Thermoregulatory behavior and orientation preference in bearded dragons

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Abstract

The regulation of body temperature is a critical function for animals. Although reliant on ambient temperature as a heat source, reptiles, and especially lizards, make use of multiple voluntary and involuntary behaviors to thermoregulate, including postural changes in body orientation, either toward or away from solar sources of heat. This thermal orientation may also result from a thermoregulatory drive to maintain precise control over cranial temperatures or a rostrally-driven sensory bias. The purpose of this work was to examine thermal orientation behavior in adult and neonatal bearded dragons (*Pogona vitticeps*), to ascertain its prevalence across different life stages within a laboratory situation and its interaction with behavioral thermoregulation. Both adult and neonatal bearded dragons were placed in a thermal gradient and allowed to voluntarily select temperatures for up to 8 hours to observe the presence and development of a thermoregulatory orientation preference. Both adult and neonatal dragons displayed a non-random orientation, preferring to face toward a heat source while achieving mean thermal preferences of ~33-34°C. Specifically, adult dragons were more likely to face a heat source when at cooler ambient temperatures and less likely at warmer temperatures, suggesting that orientation behavior counter-balances local selected temperatures but contributes to their thermoregulatory response. Neonates were also more likely to select cooler temperatures when facing a heat source, but required more experience before this orientation behavior emerged. Combined, these results demonstrate the importance of orientation to behavioral thermoregulation in multiple life stages of bearded dragons.

Keywords: behavioral thermoregulation, ectotherm, innate behavior, sensory preference, reptile, lizard

1. Introduction

Animals commit time and energy to achieve and maintain thermally optimality, defined as the range of temperatures which maintains physiological processes operating at, or near, maximum conditions (Dewitt, 1967; Huey and Slatkin, 1976). For ectotherms which depend on environmental heat absorption, behaviors that adjust the rate of body temperature (T_b) change are crucial to thermoregulation (Cowles and Bogert, 1944). Although thermoregulatory behaviors are known to present during early life (Blumberg et al., 2002; Lang, 1981; Stahlschmidt et al., 2015; Vollset et al., 2013; Zhao et al., 2013), how thermoregulatory behaviors change through ontogeny is not well studied. Shuttling and basking behaviors, which have a high impact on body temperature, are likely present from an animal's first exposure to a novel thermal environment, although these behaviors are also subject to change with experience. For example, shuttling behaviors show lower precision in bearded dragons that are naïve to an operant conditioning thermoregulatory paradigm compared to those with prior experience or when the locomotory costs of thermoregulation are increased (Cadena and Tattersall, 2009). Indeed, that lizards dedicate time to exploring and adjusting to a thermal gradient in the lab suggests that learning plays a role in behavioral thermoregulation, especially in novel environments (Cadena and Tattersall, 2009). Subtle thermoregulatory responses might, therefore, also require time and may even need to be learned well after hatching.

Unlike birds and mammals, squamates do not typically display parental care behaviors after their young hatch (Reynolds et al., 2002). After hatching, neonates meet their needs on their own, but not all behaviors are present during every phase of an animal's life (Dawkins, 1995; Khan et al., 2010). Innate behaviors are responses that prepare an animal for adaptive reactions to the world around them, and are generally fully formed from the outset without the need for experience or learning; this is also referred to as inbuilt adaptiveness (Dawkins, 1995). Learned behaviors are responses that develop through the accumulation of experience and the retention of information (Barnard, 2003). For the purposes of this work, innate thermoregulatory behaviors are those present from the neonatal stage that do not generally require experience. Examples of both innate and learned responses can be found in voluntary, involuntary, and autonomic behaviors (Dawkins, 1995), and thus thermoregulatory behaviours can be expected to reflect both innate and learned responses.

Aside from morphological and developmental differences, neonatal bearded dragons differ from their adult counterparts, especially with respect to social behaviors (Khan et al., 2010). Neonates are more prone to gregarious behavior, and often observed in aggregations (Khan et al., 2010). Gregarious behavior, while common in mammals (Aureli et al., 2002), is less prevalent in reptiles and is not necessarily driven by sociality. Instead, aggregation could be related to other fitness demands, such as gestation, oviposition, parasitism, predation protection, or even thermoregulation (Gautier et al., 2006; Graves and Duvall, 1995; Wikelski, 1999). When solitary and groups of neonatal bearded dragons were allowed to thermoregulate, both isolated and aggregated neonates were observed to select similar temperatures, however, individuals within a group context showed lower thermoregulatory precision than those in isolation (Khan et al., 2010). Khan et al. (2010) suggested that this aggregation results from a mutual attraction to a limited and valuable resource (e.g., an optimal temperature), and that the drop in precision results from agonistic interactions (Khan et al., 2010). Agonistic behaviors over access to preferred temperatures are known to occur in other ectothermic species, and are also dependent on familiarity and experience (Tattersall et al., 2012b), suggesting that both social context and learning contribute to thermoregulatory behaviors. In short, although thermoregulatory behaviors are guided by innate, sensory driven mechanisms, they can be shaped and influenced by experience.

Due to the importance of temperature regulation, it is plausible that thermoregulatory behaviors will show some level of innateness and therefore be conserved between adults and neonates. Behaviors such as aggregation are likely to be lost at the adult stages due to increased competition between individuals that have reached sexual maturity. Critical thermoregulatory behaviors, such as shuttling and basking are likely observed across all life stages. Subtler, yet equally important thermoregulatory behaviors, such as body orientation toward a heat source (referred to hereafter as orientation preference), may instead be partially learned through growth and development, since body size is strongly implicated in the effectiveness of orientation (Lactin and Johnson, 1997). Orientation preference, as a thermoregulatory behavior, has been documented in select mammals as an energy savings strategy (Hetem et al., 2011), but most notably in several invertebrates and certain reptiles (Bartholomew, 1966; Fraser et al., 2016; Martin et al., 1995; McMaster and Downs, 2006; Tattersall et al., 2012b). Adult lizards of a species well known to exhibit distinct thermoregulatory behaviors, such as the bearded dragon, are the best option for examining the presence of any orientation preference, as they are larger than neonates and therefore orientation is more likely to have a direct impact on heating and cooling rates, and therefore thermoregulation. Additionally, adults have had time to acquire any learned aspects of the behavior. On the other hand, cutaneous thermosensory feedback may be over-emphasized in the cephalic region, resulting in an innate, sensory bias-based preference to face toward or away from the source of the stimulus. Ion channels implicated in thermotaxis are highly expressed in the rostral margin of the head in flatworms, compared to lateral margins or the rest of the body (Inoue et al., 2014), emphasising the role of rostral sensory information to locomotion in bilateral animals. Furthermore, sensory representation and organization within the somatosensory cortex often reflects adaptive functionality and may contribute to enhanced sensory capacity (Catania, 2005); whether similar overrepresentation with respect to temperature exists in an animal that relies heavily on thermosensation is unknown.

This work seeks to address the presence of a thermoregulatory orientation bias in bearded dragons. By observing orientation behavior at an early and mature life stage, a better understanding of the innateness of orientation as a thermoregulatory strategy will be gained. We hypothesized that orientation would present as a thermoregulatory mechanism in bearded dragons. Therefore, we expected that bearded dragons would display non-random orientation behavior in a thermal gradient, choosing to face towards a heat source rather than towards a cold source. We also hypothesized that a preference for orienting towards a heat source would be conserved across multiple life stages, which would support an innate hypothesis for orientation behavior. Since orientation also informs about the direction in which an animal has been moving while selecting preferred temperatures, we examined orientation in combination with movement and selected temperature in a thermal gradient.

2. Methods

2.1 Animal Husbandry

All animals were captive reared and kept at Brock University in an environmentally controlled room dedicated exclusively to bearded dragons (*Pogona vitticeps*) and a small cockroach colony. A total of 43 dragons were maintained and used during this time. Of the 43 dragons, 17 were adults (10 Male and 7 Female of 1-4 years of age) and 26 were neonates (less than 2 weeks old). Each adult dragon, was housed singly in a terrarium (custom built by Brock University Machine Shop; dimensions 76 cm x 76 cm x 42 cm) with either a corn cob or a coconut husk bedding and equipped with a 40W light bulb set over a stone basking plate, which provided a maximum temperature of 45^{o}C compared to a minimum temperature of 25^{o}C at the far side of the terrarium. In addition to a standard 40 W light bulb, a UV light (13W Reptisun® 10.0 mini compact fluorescent) was also installed to provide UV required for vitamin D synthesis. All cages were given extra enrichment in the form of cardboard packing material, which was used for shelter or as a climbing surface, and Polyvinyl chloride (PVC) pipe sections, used as hiding spots. The neonatal animals were kept in small cages until they grew large enough to move to an adult cage. These smaller terraria were 45 cm x 24 cm x 20 cm and had paper towel bedding. Heating pads were laid down under the cages and set to provide half of each enclosure with floor temperatures from 25 to 45°C. Smaller PVC pipe sections were also supplied as additional enrichment. In addition, neonates were placed two to a cage unless they showed aggressive behaviors, e.g., biting or attacking cage mates, in which case they were placed in individual cages.

All lizards were under a 12:12 light:dark cycle, such that cage temperature declined to 24^{o}C in the dark. Animals were fed a diet of assorted chopped fruits and vegetables which they ate *ad libitum* and which were replaced three times a week and were fed cockroaches once or twice a week. Once a week all lizards received a water bath for sanitation and hydration.

2.2. Series I: Thermal Preference in Adult Bearded Dragons

Thermal and orientation preferences were determined using video footage and temperature sensors. During Series I (see below), data loggers (iButton Thermochron^{TM}) were affixed to the lizards and gave a measurement of ambient/skin temperature preference. All iButtons were calibrated to the computer's clock. Each iButton was set to record every 30 seconds starting immediately. Once the iButtons was programed, it was attached to the lizard using 3M Transpore^{TM} tape, to the ventral side of the abdomen.

To examine orientation and any other behaviors, animals were placed in a thermal gradient. The thermal gradient had two water baths connected to either end to create a range of temperatures, from 15^{o}C to 45^{o}C along the floor of the experimental chamber (~0.18°C /cm). In addition to the floor, an air gradient was also created by using fans, connected to radiators receiving water from the water baths, at either end of the sheet. The gradient had walls set 18 cm apart and 10 cm high while the length of the gradient itself was 163 cm. This created a somewhat narrow lane that encouraged each individual lizard to choose a direction to face during the experiment, either cold or hot. The animal was then placed in the center of the gradient facing either left or right, and was allowed to move freely. When placing animals in the gradient, the direction they were facing was randomly alternated, as was the warm and cold sides of the gradient itself.

To ensure a more consistent air gradient within the experiment, transparent plastic was placed on top of the walls to prevent the animal from escaping and to also inhibit heat exchange between the gradient and outside. The gradient set-up allowed the animal more than enough room to manoeuver but encouraged it to choose one of two possible orientations when at rest. A web camera (Microsoft LifeCam® VX-1000) was placed facing down perpendicular to the gradient, and set to take an image every 30 seconds, timed to coincide with the iButtons' temperature sampling. Once an animal was prepared, it was placed in the thermal gradient and allowed to move freely for six to eight hours. The first 3-4 hours made up the exploration phase, which allowed the lizards to habituate to their new environment (Cadena and Tattersall, 2009), followed by another two to four hours of data to capture thermoregulatory behavior in the absence of exploratory behavior.

2.3. Series II: Thermal Preference in Neonatal Bearded Dragons

The chosen animals were all two weeks old, and due to their smaller size, were placed in a smaller thermal gradient that was only 53 cm in length (thermal gradient ~0.47^{o}C/cm). Furthermore, iButtons were not used for this trial as they were too large to be easily attached to the bodies of the subjects. To collect body temperature, a thermal imaging camera (Model 7515, Mikron Instruments) was suspended above the gradient to record time lapsed thermal videos for subsequent measurement of skin temperature. Each trial ran four lizards at a time, where each lizard was placed into an individual lane separated by a 10 cm high opaque plastic wall. Once this was set up, the animals could behaviorally thermoregulate for 6-8 hours. Due to the time constraint on this particular set of experiments, the neonates were tested in batches of 10 at a time over a four month period for a total of 26 animals, and all trials were completed within three days after their arrival in the lab.

2.4. Data Analysis

2.4.1. Thermal preference in adults

The temperature data were taken from the iButtons and aligned with the corresponding time point (the ventral belly surface was taken as an indicator of selected temperature). Next, each frame of the video footage (taken every 30 seconds) was studied to observe orientation and movement. Behavior was scored in a binary format; orientation was scored as either facing heat (H) or facing away from heat (C) per frame, and movement was scored as either moving (Y) or stationary (N), depending on whether the animal had moved since the previous frame.

2.4.2. Thermal preference in neonatal bearded dragons

Since these trials were performed using a thermal imaging camera, the surface temperature of the animal, orientation, and movement were recorded from the video, using thermal imaging software (Mikrospec-RT; see Figure 1 for a sample thermal image). To calculate neonatal surface temperature, a region of interest (ROI) analysis was used, where the average surface temperature was calculated for each lizard starting from the middle of the head down the body to the base of the tail. As with the Series I trials, each frame was studied and orientation and movement recorded.

2.4.3. Statistical Analysis

Statistical analyses used R (R Core Team, 2016) and lme4 (Bates et al., 2015) to perform separate linear mixed effects analyses on the impact of multiple terms (e.g., period, body mass, sex, movement) on selected ambient temperature or orientation preference on adult and neonates separately. The data were divided into a habituation and final phase (referred to as period). For the analysis of selected temperature, we entered orientation preference, movement, body mass and sex into a global model, including select interactions with period that were chosen for biologically justifiable reasons, as fixed effects. For the analysis of orientation preference, we entered selected temperature, movement, body mass and sex into a global model, including select interactions that were chosen for biologically justifiable reasons, as fixed effects. As random effects, we included intercepts for animal ID and slopes over time within each experimental period to account for the repeated measures design, into all models. To avoid autocorrelation of model residuals, the data were resampled at every 40th time point (every 20 minutes). Neonatal data were analysed similarly, except that mass and sex were not assessed.

For both series (Series I and II), we fit all possible models that nested within a global model, calculated, and ranked ΔAICc values (Akaike, 1973), and choose the most comprehensive model with a ΔAICc <2. Model selection and the information-theoretic approach was implemented using the MuMIn package in R (Bartoń, 2016). We present parameter importance (fraction of models containing parameter) and parameter weights summed over all models containing each parameter as measures of support. Visual inspection of residuals and QQ plots did not reveal any obvious deviations from homoscedasticity or normality. P-values were obtained using likelihood ratio tests (Type II Wald's chi-square tests) using the car package in R (Fox and Weisberg, 2011). For summary purposes, thermal preference and thermal precision data from the final 4 hours were calculated according to convention (Cadena and Tattersall, 2008, 2009; Dewitt, 1967) and compared across the two age classes using simple linear models.

3. Results

3.1. Series I: Behavioral Responses in Adult Bearded Dragons

In the adult dragons, two behavioral explanatory variables were examined (selected temperature and orientation) as influenced by mass, sex, and experimental period (habituation vs. final). Selected temperature was best described by the model including orientation, period, and sex (Table S1). Selected temperature increased over the course of the experimental following the habituation period, was negatively associated with orientation to the heat, and was lower in males compared to females (Table 1; Figure 2). Orientation to heat was best described by movement, period, selected temperature and sex (Table S2). Adult bearded dragons oriented strongly toward the heat when at cool temperatures, but as they approached their selected temperature, orientation fell toward random chance (Figure 3a). During the habituation period, orientation to heat was more random, but increased to ~75% of the time during the final phase of the measurement period (Figure 3b). Movement decreased the orientation toward random chance, although stationary lizards were more likely to face toward the heat (Figure 3c). Finally, males were 0.85 times less likely to face the heat than females, although this effect was not significant at alpha = 0.05 (Table 2).

3.2. Series II: Behavioral Responses in Neonatal Bearded Dragons

In the neonates, two response variables were examined, selected temperature and orientation preference. Selected temperature was best described by a model including movement, orientation, and an interaction between period and orientation behavior (Table S3). Although there were weak effects of orientation and period on selected temperature, the interaction between orientation and experimental period predominated (Table 3; Figure 4a); during the habituation phase, selected temperature was not influenced by orientation, however during the final phase of the experiment, selected temperature was higher when neonates were facing the cold, compared to when facing toward the warmth. Selected temperature in neonates was low when they were moving (B=-3.09), compared to when they were stationary (Table 3; Figure 4b). The second response variable to be examined was the preferred orientation of neonatal bearded dragons. Orientation was strongly influenced by an interaction between selected temperature and period (Table S4); during the habituation period, orientation was positively associated with selected temperature, but during the final stage, this relationship was reversed (Table 4; Figure 5). Orientation was, however, substantially different from that expected by random chance (50%), with neonates being 3.8 times more likely to be facing toward warmth than toward cool temperatures, corresponding an overall probability of 79%.

3.3. Thermoregulatory Set-Points

Thermoregulatory set-points and measures of precision in behaviorally thermoregulating adult and neonatal bearded dragons are depicted in Table 5. These data are derived from the final four hours of the experimental period. None of thermoregulatory parameters were significantly influenced by age class (p>0.65 for all linear models performed).

4. Discussion

We hypothesized that thermal orientation would present as a thermoregulatory response in bearded dragons. In adults, our data clearly supports orientation as a behavior related to thermoregulation, which appears consistent with that observed in the wild in other species of reptile (Bartholomew, 1966; Cowles and Bogert, 1944; Gibson et al., 2015; Sartorius et al., 2002). In the morning and especially during the afternoon, marine iguanas preferentially orient perpendicularly to the sun's rays to avoid overheating and to increase exposure to cooler trade winds (Bartholomew, 1966). In contrast, the Otago/Southland gecko uses orientation to expose portions of the abdomen to direct solar radiation in order to heat those sections up faster (Gibson et al., 2015). The orientation preference displayed by bearded dragons in the absence of solar radiation suggests that they either orient to prevent over cooling/heating of the head or to expedite heating and cooling of the posterior tail region. The presence of thermoregulatory orientation behaviors at the relatively young neonatal stages has never been previously described in bearded dragons or in other reptiles. The neonatal data outlined in this work suggests a high degree of importance for orientation behavior with regard to thermoregulation. The data from the neonates also support the possibility that orientation behaviors are innate, or at least, require minimal experience. Due to the larger variety of available microenvironments and possible orientation and postural changes available in nature as opposed to the lab, it is plausible that this behavior would be more difficult to tease out in nature; nevertheless, the fact that neonates exhibit similar behaviours to the adults speaks to the inherent relevance of orientation as a thermoregulatory behavior in bearded dragons.

The variation in selected ambient temperature that the adult and neonatal bearded dragons showed is consistent with what we would expect to find in behaviorally thermoregulating lizards (Cadena and Tattersall, 2008, 2009). During the earlier time periods of each trial the dragons were selecting lower ambient temperatures, suggesting that they were exploring the gradient. As time increased, selected ambient temperature rose to similar levels reported previously (~33-34°C), suggesting that the bearded dragons were thermoregulating more consistently in the latter part of the measurement period. In addition, the probability of facing a heat source declined as selected temperature rose, showing that orientation to heat is thermoregulatory by the very fact that this behavior counter balances the lizard's selected temperature. It is possible that lizards reduce orientation to heat as they get warm to control and/or reduce head temperature (Scarpellini et al., 2015; Tattersall et al., 2006). Interestingly, the neonates required at least a 3 hour habituation period before they adhere to a similar orientation pattern to the adults, despite selecting similar temperatures to adults. Initially, neonates show increasing orientation to the heat as they select warmer temperatures (i.e. keeping the head oriented hotter than the rest of the body). By the final portion of the measurement period, the neonates show a pattern of orientation that counters that which they select, converging on the counter balancing pattern seen in the adults. Therefore, facing heat less at high temperatures is possibly a response to cool the head. Both adult and neonatal bearded dragons face a heat source more often than what would be expected from random chance. Furthermore, since selected temperature can influence and be influenced by orientation, it is plausible that orientation is used to facilitate both warming (of the head) and cooling (of the tail), and thus is well integrated with bearded dragons' suite of thermoregulatory responses.

5. Conclusions and Perspectives

The importance of behavioral thermoregulation has been well documented in numerous ectothermic groups (Angilletta, 2009; Blumberg et al., 2002; Christian and Tracy, 1981; Tattersall et al., 2012a; Vandamme et al., 1991), therefore, it is not surprising that bearded dragons and other reptiles would exhibit multiple voluntary and involuntary responses to aid in thermoregulation, such as gaping (Crawford, 1972; Tattersall et al., 2006), orientation (Bartholomew, 1966; Gibson et al., 2015) and shuttling (Cadena and Tattersall, 2008, 2009; Cowles and Bogert, 1944). In the present study, orientation preference was shown to be associated with selected ambient temperature in adult bearded dragons, suggesting that these animals do use orientation as a thermoregulatory response. By using orientation as a buffering mechanism, lizards can bask in extremely warm areas without overheating or absorb as much heat as possible in cooler areas (such as from the sun during cooler parts of the day) to prevent overcooling (Bartholomew, 1966; Gibson et al., 2015; Sartorius et al., 2002). The adult bearded dragon results suggest two possible explanations: either bearded dragons use orientation as a possible means of fine tuning regulation of head or brain temperature, or orientation is used as a means of heating up or cooling down the large posterior tail region of the animal. The most likely scenario is that the dragons use orientation to regulate head temperature separately from body temperature, similar to how certain reptiles use gaping and respiratory control (Crawford, 1972; Tattersall et al., 2006). It is also possible that orientation behavior is used to prioritize multiple thermoregulatory requirements at the same time, such as keeping the head warmer while losing heat through the tail. Given the typical rostral bias in sensory feedback and processing, and large surface area of the tail, the optimal way to maintain neural function would be to orient the head towards the heat, while leaving the potential for the tail to serve as an appendage to dump excess heat (Bartholomew and Tucker, 1963).

Orientation as a thermoregulatory behavior in neonatal bearded dragons, while present, does not appear to be as precise or as impactful on selected temperature as it does in adults. The presence of orientation as a thermoregulatory response in the early life stages suggests that this behavior is innate, and requires minimal experience (Barnard, 2003). It is likely that as size increases, the proximate drivers for orientation behaviors change. Larger animals take longer to change temperature and may require specific postural orientation in the wild that maximize their rates of heating, or minimizes their rates of cooling. Future research into behavioral thermoregulation could utilise orientation to heat to inform about thermoregulatory set-points.

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Table 1. Coefficients estimating the following model in adult bearded dragons: SelTemperature ~ Orientation + Period + Sex + (1 + Time/Period | LizardID)

Parameter	**Estimate**	**SE**	**LL**	**UL**	**P value**
Intercept	33.015	1.1447	30.7714	35.2591	-
OrientationW	-1.138	0.3689	-1.8612	-0.4152	0.00203
PeriodFinal	2.093	0.6178	0.8815	3.3036	0.00071
SexM	-1.782	1.1144	-3.9669	0.4021	0.10974

Parameter estimates (B) ± standard errors (SE) represent the model coefficients. The 95% confidence limit for each parameter is indicated by LL and UL. P values are derived from type II Wald's χ^2 tests.

Table 2. Coefficients estimating the following model in adult bearded dragons: Orientation ~ Movement + Period + SelTemperature + Sex + (1 + Time/Period | LizardID)

Parameter	**Estimate**	**OR**	**SE**	**LL**	**UL**	**P Value**
Intercept	0.8509	2.3418	0.6364	-0.3966	2.0984	-
MovementYes	-0.9844	0.3737	0.3890	-1.7468	-0.2219	0.0139
PeriodFinal	1.2459	3.4760	0.4634	0.3375	2.1543	0.0078
SelTemperature	-0.6815	0.5059	0.2243	-1.1211	-0.2418	0.0049
SexM	-1.0052	0.3660	0.7345	-2.4450	0.4345	0.1787

Parameter estimates (B) ± standard errors (SE) represent the model coefficients. Odds ratio (OR) is calculated from the parameter estimate. The 95% confidence limit for each parameter is indicated by LL and UL. P values are derived from type II Wald's χ^2 tests.

Table 3. Coefficients estimating the following model in neonatal bearded dragons: SelTemperature ~ Movement + Orientation + Period + Orientation:Period + (1 + Time/Period | LizardID)

Parameter	Estimate	SE	LL	UL	P value
Intercept	32.3881	0.6097	31.1929	33.58335	-
MovementYes	-3.0899	0.4940	-4.0581	-2.12164	4e-10
OrientationWarm	0.2449	0.3969	-0.5330	1.02284	0.109
PeriodFinal	1.4492	0.5250	0.4201	2.47822	0.068
OrientationWarm: PeriodFinal	-1.0543	0.5044	-2.0431	-0.06559	0.037

Parameter estimates (B) ± standard errors (SE) represent the model coefficients. The 95% confidence limit for each parameter is indicated by LL and UL. P values are derived from type II Wald's χ^2 tests.

Table 4. Coefficients estimating the following model in neonatal bearded dragons: Orientation ~ Period + SelTemperature + Period: SelTemperature + (1 +Time/Period | LizardID)

Parameter	**Estimate**	**OR**	**SE**	**LL**	**UL**	**P value**
(Intercept)	1.2900	3.6330	0.3326	0.63803	1.9421	-
PeriodFinal	0.2264	1.2541	0.3525	-0.46447	0.9174	0.8128
SelTemperature	0.3567	1.4286	0.1894	-0.01452	0.7279	0.6266
PeriodFinal : SelTemperature	-0.9713	0.3786	0.3297	-1.61749	-0.3250	0.0032

Parameter estimates (B) ± standard errors (SE) represent the model coefficients. The 95% confidence limit for each parameter is indicated by LL and UL. P values are derived from type II Wald's χ^2 tests.

Table 5. Descriptive statistics (mean ± sd) of behavioral thermoregulatory parameters in adult and neonatal bearded dragons taken from the final 4 hours of measurement.

	Mean	**Median**	**Standard Deviation**	**25th Percentile**	**75th Percentile**
Adult	33.6 ± 2.6	34.1 ± 2.4	2.02 ± 1.11	32.5 ± 3.0	35.0 ± 2.2
Neonate	33.4 ± 1.9	33.7 ± 1.8	1.77 ± 1.17	32.1 ± 3.1	34.7 ± 1.4

Figure Legends

Figure 1. Infrared thermal images depicting an adult dragon in a thermal gradient (a) and two neonatal bearded dragons in a sub-divided thermal gradient (b). Arrows point to the tails of each animal as well as the orientation (in this sample image, all 3 animals are orienting toward the heat). Lizard skin temperature is not identical to the gradient floor temperature due to volitional movement throughout the chamber. Given the different sizes of adults and neonates, images are presented at different sizes for clarity, and limited by resolving power of the thermal camera. Scale bars denote 5 cm.

Figure 2. Influence (model fits ± se) of period (a), orientation (b), and sex (c) on selected ambient temperature of adult Bearded Dragons (*P. vitticeps*). Period refers to experimental period, broken into a habituation (first 3 hours) and final period (final 4 hours), while orientation is expressed as facing towards (H) or away from (C) a heat source, and sex is coded as male (M) or female (F). Data were collected from animals in a thermal gradient over a maximum of 8 hours. A total of 17 animals were used, 10 males and 7 females.

Figure 3. The model predicted probability (±se) that adult Bearded Dragons (*P. vitticeps*) will orient towards a heat source, as a function of selected temperature (a), experimental period (b), and movement (c). Period refers to experimental period, broken into a habituation (first 3 hours) and final period (final 4 hours), while movement is coded as yes or no. Data were collected from animals in a thermal gradient over a maximum of 8 hours. Orientation is expressed as the probability of an animal facing the warm side of the gradient (dotted line at 50% random chance).

Figure 4. Influence (model fits ± se) of the interaction between period and orientation (a), and movement (b) on selected ambient temperature of neonatal Bearded Dragons (*P. vitticeps*).

Period refers to experimental period, broken into a habituation (first 3 hours) and final period (final 4 hours), while orientation is expressed as facing towards (H) or away from (C) a heat source. Data were collected from animals in a thermal gradient over a maximum of 8 hours.

Figure 5. The model predicted probability (±se) that neonatal Bearded Dragons (*P. vitticeps*) will orient towards a heat source, as a function of the interaction between selected temperature and experimental period. Period refers to experimental period, broken into a habituation (first 3 hours) and final period (final 4 hours). Data were collected from animals in a thermal gradient over a maximum of 8 hours. Orientation is expressed as the probability of an animal facing the warm side of the gradient (dotted line at 50% random chance).

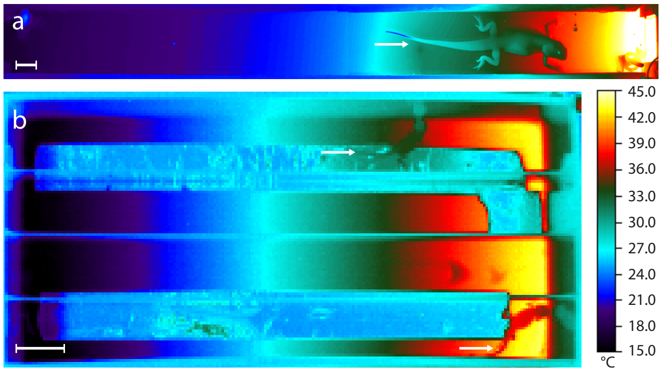

Figure 1.

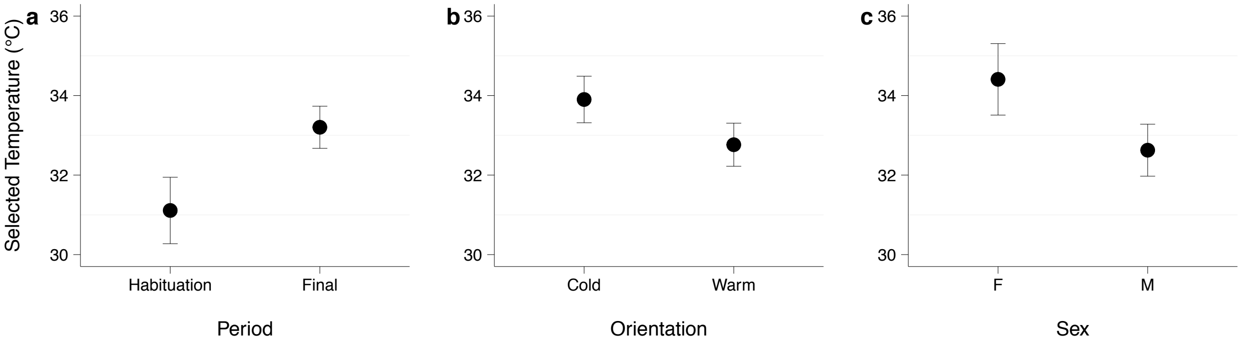
a
b
c
Selected Temperature (°C)
36
34
32
30
Habituation
Final
Period
Cold
Warm
Orientation
F
M
Sex

Figure 2.

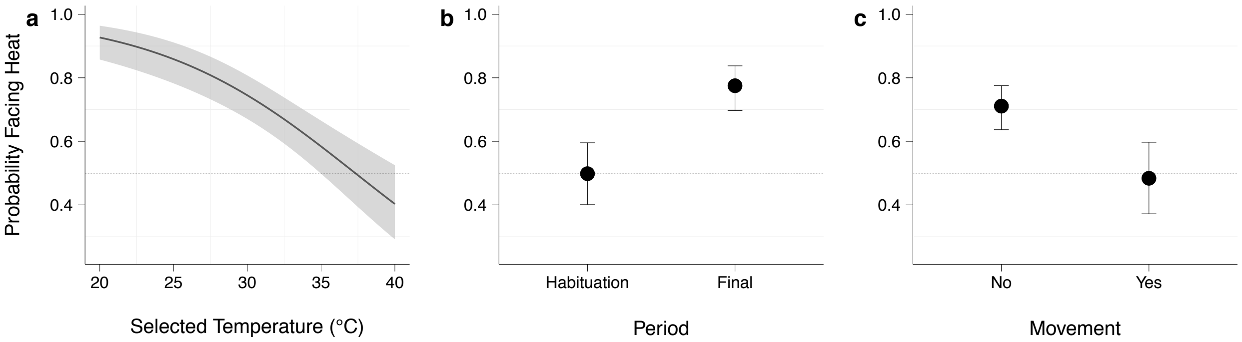
a
b
c
Probability Facing Heat
1.0
0.8
0.6
0.4
20
25
30
35
40
Selected Temperature (°C)
Habituation
Final
Period
No
Yes
Movement

Figure 3.

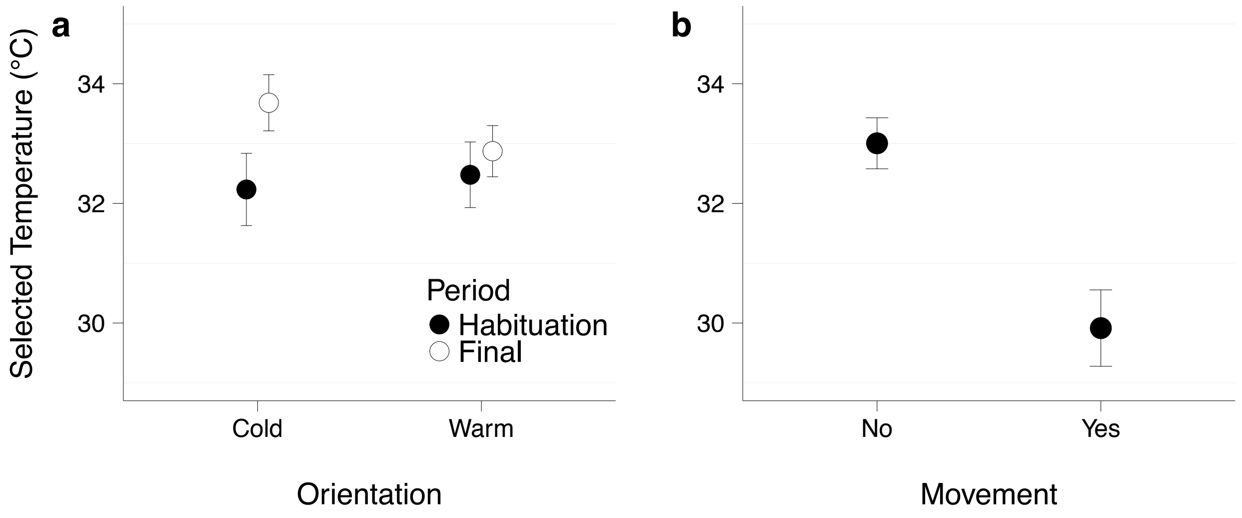
a
b
Selected Temperature (°C)
34
32
30
Period
● Habituation
○ Final
Cold
Warm
Orientation
No
Yes
Movement

Figure 4.

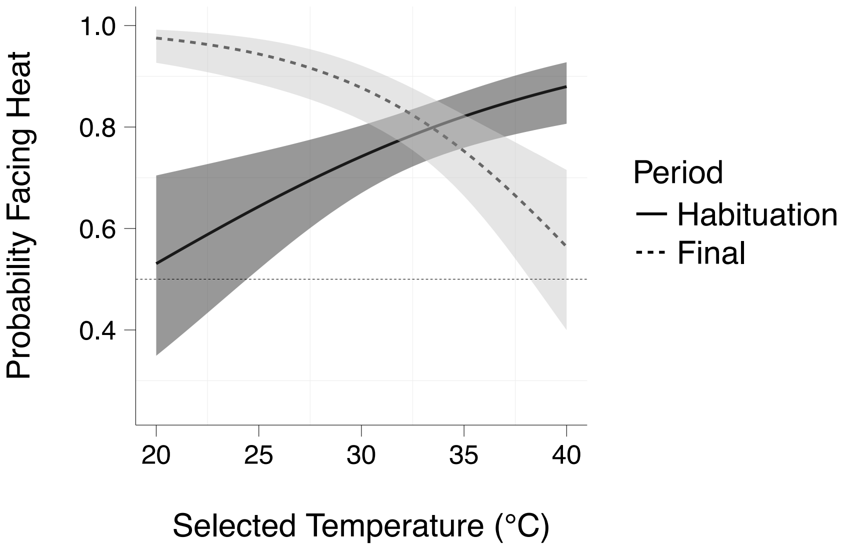
Probability Facing Heat
1.0
0.8
0.6
0.4
20
25
30
35
40
Selected Temperature (°C)
Period
— Habituation
--- Final

Figure 5.