RESEARCH ARTICLE

Impact of temperature on performance in two species of South African dwarf chameleon, *Bradypodion pumilum* and *B. occidentale*

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SUMMARY

Temperature is an extrinsic factor that influences reptile behavior because of its impact on reptile physiology. Understanding the impact of temperature on performance traits is important as it may affect the ecology and fitness of ectothermic animals such as reptiles. Here, we examined the temperature dependence of performance in two species of South African dwarf chameleon (*Bradypodion*): one adapted to a semi-arid environment and one to a mesic environment. Ecologically relevant performance traits were tested at different temperatures to evaluate their thermal dependence, and temperature–performance breadths for 80% and 90% of each performance trait were calculated. Our results show distinct differences in the thermal dependence of speed- *versus* force-related performance traits. Moreover, our results show that the semi-arid species is better adapted to higher temperatures and as such has a better chance of coping with the predicted increases in environmental temperature. The mesic area-adapted species seems to be more sensitive to an increase in temperature and could therefore potentially be threatened by the predicted future climate change. However, further studies investigating the potential for acclimation in chameleons are needed to better understand how animals may respond to future climate change.

Key words: behavior, temperature, reptile, climate change, adaptation.

INTRODUCTION

Anthropogenically induced climate change is a primary concern for the continued well-being of our planet. The Intergovernmental Panel on Climate Change (IPCC) predicts that global temperatures will increase by 1–3°C over this century (IPCC, 2007). Moreover, an increase in the frequency of heat waves, extreme heat and droughts is predicted. If organisms are to persist in the face of such rapid climate change they will need to either shift their distribution to areas with appropriate climatic conditions and habitat (Parmesan, 2006; Thomas et al., 2004; Wilson et al., 2005), or adapt to changing local conditions (Hughes, 2000; Parmesan et al., 2000). Reptiles and amphibians, being ectotherms, are considered especially vulnerable to climate change as their physiology and function are dependent on variation in environmental temperature. Consequently, climate change could have a substantial impact on the distribution and long-term persistence of reptiles and amphibians, some species of which are already in decline (Araújo et al., 2006; Gibbon et al., 2000).

South Africa has the third richest lizard biodiversity globally (Myers et al., 2000) and some climate scenarios predict that this region will be markedly impacted by climate change (Beaumont et al., 2011), with an increase of 3–7°C in temperature and a 20% increase or decrease in precipitation by 2100 (Boko et al., 2007). Previous studies (Houniet et al., 2009; Tolley et al., 2009) have predicted shifts in the available niches of some South African reptiles based on different climate change scenarios. For example, a loss of

suitable habitat for *Bradypodion pumilum* by 2080 was predicted whereas the potential suitable habitat for another chameleon, *Bradypodion occidentale*, may increase by 2080. However, these inferences were based only on environmental variables and species presence/absence records. Yet, the potential for species to respond to shifts in climate (e.g. temperature) is unclear and therefore it is crucial to refine predictions about the adaptive potential of species by investigating the thermal dependence of ecologically relevant traits, information that is rarely incorporated into species distribution models.

Chameleons, like other reptiles, are poikilotherms and consequently their body temperature is dependent on environmental temperature within the limits of behavioral thermoregulation. As muscle performance is dependent on temperature (Bennett, 1985), performance and behavior are also dependent on environmental temperature. To understand how temperature affects ecologically relevant behaviors, we measured a number of ecologically relevant performance traits under different temperature regimes. Performance is defined here as the ability of an animal to execute an ecologically relevant task, involving the physiological and morphological limits of an individual (Lande and Arnold, 1983). Performance traits are considered as ecologically relevant if they are involved in vital activities like foraging behavior, intraspecific interactions and defense against predators (Herrel et al., 2011; Herrel et al., 2013; Measey et al., 2009; Measey et al., 2011). The determination of the effect of temperature on performance traits allows inferences on the

physiological flexibility of animals in response to potential climatic shifts. Relationships between the thermal dependence of isolated muscle and that of performance are thought to be linear (Bennett, 1985), suggesting that the underlying physiology may be driving whole-organism responses to variation in temperature.

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

In addition, we predicted that these two species would respond differently to different temperatures. To examine this prediction, we evaluated preferred temperatures, temperature optima and temperature performance breadths at 80% and 90% for each performance trait in each species. Temperature performance breadths correspond to ranges of temperatures over which animals are able to achieve at least 80% (T_{pb80}) or 90% (T_{pb90}) of their maximal performance. T_{pb80} is considered as the range of temperatures beyond which an animal cannot fulfill vital activities (foraging, escaping predators, etc.), and T_{pb90} is considered as the range of ideal temperatures for vital activities. Given the different habitats in which the two species live, we predicted that the xeric environment-adapted *B. occidentale* would be able to perform better at higher temperatures than the mesic area-adapted *B. pumilum*. Additionally, we compared temperature breadths of each performance trait with climatic predictions to explore the impact of predicted climate change scenarios. By providing data on optimal temperatures and physiological flexibility in addition to behavioral thermoregulation, we aimed to understand how these species could potentially cope with future climate change. As the migration potential of chameleons is considered to be low, physiological flexibility in response to temperature variation is crucial if these animals are to respond to rapid changes in temperature and persist in the face of climate change.

MATERIALS AND METHODS
Animals
Bradypodion pumilum and *B. occidentale* live in areas near Cape Town that differ significantly in their climatic and habitat characteristics, as mentioned above (Tolley et al., 2004). Ten Cape dwarf chameleons (*B. pumilum*) were caught in Stellenbosch near the Eerste River, and 10 Namaqua dwarf chameleons (*B. occidentale*) were caught at the Tygerberg Nature Reserve, Cape Town, in January. Collecting permits were provided by Cape Nature (permit no. AAA008-00009-0056). One male and nine females were captured for each species. Mean (±s.e.m.) mass and snout–vent length were, respectively, 9.77±1.02 g and 66.53±1.87 mm for *B. pumilum* and 15.96±1.44 g and 78.87±1.98 mm for *B. occidentale*. Seven *B. occidentale* females and one of the *B. pumilum* females were gravid. The gravid *B. pumilum* gave birth during the second week of the trials. For each animal, GPS coordinates were recorded and used to release the animals at the exact place of capture at the end of the experiments. Animals were brought back to the Kirstenbosch Research Centre, in Cape Town, and kept in Exo Terra Explorarium cages (Hagen, Montréal, QC, Canada), furnished with branches, and housed in a climate-controlled chamber set at 25°C. Cages were sprayed profusely with water once daily before animals were fed. Chameleons were fed two crickets enriched with vitamins each day following the daily experiments. On rest days, the cages were placed outdoors around 16:00h, for 1 or 2h, to provide the animals with natural sunlight. All the experiments were approved by the SANBI Ethics committee (Clearance Certificate no. 003/2011).

Performance
Performance was tested at five different temperatures: 15, 20, 25, 30 and 35°C, for bite force and gripping forces, and one extra temperature (40°C) for measurements of sprint speed. Before each trial, a climate-controlled room was set at the desired temperature; chameleons were placed into the room 1h before experiments to equilibrate. After 1h, the room temperature was adjusted if the body (cloacal) temperature of the chameleon was still different from the desired test temperature (±1°C). The cloacal temperature of each chameleon was measured before each session using a K-type thermocouple (Digital Thermometer Nicety DT804A; Shenzen AOEOM Technology Co., Shenzen, Guangdong, China). The order of the test temperatures was randomized using Research Randomizer (http://www.randomizer.org) for every performance metric. Maximal performance at each temperature was recorded and used in statistical analysis.

Running speed was tested on a 1m long padded surface that prevented chameleons from slipping. Animals were stimulated to run maximally by tapping on the padded surface right behind them or by clapping. Lines were drawn every 25 cm and the time needed to travel each 25 cm interval was recorded using a stopwatch (see Herrel et al., 2013). Speed was calculated as the fastest speed over 25 cm (speed$_{25}$) and 1 m (speed$_{100}$). A run of 1 m was considered to be a session. Three measurement sessions took place at each temperature. After each session, chameleons were allowed to rest for 1h to avoid fatigue. Performance was recorded between 09:00h and 17:00h.

An isometric Kistler force transducer (type 9203, Kistler, Winterthur, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058 A) was used to measure bite force (in N) (Herrel et al., 1999; Herrel et al., 2001a; Herrel et al., 2001b; Measey et al., 2011). Chameleons were manually stimulated to open their mouth by touching the side of the jaw. When five good bites per chameleon were recorded, the session was ended. Animals were given 1h between sessions and three sessions took place at each temperature.

Tail and hand gripping forces were recorded using a piezo-electric platform (Kistler Squirrel force plate, 0.1 N). A narrow dowel (5 mm diameter) was mounted on the force platform to allow the chameleons to grip (Herrel et al., 2012; Herrel et al., 2013). The

force platform was connected to a charge amplifier (Kistler Charge Amplifier type 9865) and forces were recorded at 500 Hz, transferred to the computer, and recorded using Bioware software (Kistler). Recording sessions lasted for 30 s for hand forces and 45 s for tail forces (Herrel et al., 2012). For hand force trials, animals were held horizontally above the set-up. They voluntarily gripped the dowel with their hands and were pulled in the horizontal direction until they released the dowel. For tail force trials, chameleons were held vertically above the set-up to promote voluntary tail gripping on the dowel. Next, they were pulled vertically, until they released the dowel. A low-pass filter (10 Hz) was applied to the force traces to remove high frequency noise and facilitate extraction of peak forces. The largest Z-peaks (for tail forces) and Y-peaks (for hand forces) were measured on the graph and used in the analyses.

Thermal preference

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

Critical temperature

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

Critical maximal temperature (CT_{max}) was tested in the climate-controlled rooms. First, the room temperature was set at 42°C, based on CT_{max} data (43°C) previously obtained (Burrage, 1973) for *Bradypodion* sp., and a vertical stick was used as a support for chameleons to cling to. Individuals were tested individually until they panted or until they presented signs of hyperactivity and stress (Langlois, 1902); these were considered as signs of discomfort and

at this point the trials were ended. After 10 min, if none of these signs appeared, chameleons were removed from the room and tested again in a subsequent session in which the same set-up was used, but the room temperature was set at 43°C. The time was recorded when chameleons showed signs of discomfort and the corresponding temperature of the iButton was recorded and considered as the animal's CT_{max}. After trials, animals were returned to their cages at 25°C and allowed to rest for 1 day.

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

Critical temperatures were obtained using the iButtons. The mean temperature of the two iButtons at the cessation times of the experiment were calculated and used in the analysis as critical temperatures. CT_{min} was 7.1±2.08°C for *B. pumilum* and 7.7±2.74°C for *B. occidentale*; CT_{max} was, respectively, 41.5±0.13 and 42.3±0.22°C. These critical temperatures were then used to establish the temperature–performance curves.

Analyses

For each individual, its maximal performance across all temperatures was considered as 100% and was used to calculate the percentage performance of the maxima at the other temperatures. Performances curves were plotted using the species means (%) of the relative performance at each temperature and the minimum convex polygon method was used (Van Berkum, 1986) as it avoids discontinuities in the temperature–performance relationships. CT_{min} and CT_{max} means, for each species, were used as 0 performance points. From these curves, temperature optima (T_{opt}), T_{pb80} and T_{pb90} were obtained (Fig. 1).

Statistical analyses were performed using R (2.15.0 version); sample size was N=10 for each species. The normality of the data was tested using Shapiro–Wilk's tests; if data were not normally distributed, transformations were applied ($\log_{10}$ or power transformations). Effects of temperature on performance were tested for each species separately using repeated measures ANOVA. Differences in temperature performance breadths, between species and between performance traits, were tested using multivariate ANOVA for repeated measures with performance type and species as factors. The interaction between the two
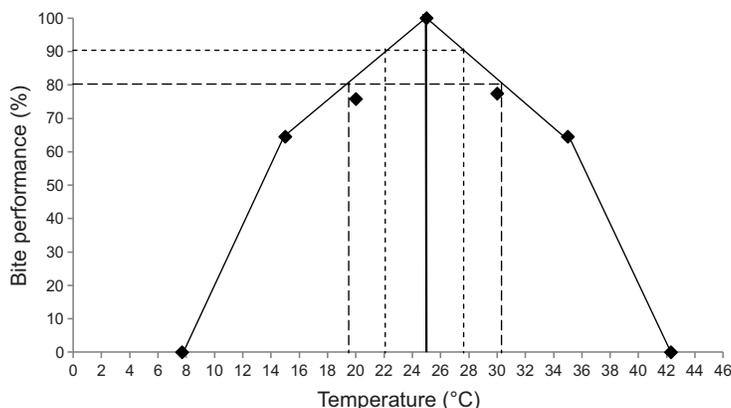

Fig. 1. Dependence of bite force performance on temperature for chameleon no. 428, illustrated using the minimum convex polygon method.

Table 1. Temperature dependence of performance traits for *Bradypodion pumilum* and *B. occidentale*

Species	Temperature	Speed$_{25}$	Speed$_{100}$	Bite force	Hand force	Tail force
B. pumilum	15°C	0.67±0.04	0.52±0.03	10.81±0.98[a]	1.62±0.10	1.17±0.12[a]
	20°C	1.07±0.04	0.85±0.05	10.88±1.04[a]	1.64±0.17	1.80±0.12
	25°C	1.47±0.04[a]	1.10±0.07[b]	13.33±0.70	1.43±0.13	1.27±0.17[a]
	30°C	1.71±0.14[a]	1.29±0.08[a,b]	9.67±0.85[a,b]	1.27±0.09	1.38±0.15[a]
	35°C	2.02±0.15[b]	1.42±0.10[a]	9.02±0.83[b]	1.32±0.09	1.09±0.17[a]
	40°C	2.04±0.18[a,b]	1.47±0.14[a]	–	–	–
B. occidentale	15°C	0.60±0.05	0.50±0.04	12.15±0.93	1.23±0.07	1.21±0.09[a]
	20°C	0.90±0.05[a]	0.70±0.04[b]	12.76±0.84	1.20±0.10	1.88±0.14
	25°C	1.08±0.08[a,c]	0.87±0.07[a]	13.80±1.01	1.09±0.05	1.36±0.12[a]
	30°C	1.31±0.09[b,c]	1.09±0.07[a]	13.39±1.17	1.14±0.08	1.35±0.10[a]
	35°C	1.31±0.09[b]	0.99±0.09[a]	12.28±0.86	0.96±0.06	1.23±0.12[a]
	40°C	1.22±0.09[a,b]	0.87±0.06[a,b]	–	–	–

Data are means ± s.e.m., *N*=10 per species. Speed$_{100}$ and speed$_{25}$ represent the fastest speed over 1 m and 25 cm, respectively, in m s^{-1}; force is in N.
For each species, means without letters are significantly different from others of the same performance trait; means with the same letter are not significantly different from one another.

factors was also included in the model. Interactions were tested using one-way ANOVA. *Post hoc* comparisons between performance traits and temperatures were performed using pairwise *t*-tests and *P*-values were adjusted with a sequential Bonferonni correction for normally distributed data.

As the distribution of T_{opt} and $T_{pb80,min}$ was not normal even after transformation, Friedman tests were used to compare differences between performance traits for these temperatures, and Wilcoxon signed rank tests were used as *post hoc* comparison tests. A sequential Bonferonni correction was used. Differences between species were tested using Mann–Whitney *U*-tests. Friedman tests

were used to test for differences in preferred body temperature between hours, for each species, and Mann–Whitney *U*-tests were used to compare mean preferred body temperature between species and preferred body temperature between species for each hour. The significance level of the tests was set at 5%.

RESULTS
Thermal sensitivity of performance traits
Speed was affected by temperature (ANOVA; *B. pumilum*: speed$_{25}$: $F_{5,45}$=33.92, *P*<0.001; speed$_{100}$: $F_{5,45}$=33.64, *P*<0.001; *B. occidentale*: speed$_{25}$: $F_{5,45}$=24.85, *P*<0.001; speed$_{100}$: $F_{5,45}$=21.29,

Table 2. *P*-values of *post hoc* comparisons of temperature for each performance trait in each species

Species	Temperature (°C)	Speed$_{25}$	Speed$_{100}$	Bite force	Hand force	Tail force
B. pumilum	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			
B. occidentale	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 were adjusted using a sequential Bonferonni correction.
*Significant difference.

Table 3. Temperature optima and temperature performance breadths at 80% and 90% for each performance trait in each species

		Speed25	Speed100	Bite	Hand force	Tail force
B. pumilum	T_{opt}	35.95±1.74	37.05±1.11	23.70±1.00	17.85±1.12	22.00±1.53
	$T_{pb80,min}$	27.91±1.22	27.73±0.99	16.20±0.80	**13.97±0.40**	**16.95±0.42**
	$T_{pb80,max}$	40.05±0.22	39.51±0.64	30.97±0.55	30.85±1.52	31.00±1.00
	$T_{pb90,min}$	31.00±1.43	31.68±1.05	19.18±0.91	**15.43±0.63**	**18.75±0.40**
	$T_{pb90,max}$	*38.86±0.62*	*38.69±0.81*	*27.98±0.42*	*26.28±1.72*	*27.80±1.46*
B. occidentale	T_{opt}	34.00±1.45	33.50±1.30	23.00±1.53	21.00±2.45	20.50±0.50
	$T_{pb80,min}$	25.55±1.00	24.50±0.55	16.00±0.71	**14.50±0.51**	**17.10±0.18**
	$T_{pb80,max}$	39.45±0.44	38.40±0.64	**34.60±0.59**	32.00±1.16	**30.55±1.21**
	$T_{pb90,min}$	29.00±1.18	28.25±0.64	18.90±1.04	16.25±0.99	18.70±0.08
	$T_{pb90,max}$	*37.85±0.79*	*36.45±0.80*	*32.45±1.00*	*27.75±1.59*	*26.95±1.36*

Data are means ± s.e.m., N=10 per species. Temperature performance breadths (T_{pb}) are given in °C; T_{opt}, optimum temperature.
Underlined means represent differences in temperature within performance traits between species.
Means for speed- and force-related performance traits are significantly different for both species, except $T_{pb90,max}$ (italic).
Means for speed-related performance traits are not significantly different; most means for force-related performance traits are not significantly different (exceptions are indicated in bold).

$P<0.001$), with a trend for increasing speed as temperature increased. *Post hoc* comparisons showed differences between most temperatures, for both species (Tables 1, 2). Speed performance curves reached a plateau between 30 and 40°C. For speed$_{25}$, T_{opt} was 35.95±1.74°C for *B. pumilum* and 34.00±1.45°C for *B.*

occidentale (Table 3, Fig. 2). For speed$_{100}$, T_{opt} was 37.05±1.11°C for *B. pumilum* and 33.50±1.30°C for *B. occidentale* (Table 3, Fig. 2).

The grip force data show differences between temperatures for both species (ANOVA; *B. pumilum*: hand force: $F_{4,36}$=4.02, P=0.008; tail force: $F_{4,36}$=7.09, $P<0.001$; *B. occidentale*: hand force:
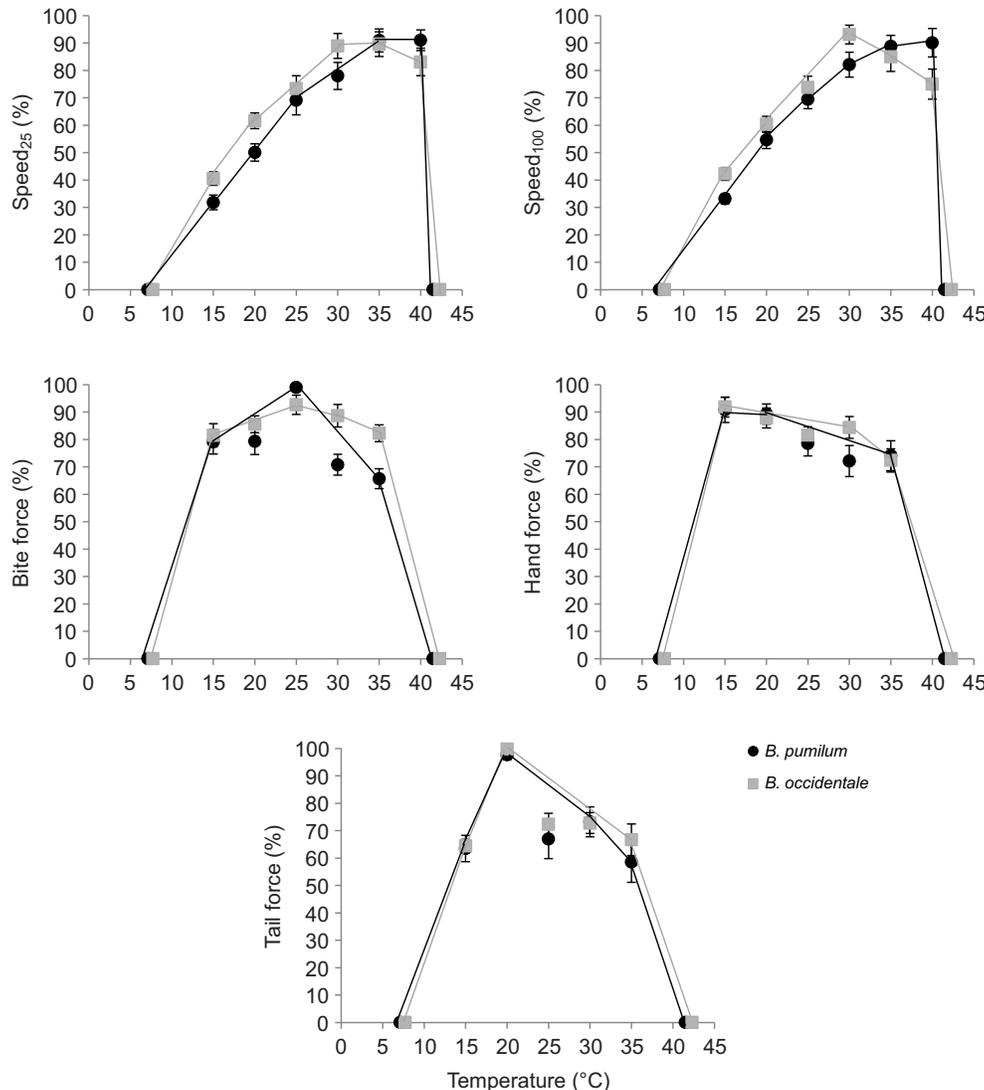

Fig. 2. Means (±s.e.m.; N=10) of relative performance curves depending on temperature for *Bradypodion pumilum* and *B. occidentale*. Points were linked using the minimum convex polygon method. Speed$_{100}$ and speed$_{25}$ represent the fastest speed over 1 m and 25 cm, respectively.

● *B. pumilum*
■ *B. occidentale*

Table 4. *P*-values of *post hoc* comparisons of temperature optima and temperature performance breadths at 80% and 90% between species for each performance trait

Species	Performance	T_{opt}	$T_{pb80,min}$	$T_{pb80,max}$	$T_{pb90,min}$	$T_{pb90,max}$
B. pumilum/B.occidentale	Speed$_{25}$	0.41	0.14	0.24	0.29	0.41
	Speed$_{100}$	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

*Significant difference.

$F_{4,36}$=3.98, *P*=0.008; tail force: $F_{4,36}$=12.62, *P*<0.001). However, *post hoc* comparisons showed no difference between temperatures for hand force, in contrast to tail force, which was temperature dependent (Table 2).

Temperature dependence of bite force performance was species dependent. Whereas there were no differences between temperatures for *B. occidentale* (ANOVA; $F_{4,36}$=2.15, *P*=0.094), in *B. pumilum* bite force was affected by temperature (ANOVA; $F_{4,36}$=25.69, *P*<0.001) and showed an optimum at 25°C (Fig. 2). This peak at 25°C was present for *B. occidentale* as well but bite force at this temperature was not significantly different from performance levels at other temperatures.

Comparison of T_{opt} and T_{pb}
Interactions between performance type and species were significant for $T_{pb80,max}$ (MANOVA; $F_{4,85}$=3.94, *P*=0.005), $T_{pb90,min}$ (MANOVA; $F_{4,85}$=2.58, *P*=0.04) and $T_{pb90,max}$ (MANOVA; $F_{4,85}$=3.45, *P*=0.01) and thus performance effects were tested within species and species effects were tested within each type of performance.

Comparison between species
T_{opt} was not different between species for each performance trait (Tables 3, 4). Performance breadths for speed$_{25}$, and hand and tail forces were not different between species (Tables 3, 4). There were, however, differences between species for speed$_{100}$ with *B. pumilum* having a higher $T_{pb80,min}$ (*t*-test; *P*=0.009), $T_{pb90,min}$ (ANOVA; $F_{1,18}$=7.16, *P*=0.01) and $T_{pb90,max}$ (ANOVA; $F_{1,18}$=4.59, *P*=0.04) than *B. occidentale*. In contrast, for bite force, $T_{pb80,max}$ (ANOVA; $F_{1,18}$=19.2, *P*<0.001) and $T_{pb90,max}$ (ANOVA; $F_{1,18}$=18.3, *P*<0.001) were higher for *B. occidentale* than for *B. pumilum* (Tables 3, 4).

Comparison between performances traits
Friedman tests performed for $T_{pb80,min}$ and T_{opt} for *B. pumilum* and *B. occidentale* showed differences between performance traits

(d.f.=4, *P*<0.001 for all tests), and ANOVA showed differences between performance traits for $T_{pb80,max}$ ($F_{4.40}$=3.6, *P*=0.01) and $T_{pb90,min}$ ($F_{4.40}$=3.2, *P*=0.02) but not for $T_{pb90,max}$ ($F_{4.40}$=0.9, *P*=0.44) for *B. pumilum*. There were no differences between $T_{pb80,max}$ ($F_{4.40}$=0.4, *P*=0.8), $T_{pb90,min}$ ($F_{4.40}$=1.4, *P*=0.26) and $T_{pb90,max}$ ($F_{4.40}$=0.8, *P*=0.52) between performance traits for *B. occidentale*. Speed-related traits showed higher T_{opt} and T_{pb} minima and maxima than force-related traits (Tables 3, 5), except for $T_{pb90,max}$, which was not different between performance traits for both species. Yet, T_{pb} was narrower for speed than for force (Fig. 3). There were no differences among different measures of speed, over 25 cm and 1 m (*P*>0.05 for all comparisons), or among measures of force (*P*>0.05 for most of the comparisons). There were some exceptions, however, with tail forces presenting higher $T_{pb80,min}$ for both species and higher $T_{pb90,min}$ for *B. occidentale* than hand forces (Tables 3, 5). $T_{pb80,max}$ of *B. occidentale* was higher for bite force than for tail force (Tables 3, 5). These statistical results show two main types of temperature–performance profiles: one for speed- and another for force-related performance traits.

Thermal preference
Preferred body temperature did not vary during the day for either species (Friedman tests; *B. pumilum*: d.f.=8, *P*=0.29; *B. occidentale*: d.f.=8, *P*=0.47) and was not different between species at each hour (Mann–Whitney *U*-tests; *P*>0.1 for all comparisons). Yet, mean preferred body temperature of *B. occidentale* (30.59±1.39°C) was higher than that of *B. pumilum* (29.30±1.30°C) (Mann–Whitney *U*-test; *W*=4866.5, *P*=0.02).

DISCUSSION
T_{opt} and T_{pb} at 80% and 90% divide performance traits in two groups: speed-related traits and force-related traits. Moreover, temperature dependence of performance accords well to our *a priori* predictions;

Table 5. *P*-values of *post hoc* comparisons of temperature optima and temperature performance breadths at 80% and 90% for each performance trait in each species

Compared performances	B. pumilum				B. occidentale			
	T_{opt}	$T_{pb80,min}$	$T_{pb80,max}$	$T_{pb90,min}$	T_{opt}	$T_{pb80,min}$	$T_{pb80,max}$	$T_{pb90,min}$
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
Speed$_{25}$/speed$_{100}$	0.1	0.72	1	0.95	0.85	0.19	0.06	0.7
Hand/speed$_{25}$	0.005*	0.005*	<0.001*	<0.001*	0.007*	0.005*	<0.001*	<0.001*
Hand/speed$_{100}$	0.005*	0.005*	0.001*	<0.001*	0.01*	0.005*	0.003*	<0.001*
Bite/speed$_{25}$	0.007*	0.005*	<0.001*	<0.001*	0.005*	0.005*	0.001*	<0.001*
Bite/speed$_{100}$	0.005*	0.005*	<0.001*	<0.001*	0.008*	0.005*	0.02*	<0.001*
Speed$_{25}$/tail	0.01*	0.002*	<0.001*	<0.001*	0.005*	0.005*	<0.001*	<0.001*
Speed$_{100}$/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.
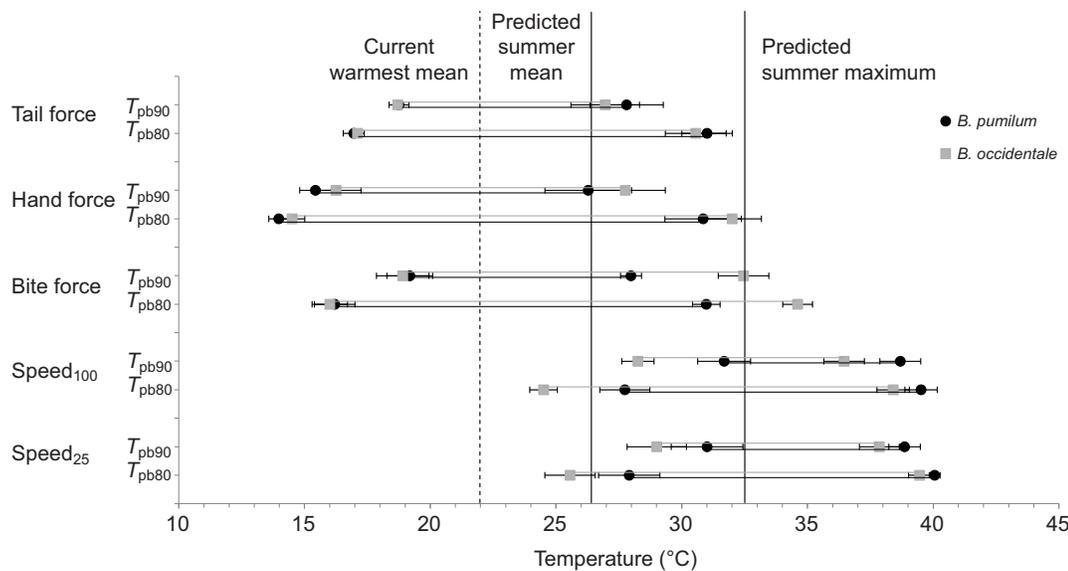
Fig. 3. Temperature performance breadths (T_{pb}) at 80% and 90% of the different tested performance traits for each *Bradypodion* species ($N=10$ for both species, means ± s.e.m.). Vertical lines represent summer mean predicted temperature and the maximum predicted temperature using the climatic change scenario A2 for 2071–2100 of Hudson and Jones (Hudson and Jones, 2002). The dashed vertical line represents the current mean temperature of the hottest month; based on climatic data for the Western Cape (Schulze, 1997).

speed-related traits are highly temperature dependent whereas force-related traits are less dependent on temperature. These different performance trait profiles are consistent with studies on the influence of temperature on muscle function (Bennett, 1980; Bergh and Ekblom, 1979; Binkhorst et al., 1977; Petrofsky et al., 1981; Anderson and Deban, 2012) and whole-organism performance (Herrel et al., 2007; Anderson and Deban, 2010). Furthermore, most of the differences found in the comparison of force-related traits involved temperatures under 25°C, whereas temperature independence of force generation by muscle is known to range from 25 to 40°C (Bergh and Ekblom, 1979; Binkhorst et al., 1977; Petrofsky et al., 1981).

The T_{opt} of speed-related performance traits was largely above the mean temperature encountered by these species in the Western Cape, with a mean temperature of 22°C during the hottest month (February) and 11.8°C during the coldest month (August) (Schulze, 1997). This suboptimal strategy is common for species with low field active temperatures (Bennett, 1980), yet remains poorly understood. Natural selection may not favor individuals with an optimal running performance, given that chameleons rely on cryptic behavior more than fast escape by running when confronted with a predator (Stuart-Fox et al., 2008) (Stuart-Fox, in press). In contrast, T_{opt} of force performance traits was very close to the mean of currently encountered temperatures in the Western Cape. This result is interesting and could explain the non-optimization of speed performance traits. A previous study showed there is no trade-off between speed and gripping force in *Bradypodion* (Herrel et al., 2013). Based on these results, we can hypothesize that natural selection favors 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 the 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 (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 capacity at these preferred temperatures. Chameleons thus prefer 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 temperatures 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. T_{pb90} of speed-related traits is included in the T_{pref50} for both species, whereas just T_{pb80} of force-related traits is included in the T_{pref50} for *B. pumilum* only. 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 the 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, fecal 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.

The climatic change scenario A2 for 2071–2100 of Hudson and Jones (Hudson and Jones, 2002) for South Africa predicts an increase in temperature of 3.9°C in summer and 4.0°C in winter. Winter temperatures are predicted to fall within the range of temperatures currently encountered by both *Bradypodion* species. Predicted summer mean temperatures (26.5°C) would also fall within the T_{pb80} and T_{pb90} for each force performance trait of both species. However, potential differences in the adaptive potential of the two species appear when we consider predictions for the maximal summer temperature. The maximal summer temperature predicted (32.5°C)

will fall outside the temperature performance breadths of tail force for both species, as well as bite force and hand force for *B. pumilum*. In contrast, it is included in hand force T_{pb80} and bite force temperature breadths for *B. occidentale*. If temperatures do indeed reach these levels, chameleons might not be able to achieve adequate gripping performance. As gripping is likely more pertinent for arboreal species like *B. pumilum* than for terrestrial species like *B. occidentale*, *B. pumilum* will likely be more strongly affected by predicted temperature changes. Bite force is involved in predator defense and, first and foremost, in predation. As such, if temperatures reach their maxima as predicted, *B. pumilum* might not be able to perform vital activities; *B. occidentale*, in contrast, could maintain its activity at normal levels.

Interestingly, at the maximum predicted temperature in climate change scenarios, both species would perform at 90% of their maximal running performance, suggesting potential beneficial effects of climate change on running performance. Thus, *Bradypodion* could potentially compensate for the negative effect on bite force by running to escape predators, for example. Other strategies such as range shifts are likely important in the case of predicted changes. However, previous studies based on the same climatic scenario showed that the suitable habitat of the most probable threatened species, *B. pumilum*, will be reduced as well (Houniet et al., 2009), whereas the suitable habitat for *B. occidentale* will increase. Moreover, the migration potential of *Bradypodion* seems to be low (K.A.T., unpublished). The results from these previous studies combined with our results and climate change predictions highlight a potential threat on the continued persistence of *B. pumilum* by 2100. However, mechanisms like developmental or reversible thermal acclimation could result in a shift in thermal optima of performance traits in this species. Additional studies on the effects of temperatures encountered by females during pregnancy on the performance of their offspring are needed. Indeed, developmental thermal acclimation and reversible thermal acclimation could be potential adaptive strategies in the face of climate change, but given the results of the few studies on thermal acclimation in lizards, their potential seems to be low. Indeed, thermal acclimation is often limited or lacking entirely (Kaufmann and Bennett, 1989). However, generalists like the chameleons studied here tend to be favored in environments with predictable temperature fluctuations (Gilchrist, 1995), suggesting that these animals may show some potential for acclimation. Clearly, more data are needed to infer the true adaptive potential of *Bradypodion* chameleons in the face of potential climate change.

Based on our observations, the predicted increase in temperature should not affect *B. occidentale* performance; this prediction is consistent with the idea that chameleons that radiated in more open habitats developed physiological, morphological and behavioral adaptations to face a higher rate of solar radiation and decrease in water availability (Measey et al., in press). Our results show that *B. occidentale* had a higher preferred body temperature, and a shift toward higher temperatures of their temperature performance breadths compared with *B. pumilum*. The CT_{max} of *B. occidentale* was also higher, but given the small sample size (*N*=3) we were unable to test for statistical differences between species. Although *B. occidentale* and *B. pumilum* face the same daily maximal temperature, 29.4°C during the hottest day of February in the Western Cape region (Schulze, 1997), the habitat of *B. occidentale* is more open than the habitat of *B. pumilum*, providing more solar radiation and less shadow. Consequently, *B. occidentale* is faced with more extreme conditions compared with *B. pumilum*, which may explain the observed shift towards

higher temperatures. It should be noted, however, that most of the *B. occidentale* chameleons tested in our study were gravid females and it is known that the physiological state of these females may affect their performance (Bauwens and Thoen, 1981; Cooper et al., 1990; Garland, 1985; Qualls and Shine, 1997; Schwarzkopf and Shine, 1992; Shine, 1980), behavior (Garland and Losos, 1994; Schwarzkopf and Shine, 1992) and thermal preference (Braña, 1993; Daut and Andrews, 1993; Le Galliard et al., 2003; Mathies and Andrews, 1997), which can introduce a bias in our results for this species. Furthermore, *B. occidentale* tested in our study were collected in the extreme southern part of their distribution area. As such, individuals inhabiting more northerly regions may experience different climatic conditions and thus could present differences in their thermal optima, thermal preferences and adaptive potential.

In conclusion, our results show that chameleons are adapted to their current habitat with shifts in the preferred and critical thermal maximum temperatures. Moreover, thermal performance curves tend to be right-shifted in the xeric environment-adapted species. These results may have important implications for the future persistence of these species under predicted climate change scenarios and may provide input data for refined species distribution models under different climate change scenarios.

LIST OF ABBREVIATIONS

CT_{max}	critical thermal maximum
CT_{min}	critical thermal minimum
T_{opt}	temperature optimum
T_{pb80}	temperature performance breadth for 80%
T_{pb90}	temperature performance breadth for 90%
T_{pref50}	interval of preferred temperature

AUTHOR CONTRIBUTIONS

M.S., K.A.T. and A.H. captured animals, performed experiments and analysed data. All authors participated in setting up the study and the writing of the manuscript.

COMPETING INTERESTS

No competing interests declared.

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