

1 Thermoregulatory behavior and orientation preference in bearded dragons

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14 **Abstract**

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

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

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37 **1. Introduction**

38 Animals commit time and energy to achieve and maintain thermally optimality, defined
39 as the range of temperatures which maintains physiological processes operating at, or near,
40 maximum conditions (Dewitt, 1967; Huey and Slatkin, 1976). For ectotherms which depend on
41 environmental heat absorption, behaviors that adjust the rate of body temperature (T_b) change are
42 crucial to thermoregulation (Cowles and Bogert, 1944). Although thermoregulatory behaviors
43 are known to present during early life (Blumberg et al., 2002; Lang, 1981; Stahlschmidt et al.,
44 2015; Vollset et al., 2013; Zhao et al., 2013), how thermoregulatory behaviors change through
45 ontogeny is not well studied. Shuttling and basking behaviors, which have a high impact on body
46 temperature, are likely present from an animal's first exposure to a novel thermal environment,
47 although these behaviors are also subject to change with experience. For example, shuttling
48 behaviors show lower precision in bearded dragons that are naïve to an operant conditioning
49 thermoregulatory paradigm compared to those with prior experience or when the locomotory
50 costs of thermoregulation are increased (Cadena and Tattersall, 2009). Indeed, that lizards
51 dedicate time to exploring and adjusting to a thermal gradient in the lab suggests that learning
52 plays a role in behavioral thermoregulation, especially in novel environments (Cadena and
53 Tattersall, 2009). Subtle thermoregulatory responses might, therefore, also require time and may
54 even need to be learned well after hatching.

55 Unlike birds and mammals, squamates do not typically display parental care behaviors
56 after their young hatch (Reynolds et al., 2002). After hatching, neonates meet their needs on their
57 own, but not all behaviors are present during every phase of an animal's life (Dawkins, 1995;
58 Khan et al., 2010). Innate behaviors are responses that prepare an animal for adaptive reactions
59 to the world around them, and are generally fully formed from the outset without the need for
60 experience or learning; this is also referred to as inbuilt adaptiveness (Dawkins, 1995). Learned

61 behaviors are responses that develop through the accumulation of experience and the retention of
62 information (Barnard, 2003). For the purposes of this work, innate thermoregulatory behaviors
63 are those present from the neonatal stage that do not generally require experience. Examples of
64 both innate and learned responses can be found in voluntary, involuntary, and autonomic
65 behaviors (Dawkins, 1995), and thus thermoregulatory behaviours can be expected to reflect
66 both innate and learned responses.

67 Aside from morphological and developmental differences, neonatal bearded dragons
68 differ from their adult counterparts, especially with respect to social behaviors (Khan et al.,
69 2010). Neonates are more prone to gregarious behavior, and often observed in aggregations
70 (Khan et al., 2010). Gregarious behavior, while common in mammals (Aureli et al., 2002), is less
71 prevalent in reptiles and is not necessarily driven by sociality. Instead, aggregation could be
72 related to other fitness demands, such as gestation, oviposition, parasitism, predation protection,
73 or even thermoregulation (Gautier et al., 2006; Graves and Duvall, 1995; Wikelski, 1999). When
74 solitary and groups of neonatal bearded dragons were allowed to thermoregulate, both isolated
75 and aggregated neonates were observed to select similar temperatures, however, individuals
76 within a group context showed lower thermoregulatory precision than those in isolation (Khan et
77 al., 2010). Khan et al. (2010) suggested that this aggregation results from a mutual attraction to a
78 limited and valuable resource (e.g., an optimal temperature), and that the drop in precision results
79 from agonistic interactions (Khan et al., 2010). Agonistic behaviors over access to preferred
80 temperatures are known to occur in other ectothermic species, and are also dependent on
81 familiarity and experience (Tattersall et al., 2012b), suggesting that both social context and
82 learning contribute to thermoregulatory behaviors. In short, although thermoregulatory

83 behaviors are guided by innate, sensory driven mechanisms, they can be shaped and influenced
84 by experience.

85 Due to the importance of temperature regulation, it is plausible that thermoregulatory
86 behaviors will show some level of innateness and therefore be conserved between adults and
87 neonates. Behaviors such as aggregation are likely to be lost at the adult stages due to increased
88 competition between individuals that have reached sexual maturity. Critical thermoregulatory
89 behaviors, such as shuttling and basking are likely observed across all life stages. Subtler, yet
90 equally important thermoregulatory behaviors, such as body orientation toward a heat source
91 (referred to hereafter as orientation preference), may instead be partially learned through growth
92 and development, since body size is strongly implicated in the effectiveness of orientation
93 (Lactin and Johnson, 1997). Orientation preference, as a thermoregulatory behavior, has been
94 documented in select mammals as an energy savings strategy (Hetem et al., 2011), but most
95 notably in several invertebrates and certain reptiles (Bartholomew, 1966; Fraser et al., 2016;
96 Martin et al., 1995; McMaster and Downs, 2006; Tattersall et al., 2012b). Adult lizards of a
97 species well known to exhibit distinct thermoregulatory behaviors, such as the bearded dragon,
98 are the best option for examining the presence of any orientation preference, as they are larger
99 than neonates and therefore orientation is more likely to have a direct impact on heating and
100 cooling rates, and therefore thermoregulation. Additionally, adults have had time to acquire any
101 learned aspects of the behavior. On the other hand, cutaneous thermosensory feedback may be
102 over-emphasized in the cephalic region, resulting in an innate, sensory bias-based preference to
103 face toward or away from the source of the stimulus. Ion channels implicated in thermotaxis are
104 highly expressed in the rostral margin of the head in flatworms, compared to lateral margins or
105 the rest of the body (Inoue et al., 2014), emphasising the role of rostral sensory information to

106 locomotion in bilateral animals. Furthermore, sensory representation and organization within the
107 somatosensory cortex often reflects adaptive functionality and may contribute to enhanced
108 sensory capacity (Catania, 2005); whether similar overrepresentation with respect to temperature
109 exists in an animal that relies heavily on thermosensation is unknown.

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

121 **2. Methods**

122 2.1 Animal Husbandry

123 All animals were captive reared and kept at Brock University in an environmentally
124 controlled room dedicated exclusively to bearded dragons (*Pogona vitticeps*) and a small
125 cockroach colony. A total of 43 dragons were maintained and used during this time. Of the 43
126 dragons, 17 were adults (10 Male and 7 Female of 1-4 years of age) and 26 were neonates (less
127 than 2 weeks old). Each adult dragon, was housed singly in a terrarium (custom built by Brock
128 University Machine Shop; dimensions 76 cm x 76 cm x 42 cm) with either a corn cob or a

129 coconut husk bedding and equipped with a 40W light bulb set over a stone basking plate, which
130 provided a maximum temperature of 45°C compared to a minimum temperature of 25°C at the
131 far side of the terrarium. In addition to a standard 40 W light bulb, a UV light (13W Reptisun®
132 10.0 mini compact fluorescent) was also installed to provide UV required for vitamin D
133 synthesis. All cages were given extra enrichment in the form of cardboard packing material,
134 which was used for shelter or as a climbing surface, and Polyvinyl chloride (PVC) pipe sections,
135 used as hiding spots. The neonatal animals were kept in small cages until they grew large enough
136 to move to an adult cage. These smaller terraria were 45 cm x 24 cm x 20 cm and had paper
137 towel bedding. Heating pads were laid down under the cages and set to provide half of each
138 enclosure with floor temperatures from 25 to 45°C. Smaller PVC pipe sections were also
139 supplied as additional enrichment. In addition, neonates were placed two to a cage unless they
140 showed aggressive behaviors, e.g., biting or attacking cage mates, in which case they were
141 placed in individual cages.

142 All lizards were under a 12:12 light:dark cycle, such that cage temperature declined to
143 24°C in the dark. Animals were fed a diet of assorted chopped fruits and vegetables which they
144 ate *ad libitum* and which were replaced three times a week and were fed cockroaches once or
145 twice a week. Once a week all lizards received a water bath for sanitation and hydration.

146 2.2. Series I: Thermal Preference in Adult Bearded Dragons

147 Thermal and orientation preferences were determined using video footage and
148 temperature sensors. During Series I (see below), data loggers (iButton ThermoChron™) were
149 affixed to the lizards and gave a measurement of ambient/skin temperature preference. All
150 iButtons were calibrated to the computer's clock. Each iButton was set to record every 30

151 seconds starting immediately. Once the iButtons was programed, it was attached to the lizard
152 using 3M TransporeTM tape, to the ventral side of the abdomen.

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

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

173 followed by another two to four hours of data to capture thermoregulatory behavior in the
174 absence of exploratory behavior.

175 *2.3. Series II: Thermal Preference in Neonatal Bearded Dragons*

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

187 2.4. Data Analysis

188 *2.4.1. Thermal preference in adults*

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

195 *2.4.2. Thermal preference in neonatal bearded dragons*

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

203 *2.4.3. Statistical Analysis*

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

217 For both series (Series I and II), we fit all possible models that nested within a global
218 model, calculated, and ranked ΔAICc values (Akaike, 1973), and choose the most
219 comprehensive model with a $\Delta\text{AICc} < 2$. Model selection and the information-theoretic approach
220 was implemented using the MuMIn package in R (Bartoń, 2016). We present parameter
221 importance (fraction of models containing parameter) and parameter weights summed over all
222 models containing each parameter as measures of support. Visual inspection of residuals and QQ
223 plots did not reveal any obvious deviations from homoscedasticity or normality. P-values were
224 obtained using likelihood ratio tests (Type II Wald's chi-square tests) using the car package in R
225 (Fox and Weisberg, 2011). For summary purposes, thermal preference and thermal precision
226 data from the final 4 hours were calculated according to convention (Cadena and Tattersall,
227 2008, 2009; Dewitt, 1967) and compared across the two age classes using simple linear models.

228 **3. Results**

229 3.1. Series I: Behavioral Responses in Adult Bearded Dragons

230 In the adult dragons, two behavioral explanatory variables were examined (selected
231 temperature and orientation) as influenced by mass, sex, and experimental period (habituation vs.
232 final). Selected temperature was best described by the model including orientation, period, and
233 sex (Table S1). Selected temperature increased over the course of the experimental following the
234 habituation period, was negatively associated with orientation to the heat, and was lower in
235 males compared to females (Table 1; Figure 2). Orientation to heat was best described by
236 movement, period, selected temperature and sex (Table S2). Adult bearded dragons oriented
237 strongly toward the heat when at cool temperatures, but as they approached their selected
238 temperature, orientation fell toward random chance (Figure 3a). During the habituation period,

239 orientation to heat was more random, but increased to ~75% of the time during the final phase of
240 the measurement period (Figure 3b). Movement decreased the orientation toward random
241 chance, although stationary lizards were more likely to face toward the heat (Figure 3c). Finally,
242 males were 0.85 times less likely to face the heat than females, although this effect was not
243 significant at $\alpha = 0.05$ (Table 2).

244 3.2. Series II: Behavioral Responses in Neonatal Bearded Dragons

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

261 3.3. Thermoregulatory Set-Points

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

266 **4. Discussion**

267 We hypothesized that thermal orientation would present as a thermoregulatory response
268 in bearded dragons. In adults, our data clearly supports orientation as a behavior related to
269 thermoregulation, which appears consistent with that observed in the wild in other species of
270 reptile (Bartholomew, 1966; Cowles and Bogert, 1944; Gibson et al., 2015; Sartorius et al.,
271 2002). In the morning and especially during the afternoon, marine iguanas preferentially orient
272 perpendicularly to the sun's rays to avoid overheating and to increase exposure to cooler trade
273 winds (Bartholomew, 1966). In contrast, the Otago/Southland gecko uses orientation to expose
274 portions of the abdomen to direct solar radiation in order to heat those sections up faster (Gibson
275 et al., 2015). The orientation preference displayed by bearded dragons in the absence of solar
276 radiation suggests that they either orient to prevent over cooling/heating of the head or to
277 expedite heating and cooling of the posterior tail region. The presence of thermoregulatory
278 orientation behaviors at the relatively young neonatal stages has never been previously described
279 in bearded dragons or in other reptiles. The neonatal data outlined in this work suggests a high
280 degree of importance for orientation behavior with regard to thermoregulation. The data from the
281 neonates also support the possibility that orientation behaviors are innate, or at least, require
282 minimal experience. Due to the larger variety of available microenvironments and possible
283 orientation and postural changes available in nature as opposed to the lab, it is plausible that this
284 behavior would be more difficult to tease out in nature; nevertheless, the fact that neonates

285 exhibit similar behaviours to the adults speaks to the inherent relevance of orientation as a
286 thermoregulatory behavior in bearded dragons.

287 The variation in selected ambient temperature that the adult and neonatal bearded dragons
288 showed is consistent with what we would expect to find in behaviorally thermoregulating lizards
289 (Cadena and Tattersall, 2008, 2009). During the earlier time periods of each trial the dragons
290 were selecting lower ambient temperatures, suggesting that they were exploring the gradient. As
291 time increased, selected ambient temperature rose to similar levels reported previously (~33-
292 34°C), suggesting that the bearded dragons were thermoregulating more consistently in the latter
293 part of the measurement period. In addition, the probability of facing a heat source declined as
294 selected temperature rose, showing that orientation to heat is thermoregulatory by the very fact
295 that this behavior counter balances the lizard's selected temperature. It is possible that lizards
296 reduce orientation to heat as they get warm to control and/or reduce head temperature
297 (Scarpellini et al., 2015; Tattersall et al., 2006). Interestingly, the neonates required at least a 3
298 hour habituation period before they adhere to a similar orientation pattern to the adults, despite
299 selecting similar temperatures to adults. Initially, neonates show increasing orientation to the
300 heat as they select warmer temperatures (i.e. keeping the head oriented hotter than the rest of the
301 body). By the final portion of the measurement period, the neonates show a pattern of
302 orientation that counters that which they select, converging on the counter balancing pattern seen
303 in the adults. Therefore, facing heat less at high temperatures is possibly a response to cool the
304 head. Both adult and neonatal bearded dragons face a heat source more often than what would be
305 expected from random chance. Furthermore, since selected temperature can influence and be
306 influenced by orientation, it is plausible that orientation is used to facilitate both warming (of the

307 head) and cooling (of the tail), and thus is well integrated with bearded dragons' suite of
308 thermoregulatory responses.

309 **5. Conclusions and Perspectives**

310 The importance of behavioral thermoregulation has been well documented in numerous
311 ectothermic groups (Angilletta, 2009; Blumberg et al., 2002; Christian and Tracy, 1981;
312 Tattersall et al., 2012a; Vandamme et al., 1991), therefore, it is not surprising that bearded
313 dragons and other reptiles would exhibit multiple voluntary and involuntary responses to aid in
314 thermoregulation, such as gaping (Crawford, 1972; Tattersall et al., 2006), orientation
315 (Bartholomew, 1966; Gibson et al., 2015) and shuttling (Cadena and Tattersall, 2008, 2009;
316 Cowles and Bogert, 1944). In the present study, orientation preference was shown to be
317 associated with selected ambient temperature in adult bearded dragons, suggesting that these
318 animals do use orientation as a thermoregulatory response. By using orientation as a buffering
319 mechanism, lizards can bask in extremely warm areas without overheating or absorb as much
320 heat as possible in cooler areas (such as from the sun during cooler parts of the day) to prevent
321 overcooling (Bartholomew, 1966; Gibson et al., 2015; Sartorius et al., 2002). The adult bearded
322 dragon results suggest two possible explanations: either bearded dragons use orientation as a
323 possible means of fine tuning regulation of head or brain temperature, or orientation is used as a
324 means of heating up or cooling down the large posterior tail region of the animal. The most
325 likely scenario is that the dragons use orientation to regulate head temperature separately from
326 body temperature, similar to how certain reptiles use gaping and respiratory control (Crawford,
327 1972; Tattersall et al., 2006). It is also possible that orientation behavior is used to prioritize
328 multiple thermoregulatory requirements at the same time, such as keeping the head warmer while
329 losing heat through the tail. Given the typical rostral bias in sensory feedback and processing,

330 and large surface area of the tail, the optimal way to maintain neural function would be to orient
331 the head towards the heat, while leaving the potential for the tail to serve as an appendage to
332 dump excess heat (Bartholomew and Tucker, 1963).

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

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445 **Table 1.** Coefficients estimating the following model in adult bearded dragons: SelTemperature
 446 ~ 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

447

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

451 **Table 2.** Coefficients estimating the following model in adult bearded dragons: Orientation ~
 452 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

453

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

457

458 **Table 3.** Coefficients estimating the following model in neonatal bearded dragons:
 459 SelTemperature ~ Movement + Orientation + Period + Orientation:Period + (1 + Time/Period |
 460 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

461
 462 Parameter estimates (B) ± standard errors (SE) represent the model coefficients. The 95%
 463 confidence limit for each parameter is indicated by LL and UL. P values are derived from type II
 464 Wald's χ^2 tests.

465

466 **Table 4.** Coefficients estimating the following model in neonatal bearded dragons: Orientation ~
 467 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

468

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

472

473

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

476

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

477

478

479 **Figure Legends**

480

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

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

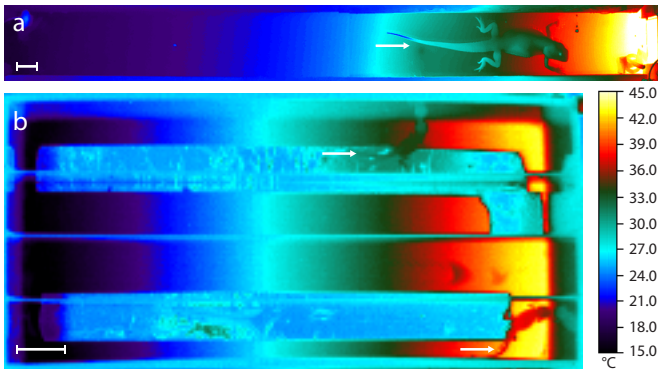
494 **Figure 3.** The model predicted probability (\pm se) that adult Bearded Dragons (*P. vitticeps*) will
495 orient towards a heat source, as a function of selected temperature (a), experimental period (b),
496 and movement (c). Period refers to experimental period, broken into a habituation (first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

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

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

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

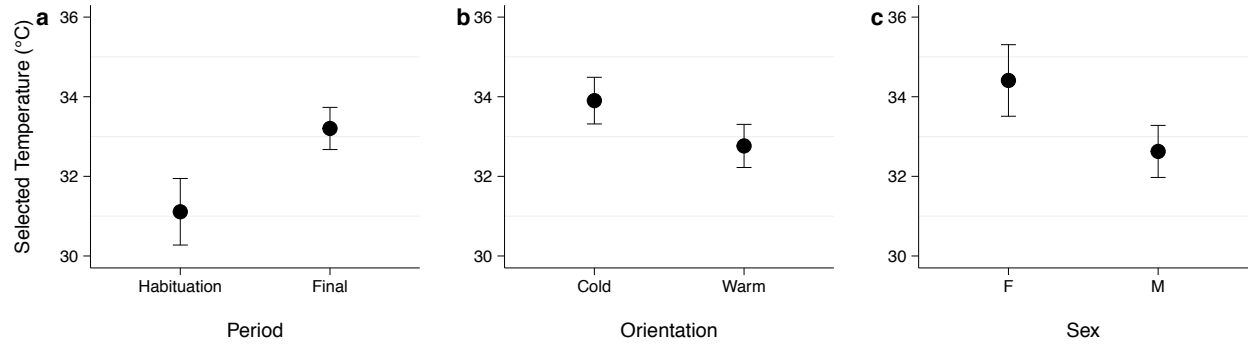
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513 Figure 1.

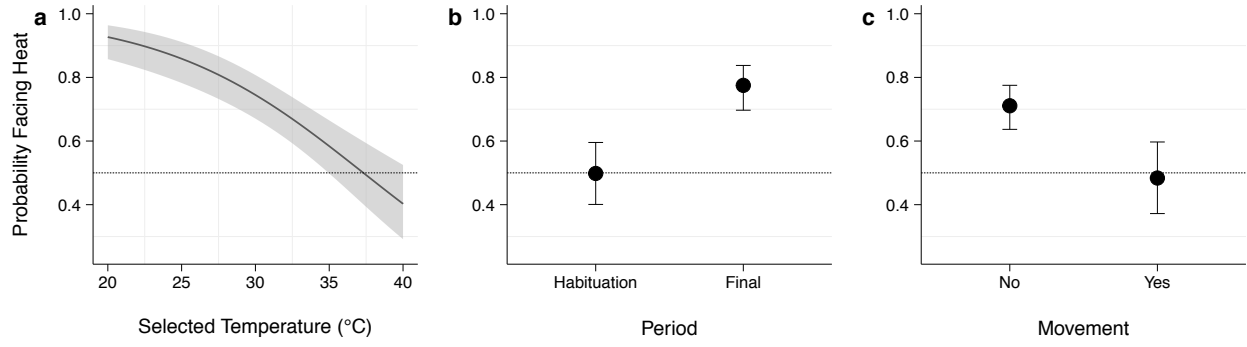
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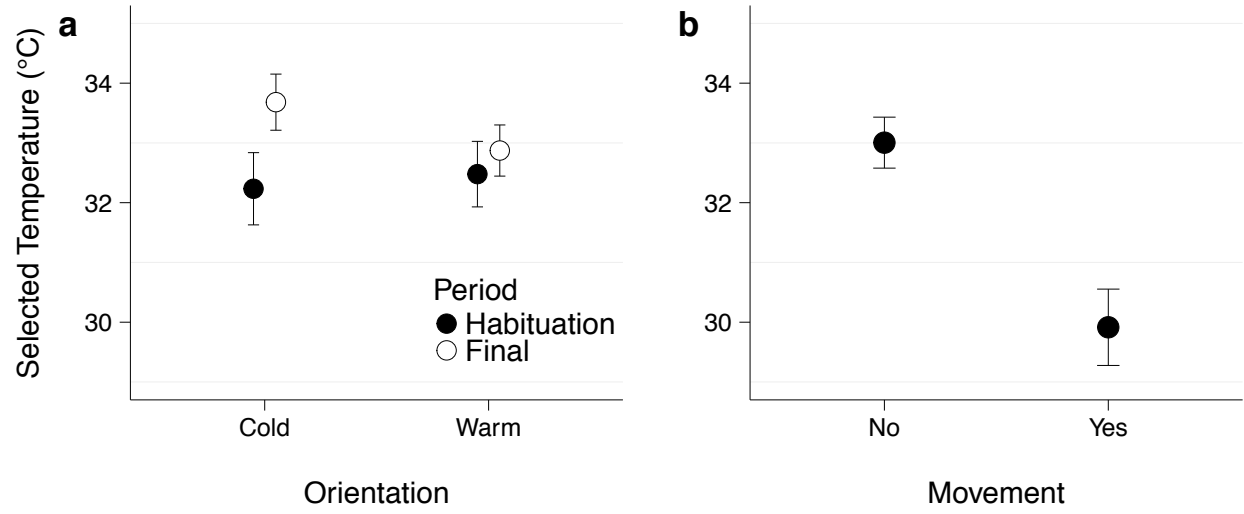
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519 Figure 3.

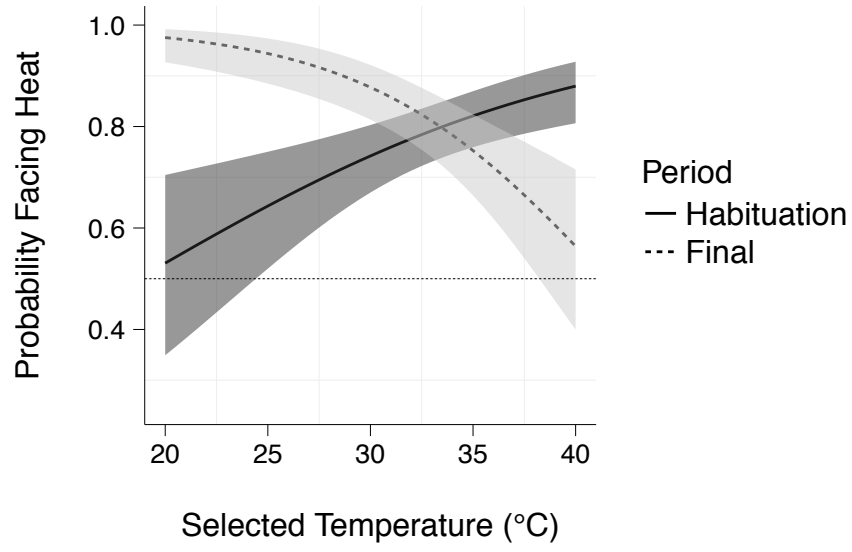
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522 Figure 4.

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525 Figure 5.

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