

1 **Impacts of temperature on performance in two species of South African dwarf**
2 **chameleons, *Bradypodion pumilum* and *B. occidentale*.**

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35 **Abstract**

36 Temperature is an extrinsic factor which influences reptile behavior given that their
37 physiology is dependent on environmental temperature. Understanding the impact of
38 temperature on performance traits is important as it may affect the ecology and fitness of
39 ectothermic animals such as reptiles. Here we examine the temperature dependence of
40 performance in two species of South African Dwarf chameleon (*Bradypodion*), a semi-arid
41 and a mesic adapted species. Ecologically relevant performance traits were tested at
42 different temperatures to evaluate their thermal dependence and temperature-performance
43 breadths for 80% and 90% of each performance trait were calculated. Our results show
44 distinct differences in the thermal dependence of speed versus force-related performance
45 traits. Moreover, our results show that the semi-arid species is better adapted to higher
46 temperatures and as such has better chances to cope with the predicted increases in
47 temperature. The mesic-adapted species seems to be more sensitive to an increase in
48 temperature and could therefore potentially be threatened by predicted future climate
49 change. However, further studies investigating the potential for acclimation in chameleons
50 are needed to better understand how animals may respond to predicted future climate
51 change.

52 Introduction

53 Anthropogenic induced climate change is a primary concern for the continued well-
54 being of our planet. The Intergovernmental Panel on Climate Change (IPCC) predicts that
55 global temperatures will increase by 1 to 3°C over this century. Moreover, an increase in
56 the frequency of heat waves, hot extremes, and droughts is predicted. If organisms are to
57 persist in the face of such rapid climate change they will need to either shift their
58 distribution to areas with appropriate climatic conditions and habitat (Parmesan et al.,
59 2006; Thomas et al., 2004; Wilson et al., 2005), or adapt to changing local conditions
60 (Hughes, 2000; Parmesan et al., 2000). Reptiles and amphibians, being ectotherms, are
61 considered especially vulnerable to climate change as their physiology and function is
62 dependent on variation in environmental temperature. Consequently, climate change could
63 have a substantial impact on the distribution and long-term persistence of reptiles and
64 amphibians, some of them being already in decline (Araújo et al., 2006; Gibbons et al.,
65 2000).

66 South Africa has the third richest lizard biodiversity globally (Myers et al., 2000)
67 and some climate scenarios predict that this region will be particularly impacted by climate
68 change (Beaumont et al., 2011), with an increase of 3-7°C in temperatures and a 20%
69 increase or decrease in precipitation by 2100 (Boko et al., 2007). Previous studies (Houniet
70 et al., 2009; Tolley et al., 2009) have predicted shifts in the available niches of some South
71 African reptiles based on different climate change scenarios. For example, a loss of
72 suitable habitat for *Bradypodion pumilum* by 2080 was predicted whereas the potential
73 suitable habitat for another chameleon (*Bradypodion occidentale*) may increase by 2080.
74 However, these inferences were based only on environmental variables and species
75 presence/absence records. Yet, the potential for species to respond to shifts in climate (e.g.
76 temperature) is unclear and therefore it is crucial to refine predictions about the adaptive
77 potential of species by investigating the thermal dependence of ecologically relevant traits,
78 information which is rarely incorporated into species distribution models.

79 Chameleons, like other reptiles, are poikilotherms and consequently their body
80 temperature is dependent on environmental temperature within the limits of behavioral
81 thermoregulation. As muscle performance is dependent on temperature (Bennett, 1985),
82 performance and behavior are also dependent on environmental temperature. To
83 understand how temperature affects ecologically relevant behaviors, we measured a
84 number of ecologically relevant performance traits under different temperature regimes.
85 Performance is defined here as the ability of an animal to execute an ecologically relevant

86 task, involving the physiological and morphological limits of an individual (Lande and
87 Arnold, 1983). Performance traits are considered as ecologically relevant if they are
88 involved in vital activities like foraging behavior, intraspecific interactions, and defense
89 against predators (Herrel et al. 2011; Herrel et al. 2013; Measey et al. 2009; Measey et al.
90 2011). The determination of the effect of temperature on performance traits allows
91 inferences on the physiological flexibility of animals in response to potential climatic
92 shifts. Relationships between the thermal dependence of isolated muscle and that of
93 performance are thought to be linear (Bennett, 1985) suggesting that the underlying
94 physiology may be driving whole-organism responses to variation in temperature.

95 Our study focuses on two species of South African dwarf chameleons, *Bradypodion*
96 *occidentale* and *B. pumilum*. *Bradypodion pumilum* (Gmelin, 1789) is strictly arboreal and
97 two morphs are recognized; one inhabiting woodland and the other inhabiting heathland
98 (Tilbury et al., 2006; Tolley and Burger, 2007). Here, we used the mesic-adapted forest
99 morph of this species. *Bradypodion occidentale* (Hewitt, 1935) is a semi-terrestrial species
100 that lives in arid regions along the west coast of South Africa (Tilbury et al., 2006; Tolley
101 and Burger, 2007) and is rather xeric-adapted. The specific aim of this study is to
102 determine the temperature-dependence of selected performance traits (bite force, hand and
103 tail force, and sprint speed), for each species. We predict that speed-related performance
104 traits should be highly temperature-dependent (Bennett, 1980), yet, force-related
105 performances should be less temperature-dependent (Bergh and Ekblom, 1979; Binkhorst
106 et al., 1977; Herrel et al., 2007; Petrofsky et al., 1981) thus differentially affecting
107 behavior. These predictions are based on previous results (e.g. Bennett, 1985) which show
108 that tetanic and twitch tension are largely temperature independent, whereas rate-
109 dependent processes show a strong thermal dependence. The thermal dependence of rate-
110 dependent processes is explained by the temperature dependence of the enzymatic
111 reactions allowing contraction and relaxation of muscle, whereas contractile proteins and
112 the number of cross-bridges per sarcomere that can be established, are not temperature-
113 dependent (Bennett, 1985).

114 Secondly, we predicted that these two species would respond differently to different
115 temperatures. To examine this prediction, we evaluate preferred temperatures, temperature
116 optima, and temperature performance breadths at 80% and 90% for each performance trait
117 in each species. Temperature performance breadths correspond to ranges of temperatures
118 over which animals are able to achieve, at least, 80% (T_{pb80}) or 90% (T_{pb90}) of their
119 maximal performance. T_{pb80} is considered as the range of temperatures beyond which

120 animal cannot fulfill vital activities (foraging, escaping predators, etc), and T_{pb90} is
121 considered as the range of ideal temperatures for vital activities. Given the different
122 habitats in which the two species live, we predict that the xeric-adapted *B. occidentale* will
123 be able to perform better at higher temperatures than the mesic-adapted *B. pumilum*.
124 Additionally, we compared temperature breadths of each performance trait with climatic
125 predictions to explore the impact of predicted climatic change scenarios. By providing data
126 on optimal temperatures and physiological flexibility in addition to behavioral
127 thermoregulation we aim to understand how these species could potentially cope with
128 future climate change. As the migration potential of chameleons is considered to be low,
129 physiological flexibility in response to temperature variation is crucial if these animals are
130 to respond to rapid changes in temperature and persist in the face of climate change.

131

132 **Material and methods**

133 Animals

134 *Bradypodion pumilum* and *B. occidentale* live in areas near Cape Town that differ
135 significantly in their climatic and habitat characteristics, as mentioned above (Tolley et al.,
136 2004). Ten Cape dwarf chameleons (*B. pumilum*) were caught in Stellenbosch near the
137 Eerste River, and ten Namaqua dwarf chameleons (*B. occidentale*) were caught at the
138 Tygerberg Nature Reserve, Cape Town, in January. Collecting permits were provided by
139 Cape Nature (permit n°AAA008-00009-0056). One male and nine females were captured
140 for each species. Average weight and average snout-vent length were respectively $9.77 \pm$
141 1.02g and $66.53 \pm 1.87\text{mm}$ for *B. pumilum* and $15.96 \pm 1.44\text{g}$ and $78.87 \pm 1.98\text{mm}$ for *B.*
142 *occidentale*. Seven *B. occidentale* females and one of the *B. pumilum* females were gravid.
143 The gravid *B. pumilum* gave birth during the second week of the trials. For each animal,
144 GPS coordinates were recorded and used to release the animals at the exact place of
145 capture at the end of the experiments. Animals were brought back to the Kirstenbosch
146 Research Centre, in Cape Town, and kept in Exo Terra® Explorarium cages (Hagen Inc.,
147 Montréal, Québec, Canada), furnished with branches, and housed in a climate-controlled
148 chamber set at 25°C. Cages were sprayed profusely with water once daily, before animals
149 were fed. Chameleons were fed two crickets enriched with vitamins each day following the
150 daily experiments. On rest days, the cages were placed outdoors around 16:00, for one or
151 two hours, to provide the animals with natural sunlight. All the experiments were approved
152 by the SANBI Ethics committee (Clearance Certificate n° 003/2011).

153

154 Performance

155 Performance was tested at five different temperatures: 15°C, 20°C, 25°C, 30°C,
156 35°C, for bite force and gripping forces, and one extra temperature was used for
157 measurements of sprint speed: 40°C. Before each trial, a climate-controlled room was set
158 at the desired temperature and chameleons were put in one hour before experiments to
159 equilibrate. After one hour, the room temperature was adjusted if the body (cloacal)
160 temperature of the chameleon was still different from the desired test temperature (+/-
161 1°C). The cloacal temperature of each chameleon was measured before each session using
162 a K-type thermocouple (Digital Thermometer Nicety® DT804A). The order of the test
163 temperatures was randomized using Research Randomizer (<http://www.randomizer.org>)
164 for every performance metric. Maximal performance at each temperature was recorded and
165 used in statistical analysis.

166 Running speed was tested on a padded surface of 1m long that prevented
167 chameleons from slipping. Animals were stimulated to run maximally by clapping hands
168 or tapping on the padded surface right behind them. Lines were drawn each 25 cm and
169 time needed to travel each 25 cm interval was recorded using a stopwatch (see Herrel et al.,
170 2013). Speed was calculated as the fastest speed over 25 cm (speed25) and 1 m
171 (speed100). A run of 1 m was considered to be a session. Three measurement sessions took
172 place at each temperature. After each session, a rest of one hour of rest was given to avoid
173 fatigue. Performance was recorded between 09:00 and 17:00.

174 An isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur,
175 Switzerland) mounted on a purpose-built holder and connected to a Kistler charge
176 amplifier (type 5058 A, Kistler Inc.) was used to measure bite force (in N) (Herrel et al.,
177 1999; Herrel et al., 2001a; Herrel et al., 2001b; Measey et al., 2011). Chameleons were
178 manually stimulated to open their mouth by touching the side of the jaw. When five good
179 bites per chameleon were recorded, the session was ended. Animals were given one hour
180 between sessions and three sessions took place at each temperature.

181 Tail and hand gripping forces were recorded using a piezo-electric platform (Kistler
182 Squirrel force plate, 0.1 N). A narrow dowel (5 mm diameter) was mounted on the force
183 platform to allow the chameleons to grip (Herrel et al., 2012; Herrel et al. 2013). The force
184 platform was connected to a charge amplifier (Kistler Charge Amplifier type 9865) and
185 forces were recorded at 500 Hz, transferred to the computer, and recorded using the
186 Bioware software (Kistler Inc.). Recording session lasted 30 sec for hand forces, and 45
187 sec for tail forces (Herrel et al., 2012). For hand forces trials, animals were held

188 horizontally above the set-up. They voluntarily gripped the dowel with their hands and
189 were pulled in the horizontal direction until they released the dowel. For tail forces trials,
190 chameleons were held vertically above the set-up to promote voluntary tail gripping on the
191 dowel. Next, they were pulled vertically, until they released the dowel. A low-pass filter
192 (10 Hz) was applied to the forces traces to remove high frequency noise and facilitate
193 extraction of peak forces. The largest Z-peaks (for tail forces) and Y-peaks (for hand
194 forces) were measured on the graph and used in the analyses.

195

196 Thermal preferences

197 The thermal preference set-up was composed of a wooden box (1.26 m x 0.73 m x
198 0.38 m) with six lanes. Five lights (Eurolux G230 M-infrared 275W) were used to create a
199 temperature gradient in which chameleons could select their preferred temperature. Room
200 temperature was set at 12°C and the height of the lights was adjusted to obtain a gradient
201 of 56°C to 17°C. Wooden sticks were mounted near the bottom of the corridors to allow
202 chameleons to hold on to and to move back and forth. The temperature gradient within the
203 lanes was recorded every 10 minutes using six iButtons® (Maxim Integrated™, San Jose,
204 California), placed in the first lane, 20 cm apart. Sessions started at 09:00 and lasted until
205 17:00. For each trial, five chameleons were put in separate lanes at 08:00, to habituate to
206 the set-up. Every hour, the body temperature of the chameleons was taken. Chameleons
207 were starved 24 hours before thermal preference trials because feeding state affects
208 temperature preference in lizards (Autumn and De Nardo, 1995; Li et al., 2010).

209

210 Critical temperatures

211 To establish critical temperatures only males and non-gravid females were used
212 given the potential danger of extreme temperatures on embryonic development. As room
213 temperatures were relatively unstable, two iButtons were placed in the room at 20 cm from
214 the test area to record room temperature every minute during the trials.

215 Critical maximal temperature (CT_{max}) was tested in the climate-controlled rooms.
216 First, the room temperature was set at 42°C, based on CT_{max} data (43°C) previously
217 obtained by Burrage (1973) for *Bradypodion sp.*, and a vertical stick was used as a support
218 for chameleons to cling to. Individuals were tested individually until they panted or until
219 they presented signs of hyperactivity and stress (Langlois, 1902); these were considered as
220 signs of discomfort and at this point the trials were ended. After 10 minutes, if none of
221 these signs appeared, chameleons were removed from the room and tested again in a

222 subsequent session in which the same set-up was used, but the room was set at 43°C. The
223 time was recorded when chameleons showed signs of discomfort and the corresponding
224 temperature of the iButton was recorded and considered as the animal's CT_{max}. After
225 trials, animals were returned to their cages at 25°C and allowed to rest for one day.

226 Critical minimum temperatures (CT_{min}) were tested in three cold rooms set at
227 different temperatures: 10, 7 and 5°C (+/- 2°C). Four chameleons of the same species were
228 tested together. They were placed in the 10°C room for 30 minutes. Every 10 minutes, they
229 were put on their back to test their righting response. When animals were no longer able to
230 right themselves the time was recorded and chameleons were returned to their cages. If
231 animals were still able to right them after 30 minutes at 10°C, they were transferred to the
232 8°C room and finally, to the 5°C room.

233 Critical temperatures were obtained using the iButtons. The mean temperature of
234 the two iButtons at the cessation times of the experiment were calculated and used in the
235 analysis as critical temperatures. The critical thermal minimum was $7.1 \pm 2.08^\circ\text{C}$ for *B.*
236 *pumilum* and $7.7 \pm 2.74^\circ\text{C}$ for *B. occidentale*, critical thermal maxima were respectively
237 $41.5 \pm 0.13^\circ\text{C}$ and $42.3 \pm 0.22^\circ\text{C}$. These critical temperatures were then used to establish
238 the temperature-performance curves.

239

240 Analyses

241 For each individual, its maximal performance across all temperatures was
242 considered as 100% and used to calculate the %performance of the maxima at the other
243 temperatures. Performances curves were plotted using the species means of the relative
244 performance at each temperature (in %) and the minimum convex polygon method was
245 used (Van Berkum, 1986) as it avoids discontinuities in the temperature-performance
246 relationships. Critical minimum and maximum temperature means, for each species, were
247 used as 0 performance points. From these curves, temperature optima (T_{opt}), temperature
248 performance breadths for 80% (T_{pb80}) and 90% (T_{pb90}) were obtained (Fig. 1).

249 Statistical analyses were performed using R (2.15.0 version), sample size was N=10
250 for each species. The normality of the data was tested using Shapiro-Wilk's tests; if data
251 were not normally distributed transformations were applied (Log₁₀ or power
252 transformations). Effects of temperature on performance were tested for each species
253 separately using repeated measurement analysis of variance (ANOVA). Differences in
254 temperature performance breadths, between species and between performances traits were
255 tested using multivariate ANOVA for repeated measurements with performance type and

256 species as factors. The interaction between both factors was also included in the model.
257 Interactions were tested using one way ANOVAs. *Post hoc* comparisons between
258 performance traits and temperatures were performed using pairwise t-tests and p-values
259 were adjusted with a sequential Bonferonni correction, for normally distributed data.

260 As the distribution of T_{opt} and $T_{pb80min}$ was not normal even after transformation,
261 Friedman tests were used to compare differences between performance traits for these
262 temperatures, and Wilcoxon signed rank tests were used as *post hoc* comparison tests. A
263 sequential Bonferonni correction was used. Differences between species were tested using
264 Mann-Whitney U tests. Friedman tests were used to test for differences in preferred body
265 temperature between hours, for each species and Mann-Whitney U tests were used to
266 compare mean preferred body temperature between species and preferred body
267 temperature between species for each hour. The significance level of the tests was set at
268 5%.

269

270 **Results**

271 Thermal sensitivity of performance traits

272 Speed was affected by temperature (ANOVA: *B. pumilum*: speed25: $F_{5,45}= 33.92$,
273 $P<0.001$; speed100: $F_{5,45}=33.64$, $P<0.001$; *B. occidentale*: speed25: $F_{5,45}= 24.85$, $P<0.001$;
274 speed100: $F_{5,45}=21.29$, $P<0.001$) with a trend for increasing speed as temperature
275 increases. *Post hoc* comparisons show differences between most of the temperatures, for
276 both species (Table 1, 2). Speed performance curves reach a plateau from 30°C to 40°C.
277 For speed over 25 cm, temperature optima were $35.95\pm 1.74^{\circ}\text{C}$ for *B. pumilum* and
278 $34.00\pm 1.45^{\circ}\text{C}$ for *B. occidentale* (Table 3, Fig. 2). For speed over 1m, temperature optima
279 were $37.05\pm 1.11^{\circ}\text{C}$ for *B. pumilum* and $33.50\pm 1.30^{\circ}\text{C}$ for *B. occidentale* (Table 3, Fig. 2).

280 The grip force data show differences between temperatures for both species
281 (ANOVA: *B. pumilum*: hand force: $F_{4,36}=4.02$, $P=0.008$; tail force: $F_{4,36}=7.09$, $P<0.001$; *B.*
282 *occidentale*: hand force: $F_{4,36}=3.98$, $P=0.008$; tail force: $F_{4,36}=12.62$, $P<0.001$). However,
283 *post hoc* comparisons show no differences between temperatures for hand force, in contrast
284 to tail force which was temperature dependent (Table 2).

285 Temperature dependence of bite force performance was species dependent.
286 Whereas there were no differences between temperatures, for *B. occidentale* (ANOVA:
287 $F_{4,36}= 2.15$, $P=0.094$), in *B. pumilum* bite force was affected by temperature (ANOVA:
288 $F_{4,36}= 25.69$, $P<0.001$) and shows an optimum at 25°C (Fig. 2). This peak at 25°C is

289 present for *B. occidentale* as well but bite force at this temperature is not significantly
290 different from performance levels at other temperatures.

291

292 Comparisons of temperature optima and temperature performance breadths

293 Interactions between performance type and species were significant for $T_{pb80max}$
294 (MANOVA: $F_{4,85}=3.94$, $P=0.005$), $T_{pb90min}$ (MANOVA: $F_{4,85}=2.58$, $P=0.04$) and $T_{pb90max}$
295 (MANOVA: $F_{4,85}=3.45$, $P=0.01$) and thus performance effects were tested within species
296 and species effects within each type of performance.

297

298 *Comparison between species*

299 Temperature optima were not different between species for each performance trait
300 (Table 3, 4). Performance breadths, for speed over 25cm, hand and tail forces are not
301 different between species (Table 3, 4). There were, however, differences between species,
302 for speed over 1 m with *B. pumilum* having higher $T_{pb80min}$ (t-test: $P=0.009$), $T_{pb90min}$
303 (ANOVA: $F_{1,18}=7.16$, $P=0.01$) and $T_{pb90max}$ (ANOVA: $F_{1,18}=4.59$, $P=0.04$) than *B.*
304 *occidentale*. In contrast, for bite force, $T_{pb80max}$ (ANOVA: $F_{1,18}=19.2$, $P<0.001$) and
305 $T_{pb90max}$ (ANOVA: $F_{1,18}=18.3$, $P<0.001$) are higher for *B. occidentale* than for *B. pumilum*
306 (Table 3, 4).

307

308 *Comparison between performances traits*

309 Friedman tests performed for $T_{pb80min}$ and T_{opt} for *B. pumilum* and *B. occidentale*
310 showed differences between performance traits ($df=4$, $P<0.001$ for all tests), and ANOVAs
311 showed differences between performance traits for $T_{pb80max}$ ($F_{4,40}=3.6$, $P=0.01$) and $T_{pb90min}$
312 ($F_{4,40}=3.2$, $P=0.02$) for *B. pumilum*, but not for $T_{pb90max}$ ($F_{4,40}=0.9$, $P=0.44$). There were no
313 differences between $T_{pb80max}$ ($F_{4,40}=0.4$, $P=0.8$), $T_{pb90min}$ ($F_{4,40}=1.4$, $P=0.26$) and $T_{pb90max}$
314 ($F_{4,40}=0.8$, $P=0.52$) between performance traits for *B. occidentale*. Speed related traits have
315 higher temperature optima and temperature performance breadth minima and maxima than
316 force-related traits (Table 3, 5), except $T_{pb90max}$ which is not different between performance
317 traits for both species. Yet, temperature performance breadths are narrower for speed than
318 for force (Fig. 3). There were no differences among different measures of speed, over
319 25cm and 1m, ($P>0.05$ for all comparisons) or among measures of force ($P>0.05$ for most
320 of the comparisons). There were some exceptions, however, with tail forces presenting
321 higher $T_{pb80min}$ for both species and higher $T_{pb90min}$ for *B. occidentale* than hand forces
322 (Table 3, 5). $T_{pb80max}$ of *B. occidentale* was higher for bite force than tail force (Table 3, 5).

323 These statistical results show two main types of temperature-performance profiles: one for
324 speed and another for force-related performance traits.

325

326 Thermal preferences

327 Preferred body temperature did not vary during the day for either species (Friedman
328 tests: *B. pumilum*: $df=8$, $P=0.29$; *B. occidentale*: $df=8$, $P=0.47$) and was not different
329 between species at each hour (Mann-Whitney U tests: $P>0.1$ for all comparison). Yet,
330 mean preferred body temperature of *B. occidentale* ($30.59^{\circ}\text{C}\pm 1.39$) was higher than *B.*
331 *pumilum* ($29.30^{\circ}\text{C}\pm 1.30$) (Mann-Whitney U test: $W=4866.5$, $P=0.02$).

332

333 **Discussion**

334 Temperature optima and temperature of performance breadths for 80 and 90%
335 divide performance traits in two groups: speed-related traits and force related traits.
336 Moreover, temperature dependence of performance accords well to our *a priori*
337 predictions; speed related traits are highly temperature-dependent whereas force related
338 traits are less dependent of temperature. These different performance trait profiles are
339 consistent with studies on the influence of temperature on muscle function (Bennett, 1980;
340 Bergh and Ekblom, 1979; Binkhorst et al., 1977; Petrofsky et al., 1981; Anderson and
341 Deban, 2012) and whole organism performance (Herrel et al., 2007; Anderson and Deban,
342 2010). Furthermore, most of the differences found in the comparison of force related traits
343 involved temperatures under 25°C , whereas temperature independence of force generation
344 by muscle is known to range from 25°C to 40°C (Bergh and Ekblom, 1979; Binkhorst et
345 al., 1977; Petrofsky et al., 1981).

346 The temperature optima of speed-related performance traits are largely above the
347 mean temperature encountered by these species in the Western Cape, with a mean
348 temperature of 22°C during the hottest month (February) and 11.8°C during the coldest
349 month (August) (Schultze, 1997). This suboptimal strategy is common for species with low
350 field active temperatures (Bennett, 1980), yet remains poorly understood. Natural selection
351 may not favor individuals with an optimal running performance given that chameleons rely
352 on cryptic behavior more than fast escape by running when confronted with a predator
353 (Stuart-Fox et al., 2008, Stuart-Fox, *in press*). In contrast, temperature optima of force
354 performance traits are very close to the mean of currently encountered temperatures in the
355 Western Cape. This result is interesting and could explain the non-optimization of speed
356 performance traits. A previous study showed there is no trade-off between speed and

gripping forces in *Bradypodion* (Herrel et al., 2013). Based on these results, we can hypothesize that natural selection favored individuals who present optimal force performance traits, low thermal dependence of these traits, and optimum performance in the range of encountered temperatures. This observation underscores the relative importance of speed and force performance traits in a chameleon's ecology. Running is an anti-predator strategy and allows escape in most animals. Chameleons, however, have developed other strategies such as physical and behavioral camouflage. Consequently, running may be less relevant to the ecology of a chameleon. In support of this hypothesis, our results show that mean temperature encountered by *Bradypodion* is not included within T_{pb80} and T_{pb90} intervals for both speed performance traits whereas it is included in those of force related traits. Huey and Bennett (1987) also found that in nature, reptiles are not always able to run at their maximal speed which could explain the development of defensive behavior involving biting which is less temperature dependent (Herrel et al., 2007). Interestingly, mean preferred body temperature for both species is included within T_{pb80} intervals for each performance trait and consequently, chameleons can perform running, biting and gripping at 80% of their maximal capacities at these preferred temperatures. Chameleons thus preferred a "trade-off temperature" at which they can perform correctly over a wide range of performance traits instead of maximizing a single type of performance. Yet, when we consider the smallest temperature interval that contained at least 50% of the preferred during the preference trials (T_{pref50} ; 30-36°C for *B. pumilum* and 32-38°C for *B. occidentale*) it becomes clear that this interval is right-shifted for both species. For both species, T_{pb90} of speed related traits are included in the T_{pref50} whereas only T_{pb80} of force related traits are included in the T_{pref50} for *B. pumilum* only. As for *B. occidentale*, tail force temperature breadths are not included within the T_{pref50} , but T_{pb80} of hand force and T_{pb90} of bite force are. This suggests that animals spend quite some time at temperatures away from the optima for force generation. Although counter-intuitive at first, data on the thermal dependence of feeding behavior (Van Damme et al., 1991) show that traits such as gut-passage time, energy intake, faecal output and body mass change, are included in the 30-35°C interval, at least for the lizard, *Lacerta vivipara*. This interval is near to the T_{pref50} of *Bradypodion* and may indicate an optimization of digestive physiological processes. Although our study focused on five different performance metrics, the physiology of an animal is clearly complex and data on the temperature-dependence of, for example, digestive physiology would be extremely insightful to better understand temperatures selected by animals.

391 The climatic change scenario A2 for 2071-2100, of Hudson and Jones (2002) for
392 South Africa predicts an increase in temperature of 3.9°C in summer and 4.0°C in winter.
393 Winter temperatures are predicted to fall within the range of temperatures currently
394 encountered by both *Bradypodion* species. Predicted summer mean temperatures (26.5°C)
395 would also fall within the T_{pb80} and T_{pb90} for each force performance trait of both species.
396 However, potential differences in the adaptive potential of the two species appear when we
397 consider predictions for the maximal summer temperature. The maximal summer
398 temperature predicted (32.5°C) will fall outside the temperature performance breadths of
399 tail force for both species, as well as bite force and hand force for *B. pumilum*. In contrast,
400 it is included in hand force T_{pb80} and bite force temperature breadths for *B. occidentale*. If
401 temperatures would indeed reach these levels, chameleons might not be able to achieve
402 adequate gripping performance. As, gripping is likely more pertinent for arboreal species
403 like *B. pumilum*, than terrestrial species like *B. occidentale*, *B. pumilum* will likely be more
404 strongly affected by predicted temperature changes. Bite force is involved in predator
405 defense, and first and foremost, in predation. As such, if temperatures reach their maxima
406 as predicted, *Bradypodion pumilum* might not be able to perform vital activities,
407 *Bradypodion occidentale*, on the other hand, could maintain its activity at normal levels.

408 Interestingly, at the maximal predicted temperature in climate change scenarios,
409 both species would perform at 90% of their maximal running performance suggesting
410 potential beneficial effects of climate change on running performance. Thus, *Bradypodion*
411 could potentially compensate for the negative effect on bite force by running to escape
412 predators, for example. Others strategies such as range shifts are likely important in the
413 case of predicted changes. However, previous studies based on the same climatic scenario
414 showed that the suitable habitat of the most likely threatened species, *B. pumilum*, will be
415 reduced as well (Houniet et al., 2009), whereas the suitable habitat for *B. occidentale* will
416 increase. Moreover, the migration potential of *Bradypodion* seems to be low (K. A. Tolley,
417 unpublished). The results from these previous studies combined with our results and
418 climate change predictions highlight a potential threat on the continued persistence of *B.*
419 *pumilum* by 2100. However, mechanisms like developmental or reversible thermal
420 acclimation could result in a shift in thermal optima of performance traits in this species.
421 Additional studies on effects of temperatures encountered by females during pregnancy on
422 the performance of their offspring are needed. Indeed, developmental thermal acclimation
423 and reversible thermal acclimation could be potential adaptive strategies in the face of
424 climate change but given the results of the few studies on thermal acclimation on lizards,

425 their potential seems to be low. Indeed, thermal acclimation is often limited or lacking
426 entirely (Kaufmann and Bennett, 1989). However, generalists like the chameleons studied
427 here tend to be favored in environments with predictable temperature fluctuations
428 (Gilchrist, 1995) suggesting that these animals may show some potential for acclimation.
429 Clearly, more data are needed to infer the true adaptive potential of *Bradypodion*
430 chameleons in the face of potential climate change.

431 Based on our observations, the predicted increase in temperature should not affect
432 *B. occidentale* performance; this prediction is consistent with the idea that chameleons who
433 radiated in more open habitats developed physiological, morphological and behavioral
434 adaptations to face a higher rate of solar radiation and decrease in water availability
435 (Measey et al., *in press*). Our results showed that *B. occidentale* had a higher preferred
436 body temperature, a shift toward higher temperatures of their temperature performance
437 breadths compared to *B. pumilum*. The CT_{max} of *B. occidentale* was also higher, but given
438 the small sample size ($N = 3$) we were unable to test for statistical differences between
439 species. Although, *B. occidentale* and *B. pumilum* face the same daily maximal
440 temperature, 29.4°C during the hottest day of February in the Western Cape region
441 (Schultze, 1997), the habitat of *B. occidentale* is more open than the habitat of *B. pumilum*,
442 providing more solar radiations and less shadow. Consequently, *B. occidentale* is faced
443 with more extreme conditions as compared to *B. pumilum* which may explain the observed
444 shift towards higher temperatures. It should be noted, however, that most of the *B.*
445 *occidentale* tested in our study were gravid females and it is known that the physiological
446 state of these females may affect their performance (Bauwens and Thoen, 1981; Cooper et
447 al., 1990; Garland, 1985; Qualls and Shine, 1997; Schwarzkopf and Shine, 1992; Shine,
448 1980), behavior (Garland and Losos, 1994; Schwarzkopf and Shine, 1992) and thermal
449 preferences (Braña, 1993; Daut and Andrews, 1993; Le Galliard et al., 2003; Mathies and
450 Andrews, 1997) which can introduce a bias in our results for this species. Furthermore, *B.*
451 *occidentale* tested in our study were collected in the extreme southern part of their
452 distribution area. As such, individuals inhabiting further north may experience different
453 climatic conditions and thus could present differences in their thermal optima, thermal
454 preferences and adaptive potential.

455 In conclusion, our results show that chameleons are adapted to their current habitat
456 with shifts in the preferred and critical thermal maximum temperatures. Moreover, thermal
457 performance curves tend to be right-shifted in the xeric-adapted species. These results may
458 have important implications for the future persistence of these species under predicted

459 climate-change scenarios and may provide input data for refined species distribution
460 models under different climate change scenarios.

461

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467

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Figure legends

Figure 1: Percentage of bite force performance of chameleon n°428 depending on temperature (°C) illustrated using the minimum convex polygon method.

Figure 2: Means (\pm s.e.m; N=10) of relative performance curves depending on temperature for *B. pumilum* (in black) and *B. occidentale* (in grey). Relative performance is in % and temperature in °C. Points are linked using the minimum convex polygon method.

Figure 3: Temperature performance breadths for 80% and 90% of the different tested performance traits for each *Bradypodion* species (N=10 for both species, means \pm s.e.m). Vertical lines represent summer mean predicted temperature and the maximum predicted temperature by the climatic change scenario A2 for 2071-2100 of Hudson and Jones (2002). The dashed line represents the current mean temperature of the hottest month; based on climatic data for the Western Cape (Schulze, 1997).

List of abbreviations

CTmin: Critical thermal minimum

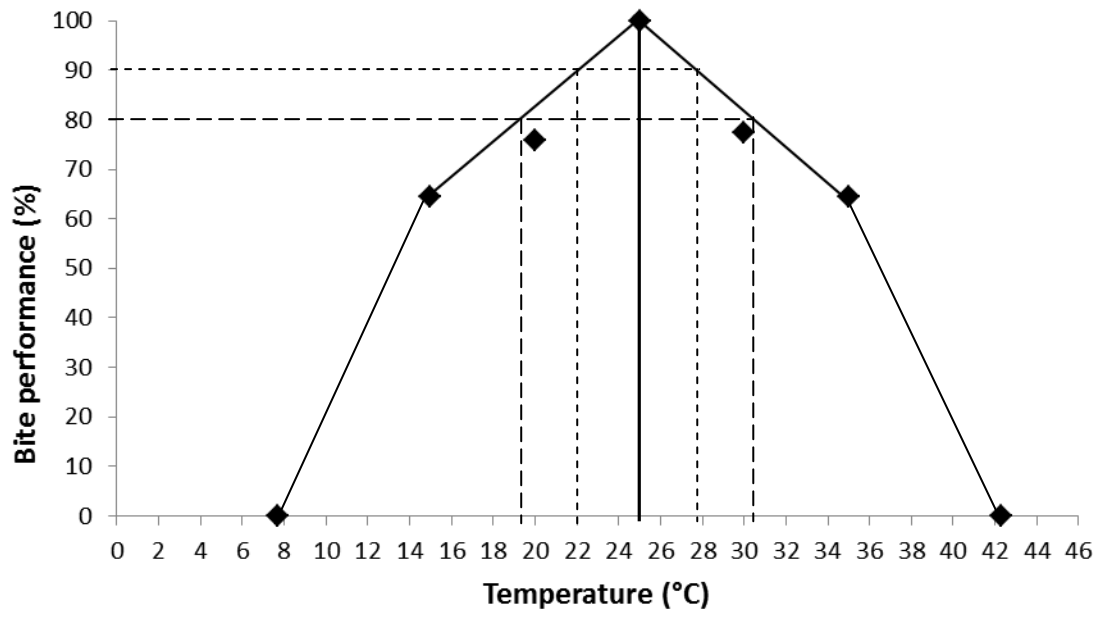
CTmax: Critical thermal maxima

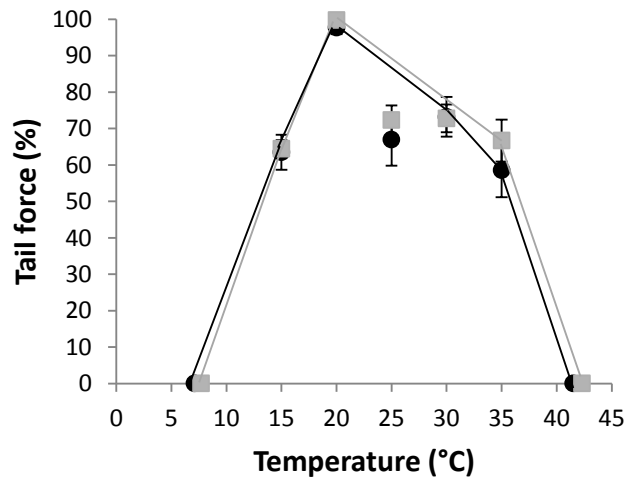
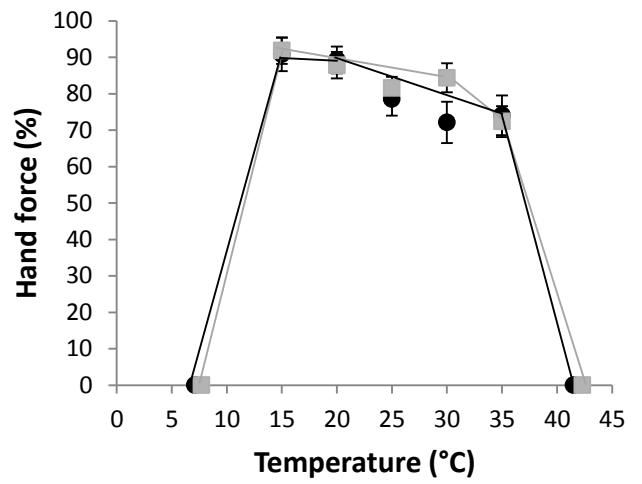
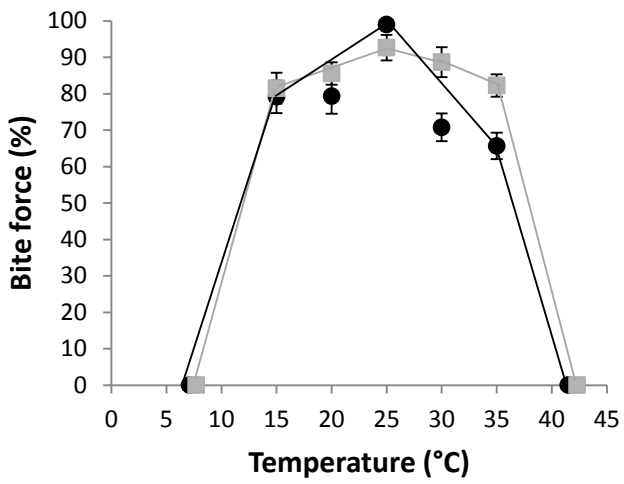
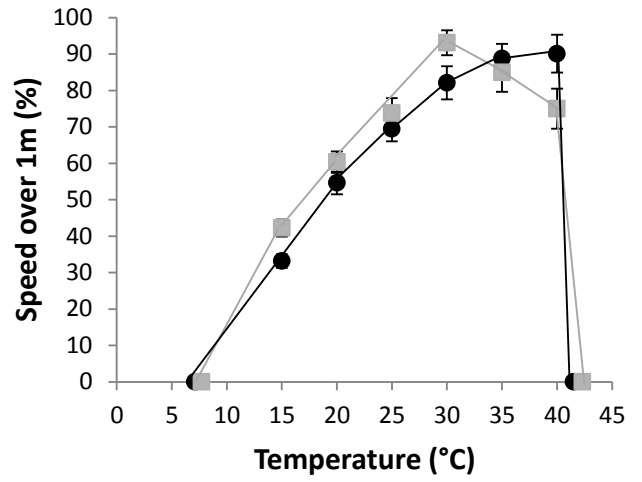
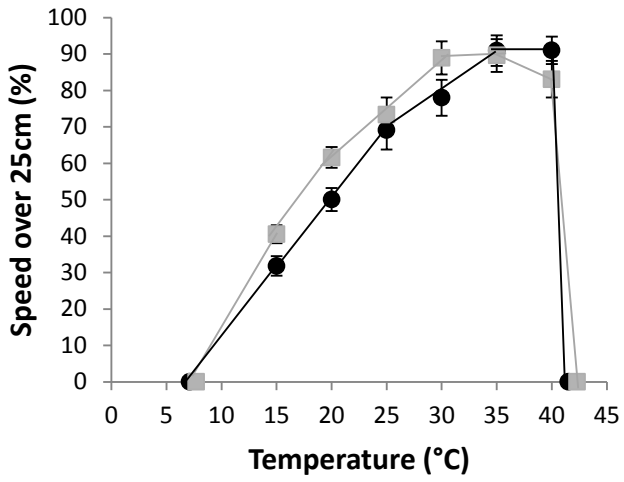
T_{opt}: Temperature optima

T_{pb80}: Temperature performance breadths for 80%

T_{pb90}: Temperature performance breadths for 90%

T_{pref50}: Interval of preferred temperature





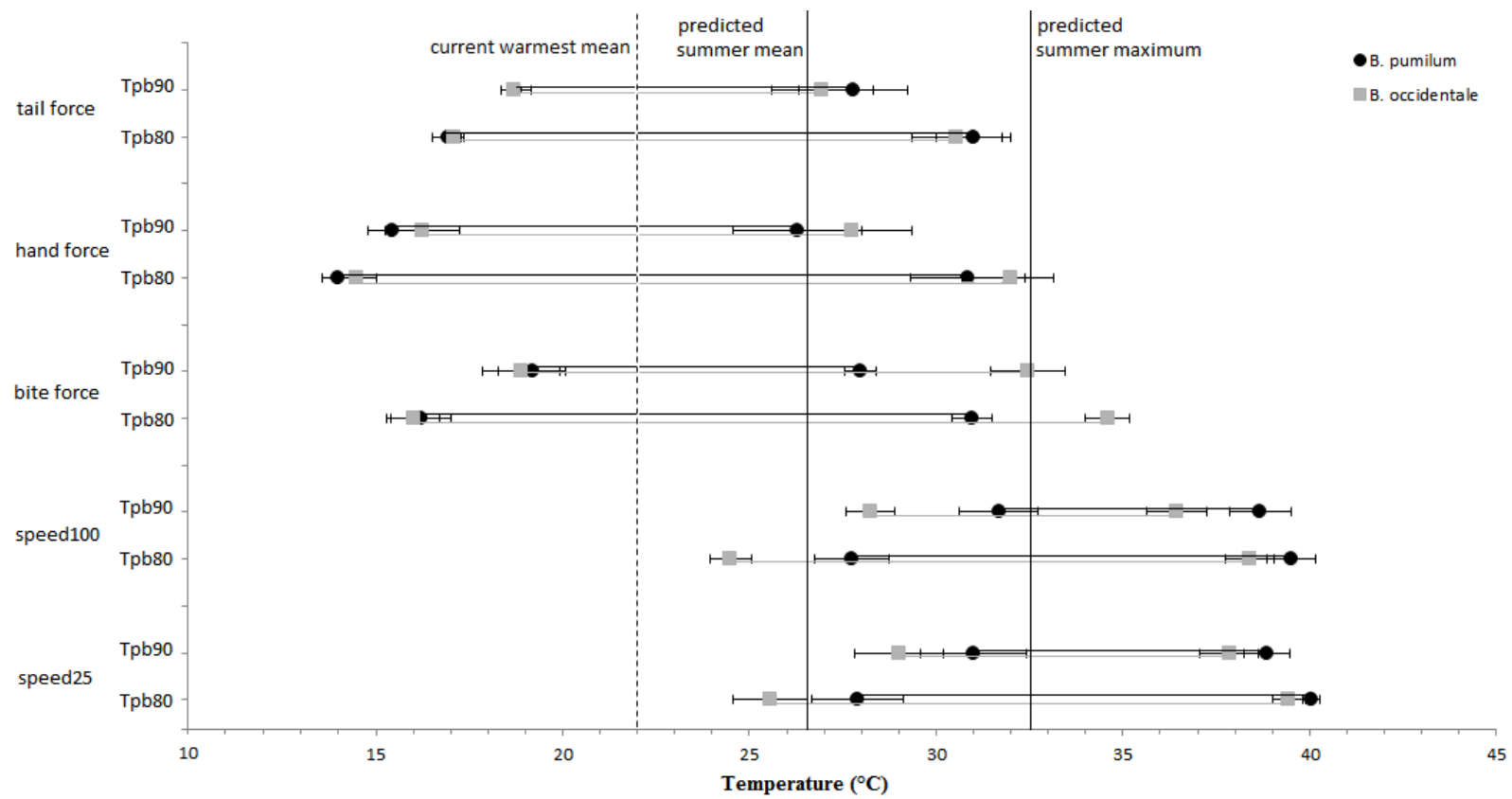


Table 1: Means (\pm s.e.m; N=10 per species) of performance traits for *B. pumilum* and *B. occidentale*, depending on temperature.

Species	Temperature	Speed25	Speed100	Bite force	Hand force	Tail force
<i>B. pumilum</i>	15°C	0.67 \pm 0.04	0.52 \pm 0.03	10.81 \pm 0.98 a	1.62 \pm 0.10	1.17 \pm 0.12 a
	20°C	1.07 \pm 0.04	0.85 \pm 0.05	10.88 \pm 1.04 a	1.64 \pm 0.17	1.80 \pm 0.12
	25°C	1.47 \pm 0.04 a	1.10 \pm 0.07 b	13.33 \pm 0.70	1.43 \pm 0.13	1.27 \pm 0.17 a
	30°C	1.71 \pm 0.14 a	1.29 \pm 0.08 ab	9.67 \pm 0.85 ab	1.27 \pm 0.09	1.38 \pm 0.15 a
	35°C	2.02 \pm 0.15 b	1.42 \pm 0.10 a	9.02 \pm 0.83 b	1.32 \pm 0.09	1.09 \pm 0.17 a
	40°C	2.04 \pm 0.18 ab	1.47 \pm 0.14 a	-	-	-
<i>B. occidentale</i>	15°C	0.60 \pm 0.05	0.50 \pm 0.04	12.15 \pm 0.93	1.23 \pm 0.07	1.21 \pm 0.09 a
	20°C	0.90 \pm 0.05 a	0.70 \pm 0.04 b	12.76 \pm 0.84	1.20 \pm 0.10	1.88 \pm 0.14
	25°C	1.08 \pm 0.08 ac	0.87 \pm 0.07 a	13.80 \pm 1.01	1.09 \pm 0.05	1.36 \pm 0.12 a
	30°C	1.31 \pm 0.09 bc	1.09 \pm 0.07 a	13.39 \pm 1.17	1.14 \pm 0.08	1.35 \pm 0.10 a
	35°C	1.31 \pm 0.09 b	0.99 \pm 0.09 a	12.28 \pm 0.86	0.96 \pm 0.06	1.23 \pm 0.12 a
	40°C	1.22 \pm 0.09 ab	0.87 \pm 0.06 ab	-	-	-

Speed is in $\text{m}\cdot\text{s}^{-1}$ and forces in N. For each species, means without letters are significantly different from others of the same performance trait and means with the same letter are not significantly different from one another.

Table 2: P-values of *post-hoc* comparisons between temperatures, for each performance trait in each species.

Species	Temperatures	Speed25	Speed100	Bite force	Hand force	Tail force
<i>B. pumilum</i>	15-20	<0.001*	<0.001*	0.87	0.96	0.001*
	15-25	<0.001*	<0.001*	0.02*	0.69	1
	15-30	<0.001*	<0.001*	0.09	0.31	0.97
	15-35	<0.001*	<0.001*	0.01*	0.37	1
	20-25	<0.001*	0.005*	0.01*	0.22	0.02*
	20-30	0.002*	<0.001*	0.11	0.24	<0.001*
	20-35	<0.001*	<0.001*	0.006*	0.31	0.01*
	25-30	0.24	0.12	<0.001*	0.69	1
	25-35	0.02*	0.01*	<0.001*	0.87	1
	30-35	0.04*	0.21	0.11	0.87	0.97
	15-40	<0.001*	<0.001*			
	20-40	0.001*	0.006*			
	25-40	0.02*	0.03*			
	30-40	0.24	0.41			
	35-40	0.87	0.61			
<i>B. occidentale</i>	15-20	<0.001*	<0.001*	-	1	<0.001*
	15-25	<0.001*	<0.001*	-	0.26	0.74
	15-30	<0.001*	<0.001*	-	1	0.56
	15-35	<0.001*	<0.001*	-	0.06	1
	20-25	0.052	0.03*	-	0.793	0.002*
	20-30	0.002*	<0.001*	-	1	0.003*
	20-35	<0.001*	0.02*	-	0.19	0.007*
	25-30	0.06	0.059	-	1	1
	25-35	0.01*	0.18	-	0.44	1
	30-35	1	0.66	-	0.21	1
	15-40	<0.001*	0.003*			
	20-40	0.052	0.18			
	25-40	0.73	0.98			
	30-40	1	0.13			
	35-40	1	0.51			

P-values are adjusted using a sequential Bonferonni correction. * indicates a significant difference.

Table 3: Means (\pm s.e.m; N=10) of temperatures optima and temperature performance breadths at 80% and 90% (in °C) for each performance trait, for both species.

		Speed25	Speed100	Bite	Hand force	Tail force
<i>B. pumilum</i>	Topt	35.95 \pm 1.74	37.05 \pm 1.11	23.70 \pm 1.00	17.85 \pm 1.12	22.00 \pm 1.53
	Tpb80 min	27.91 \pm 1.22	<u>27.73\pm0.99</u>	16.20 \pm 0.80	13.97\pm0.40	16.95\pm0.42
	Tpb80 max	40.05 \pm 0.22	39.51 \pm 0.64	<u>30.97\pm0.55</u>	30.85 \pm 1.52	31.00 \pm 1.00
	Tpb90 min	31.00 \pm 1.43	<u>31.68\pm1.05</u>	19.18 \pm 0.91	15.43\pm0.63	18.75\pm0.40
	Tpb90 max	38.86 \pm 0.62	<u>38.69\pm0.81</u>	<u>27.98\pm0.42</u>	26.28 \pm 1.72	27.80 \pm 1.46
<i>B. occidentale</i>	Topt	34.00 \pm 1.45	33.50 \pm 1.30	23.00 \pm 1.53	21.00 \pm 2.45	20.50 \pm 0.50
	Tpb80 min	25.55 \pm 1.00	<u>24.50\pm0.55</u>	16.00 \pm 0.71	14.50\pm0.51	17.10\pm0.18
	Tpb80 max	39.45 \pm 0.44	38.40 \pm 0.64	<u>34.60\pm0.59</u>	32.00 \pm 1.16	30.55\pm1.21
	Tpb90 min	29.00 \pm 1.18	<u>28.25\pm0.64</u>	18.90 \pm 1.04	16.25 \pm 0.99	18.70 \pm 0.08
	Tpb90 max	37.85 \pm 0.79	<u>36.45\pm0.80</u>	<u>32.45\pm1.00</u>	27.75 \pm 1.59	26.95 \pm 1.36

Underlined means: represent differences in temperatures within performance trait between species.

Italic means: means of temperatures of speed related performance traits and force related performance traits are significantly different for both species; excepted $T_{pb90max}$ which are not different between performance traits for each species (italic).

Bold means: temperatures of speed-related performance traits are not different between speed-related traits and most of the temperature variables of force-related performance traits are not significantly different either, exceptions are indicated in bold.

Table 4: P-values of post-hoc comparisons of temperature optima, temperature performance breadth minima and maxima for 80% and 90% between species, within performance traits.

Species	Performance	Topt	Tpb80min	Tpb80max	Tpb90min	Tpb90max
<i>B. pumilum</i> / <i>B. occidentale</i>	speed25	0.41	0.14	0.24	0.29	0.41
	speed100	0.06	0.009*	0.12	0.01*	0.04*
	Bite	0.65	0.93	<0.001*	1	<0.001*
	Hand	0.42	0.89	0.89	0.55	0.75
	Tail	0.54	0.74	0.88	0.9	0.67

* denotes a significant difference.

Table 5: P-values of *post hoc* comparisons of temperature optima, temperature performance breadth minima and maxima for 80% and 90% between performance traits, within species.

Species	<i>Bradypodion pumilum</i>				<i>Bradypodion occidentale</i>			
	Compared performances	Topt	Tpb80min	Tpb80max	Tpb90min	Topt	Tpb80min	Tpb80max
bite/hand	0.01	0.11	1	0.09	0.4	0.28	0.08	0.28
bite/tail	0.28	0.1	1	0.95	0.15	0.12	0.02*	0.84
hand/tail	0.04	0.008*	1	0.01*	1	0.008*	0.14	0.13
speed25/100	0.1	0.72	1	0.95	0.85	0.19	0.06	0.7
hand/speed25	0.005*	0.005*	<0.001*	<0.001*	0.007*	0.005*	<0.001*	<0.001*
hand/speed100	0.005*	0.005*	0.001*	<0.001*	0.01*	0.005*	0.003*	<0.001*
bite/speed25	0.007*	0.005*	<0.001*	<0.001*	0.005*	0.005*	0.001*	<0.001*
bite/speed100	0.005*	0.005*	<0.001*	<0.001*	0.008*	0.005*	0.02*	<0.001*
speed25/tail	0.01*	0.002*	<0.001*	<0.001*	0.005*	0.005*	<0.001*	<0.001*
speed100/tail	0.007*	0.002*	<0.001*	<0.001*	0.004*	0.005*	0.003*	<0.001*

*: significant difference after correction. Dashed line separates comparisons within related traits and between related traits.