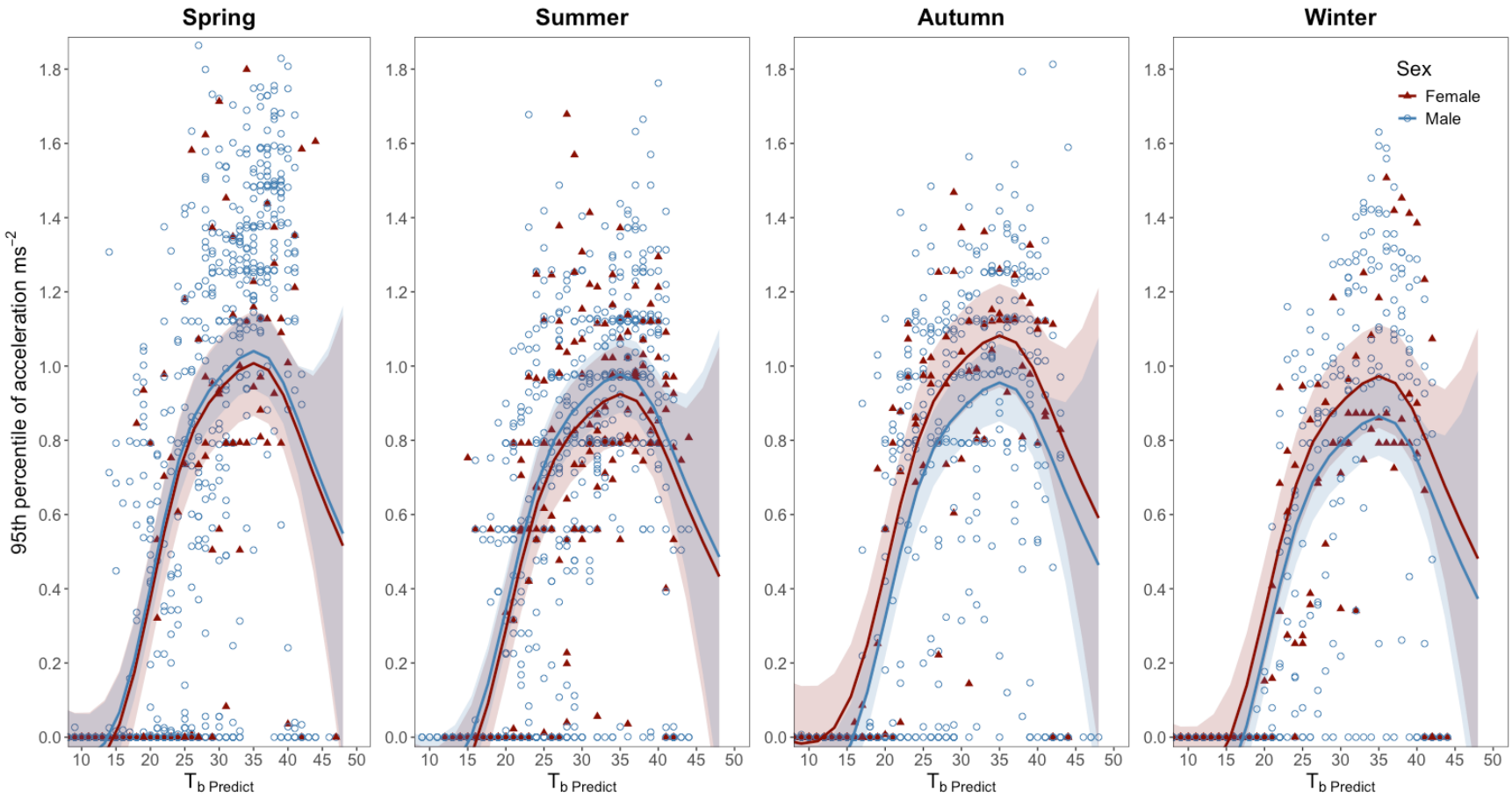

Figure 5. Thermal performance curves of free-ranging *Pogona vitticeps* across season and sex. The data were obtained from the top-performing Generalized Additive Mixed Models (GAMM) presented in Table S5. Each data point represents the average performance (95th percentile of acceleration) at a given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

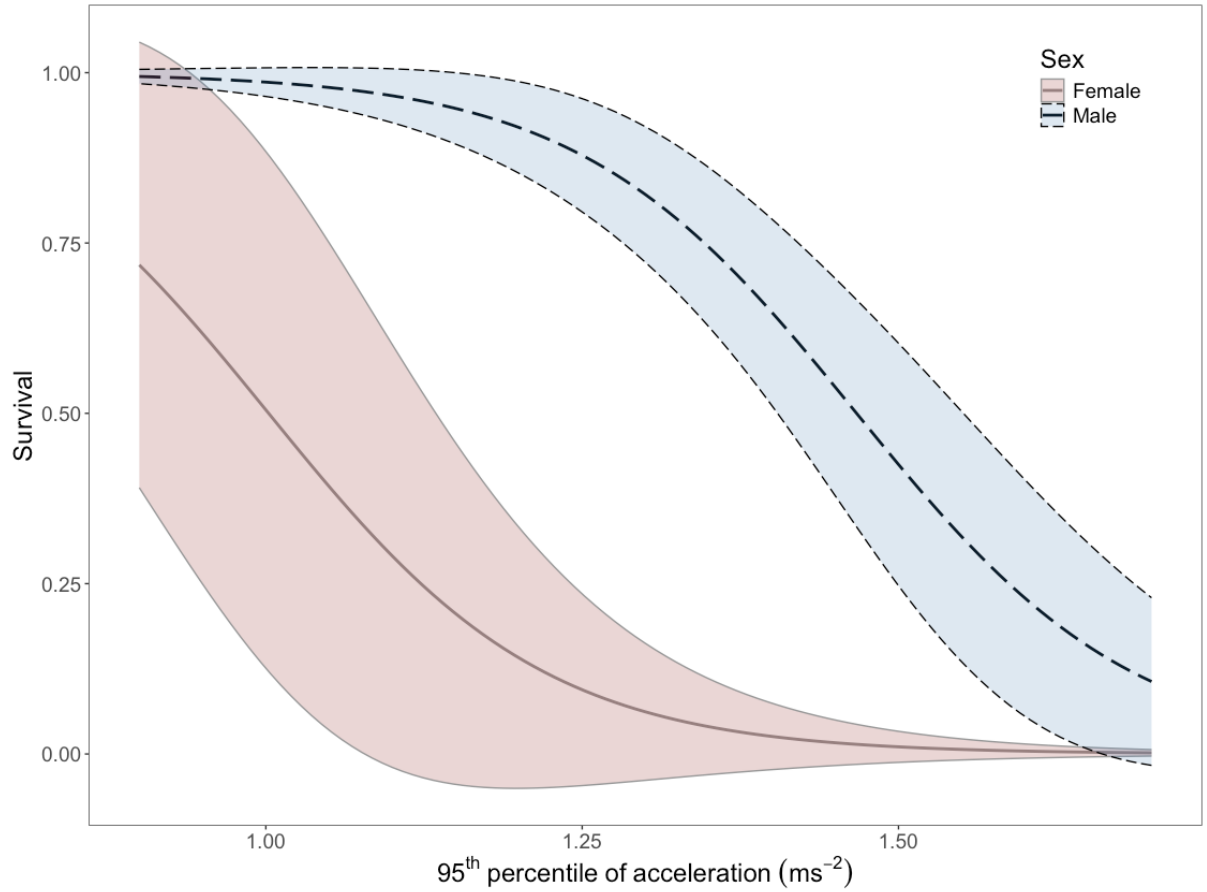

Figure 6. Survivorship as a function of the maximum performance (P_{max}) for free-ranging male and female *Pogona vitticeps* in spring (September -November). Data are extracted from the top-performing known-fates survival model in Program MARK that accounted for season and sex (Table S8). Lines represent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

Supplement Information

Surgical protocols:

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).

Environmental model calibration:

Environmental 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).

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).

Correlation between physiological traits and activity:

We explored the relationships between Pmax vs. minutes active, accuracy of thermoregulation (db) vs. minutes active, and efficiency of thermoregulation (E index) vs. minutes active by conducting correlation analyses. The results showed no significant relationships between either Pmax and minutes active ($r = -0.09$, $p = 0.665$), db and minutes active ($r = -0.23$, $p = 0.256$), or Eindex and minutes active ($r = 0.17$, $p = 0.385$) (Fig. S2). These findings suggest that performance traits such as Pmax, db, and E are not predictive of movement rates in our dataset.

Literature cited:

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Supplementary figures & tables

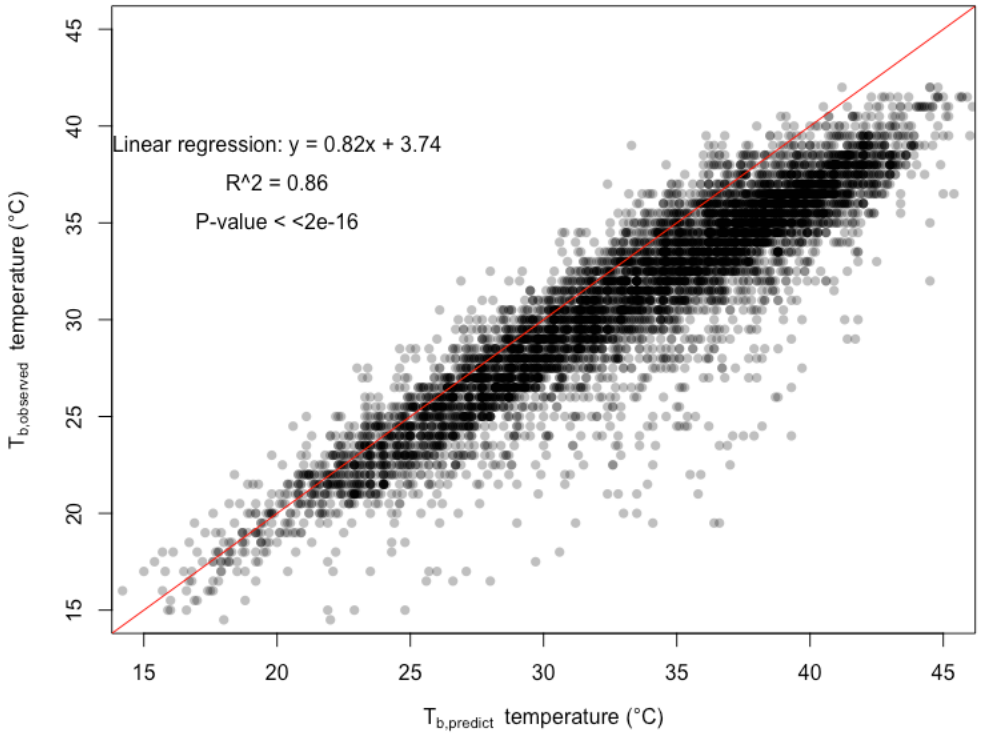

Figure S1. Comparison of predicted and core body temperatures of lizards in the field. Predicted body temperature ($T_{b,predict}$) was estimated through laboratory adjustments of surface temperature and core body temperature measured in a laboratory thermal gradient. Field core body temperature ($T_{b,observed}$)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

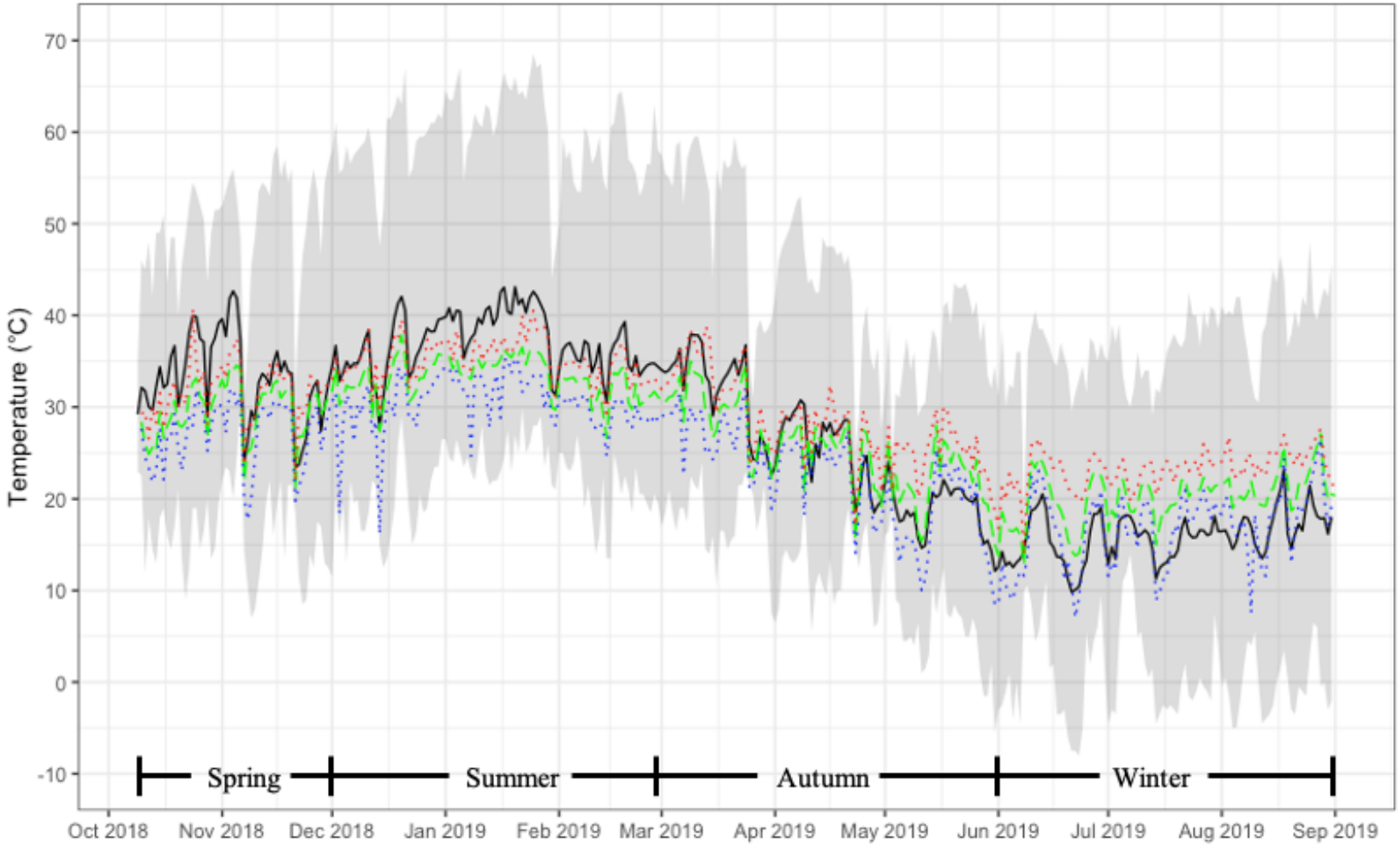

Figure S2. Environmental temperature range and how *Pogona vitticeps* thermoregulated during the duration of the study. Black solid lines represent the mean environmental temperatures (T_e) for each day, and grey bands represent the daily mean minimum and maximum of T_e. Coloured lines represent the daily mean (green), mean minimum (blue), and mean maximum (red) predicted body temperatures $T_{b\ Predict}$ for a lizards during the study

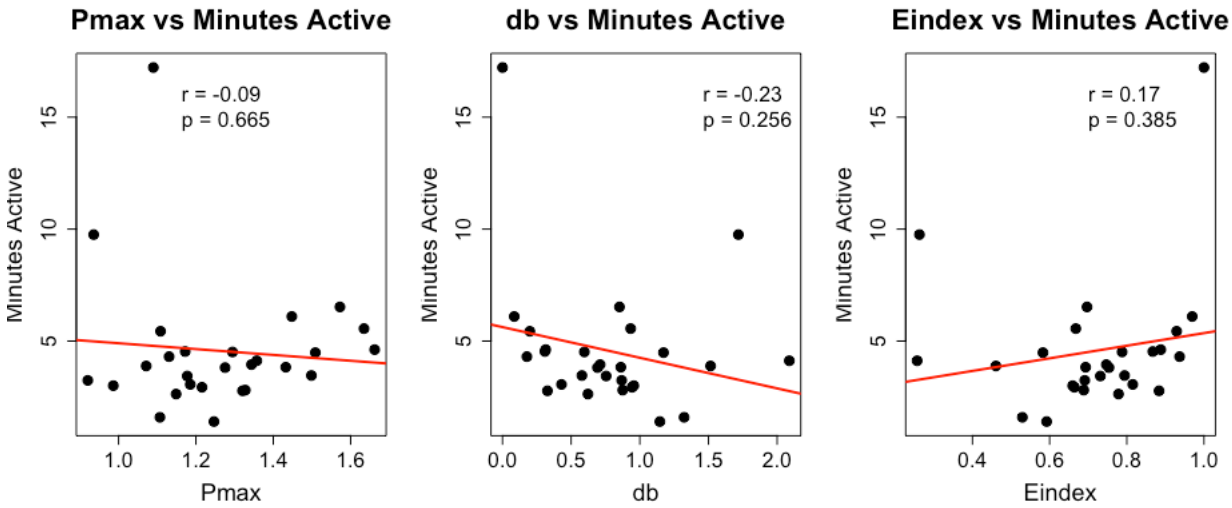

Figure S3. Relationships between maximum performance (Pmax), accuracy of thermoregulation (db), and efficiency of thermoregulation (E index) with minutes active.

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