

The actively foraging desert lizard *Pedioplanis husabensis* (Husab Sand Lizard) behaviorally optimizes its energetic economy

Ian W. Murray, Andrea Fuller, Hilary M. Lease, Duncan Mitchell, Blair O. Wolf, and Robyn S. Hetem

Abstract: The Husab Sand Lizard (*Pedioplanis husabensis* Berger-Dell'Mour and Mayer, 1989) is a recently described lacertid lizard endemic to a small region in the central Namib Desert. Although this species is of conservation concern, very little is known about how this lizard functions in its environment. We used the doubly labeled water method to measure the field energetics in this lizard species and we report on its foraging behavior. *Pedioplanis husabensis* had summer field metabolic rates ($330 \pm 140 \text{ J}\cdot\text{d}^{-1}$) that were similar to those of other similarly sized sit-and-wait foraging lizards ($360 \text{ J}\cdot\text{d}^{-1}$), but only 43% that of an active foraging lizard of the same mass ($770 \text{ J}\cdot\text{d}^{-1}$), despite using a movement-intensive, active foraging strategy. Additionally, the mean water influx rate ($0.06 \pm 0.03 \text{ mL}\cdot\text{d}^{-1}$) was 67% that of a desert reptile of the same size ($0.09 \text{ mL}\cdot\text{d}^{-1}$). Active body temperatures were significantly lower in summer ($34.3 \pm 1.7 \text{ }^\circ\text{C}$) than they were in autumn ($36.8 \pm 1.6 \text{ }^\circ\text{C}$), and daily activity of lizards increased from $2.6 \pm 0.9 \text{ h}\cdot\text{d}^{-1}$ in summer to $4.3 \pm 1.9 \text{ h}\cdot\text{d}^{-1}$ in autumn. Relative to other species of actively foraging desert lizards, *P. husabensis* has lower energy requirements.

Key words: *Pedioplanis husabensis*, Husab Sand Lizard, Namib Desert, field metabolic rate, doubly labeled water.

Résumé : Le lézard *Pedioplanis husabensis* Berger-Dell'Mour et Mayer, 1989, est un lézard lacertidé récemment décrit du centre du désert du Namib. Si l'espèce est préoccupante sur le plan de la conservation, on en sait très peu sur la manière dont ce lézard fonctionne dans son milieu. Nous avons utilisé la méthode de l'eau doublement marquée pour mesurer l'énergétique de cette espèce de lézard sur le terrain et nous faisons état d'observations sur son comportement d'alimentation. Même s'ils utilisent une stratégie d'alimentation très active, les *P. husabensis* présentaient des taux métaboliques estivaux sur le terrain ($330 \pm 140 \text{ J}\cdot\text{j}^{-1}$) semblables à ceux d'autres lézards de taille semblable employant une approche d'attente aux aguets pour s'alimenter ($360 \text{ J}\cdot\text{j}^{-1}$), mais correspondant à seulement 43 % du taux d'un lézard à quête de nourriture active de même masse ($770 \text{ J}\cdot\text{j}^{-1}$). En outre, le taux d'apport d'eau moyen ($0,06 \pm 0,03 \text{ mL}\cdot\text{j}^{-1}$) équivalait à 67 % de celui d'un reptile de milieu désertique de même taille ($0,09 \text{ mL}\cdot\text{j}^{-1}$). Les températures corporelles en action étaient significativement plus faibles en été ($34,3 \pm 1,7 \text{ }^\circ\text{C}$) qu'en automne ($36,8 \pm 1,6 \text{ }^\circ\text{C}$) et l'activité quotidienne des lézards augmentait de $2,6 \pm 0,9 \text{ h}\cdot\text{j}^{-1}$ l'été à $4,3 \pm 1,9 \text{ h}\cdot\text{j}^{-1}$ l'automne. Comparativement à d'autres espèces de lézards de milieu désertique à quête de nourriture active, *P. husabensis* a des besoins en énergie plus faibles. [Traduit par la Rédaction]

Mots-clés : *Pedioplanis husabensis*, désert du Namib, taux métabolique sur le terrain, eau doublement marquée.

Introduction

Some carnivorous lizard species are sit-and-wait foragers, which expend relatively small amounts of energy during the course of ambushing prey. Others species are active foragers that expend more energy because they actively search their environment for prey, often moving over large home ranges (Anderson and Karasov 1981, 1988; Nagy et al. 1984; Brown and Nagy 2007). Although locomotor and other costs (such as predation) may be higher for active foragers, their higher prey encounter rates often provide an advantage over sit-and-wait foragers (Anderson and Karasov 1981; Nagy et al. 1984). For example, actively foraging lizard species typically have feeding rates 2- to 6-fold higher than do sympatric sit-and-wait lizard species (Anderson and Karasov 1981; Nagy et al. 1984).

Lizards in the family Lacertidae belong to two major clades: one in Eurasia and one occurring primarily in Africa and Arabia (Verwajen and Van Damme 2008). Active foraging is the ancestral state in Lacertidae, but significant variation exists in foraging mode for both the Eurasian and the African radiations of lacertids because some species are categorized as sit-and-wait foragers,

while others are categorized as using a foraging strategy that is intermediate between that of a strict active forager and that of a sit-and-wait forager (Huey and Bennett 1986; Cooper and Whiting 1999; Verwajen and Van Damme 2008). The Husab Sand Lizard (*Pedioplanis husabensis* Berger-Dell'Mour and Mayer, 1989) is a recently described lacertid endemic to a small region of hyperarid desert in the central Namib Desert between the Swakop and the Khan rivers. It is a rupicolous lizard species and is found primarily on light-colored rocky substrates (Berger-Dell'Mour and Mayer 1989; Cunningham et al. 2012). This species currently is of conservation interest as a result of the threat that widespread uranium mining may have upon its limited distribution and habitat (Cunningham et al. 2012), as well as its potential to be negatively impacted by projected changes in climate (Thuiller et al. 2006) including the possible effects of climate change on local patterns of fog and temperature (Haensler et al. 2011). However, its ecology, physiology, and behavior are currently unstudied. Since lizard life history, physiology, and foraging behavior are closely tied to one another and animal metabolism has cascading effects on life history and population ecology (Brown et al. 2004), it is important to

Received 2 April 2014. Accepted 12 August 2014.

I.W. Murray, A. Fuller, H.M. Lease, D. Mitchell, and R.S. Hetem. Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Parktown 2193, South Africa.

B.O. Wolf. Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

Corresponding author: Ian W. Murray (e-mail: Ian.Murray@wits.ac.za).

understand how this species of management concern makes its living and interacts with the physical and biotic environments. For example, many organisms are dependent upon fog-derived moisture in the Namib Desert (Louw 1972; Henschel and Seely 2008) and any changes in the pattern of fog-water deposition could negatively impact organism fitness. Whether or not *P. husabensis* is dependent upon fog-water is currently unknown, and how temperature affects its behavior and ecology is also unknown. Both could have important consequences for better understanding how climate change may impact this lizard's already restricted distribution near the geographic edge of inland penetration of coastal fog events (Berger-Dell'Mour and Mayer 1989; Soderberg 2010). It is scenarios such as these that underlie how closely interconnected physiological ecology is to the field of conservation biology and the decisions that those concerned with the management of imperiled biota must make (e.g., Tracy et al. 2006; Tomlinson et al. 2014). Consequently, in this study we examine the field energetics, morphology, thermal biology, water balance, and foraging behavior of sand lizards by measuring field metabolic rate (FMR), mass and length, water flux rate, body temperature, and foraging activity. Other species of Namib Desert lizards are known to have very low energy use (Nagy et al. 1991, 1993), and likewise, we predict that the physiology and ecology of *P. husabensis* will reflect a similar pattern of optimization reflecting its harsh desert environment.

Materials and methods

Study site

Between December 2012 and May 2013, we studied lizards along the dry bed of the Swakop River (22°42.049'S, 14°54.890'E; 210 m above sea level), approximately 40 km east of Swakopmund, Namibia. FMRs and water flux were measured in December 2012 and January 2013 (austral summer), while lizard foraging behavior was studied during austral summer (January 2013) and autumn (May 2013), allowing us to compare activity during periods with different resource availability (food quality and availability were likely higher in autumn after precipitation), ambient temperatures, and potentially different reproductive activity. The site is warm and arid, with mean monthly maximum air temperatures ranging from 24 to 39 °C and mean monthly minimum air temperatures ranging from 6 to 20 °C. Annual rainfall averaged 25 mm between 1962 and 2011 (Eckardt et al. 2013) according to data from the closest inland long-term weather station (approximately 80 km; Gobabeb Research and Training Centre, Namibia). During our study, summer daily maximum and minimum temperatures (measured on site) averaged 30.9 ± 2.6 and 16.3 ± 1.1 °C (mean (\pm SD) temperature = 22.1 ± 1.6 °C), respectively, and although two mornings were visibly foggy with condensed moisture, no precipitation occurred. No rain had fallen for at least 4 months before we began our study in December. Mean sunrise and sunset times were 0608 and 1938, respectively. Autumn daily maximum and minimum temperatures averaged 35.3 ± 4.3 and 13.0 ± 4.4 °C (mean (\pm SD) temperature = 22.4 ± 5.0 °C), respectively, and the site received 13 mm of precipitation on 30–31 March 2013 (measured on site with a Davis Rain Collector II #7852M (Davis Instruments Corp., Hayward, California, USA) and a Hobo Pendant Event Logger #UA-003-64 (Onset Computer Corporation, Bourne, Massachusetts, USA)). Sunrise and sunset during the autumn study period averaged 0614 and 1721, respectively. Although our study site is considered to be near the inland edge of the coastal fog belt and fog input is likely to be low relative to coastal regions, fog events have not been recorded systematically there (T. Wassenaar, personal communication, 2013).

FMR

Because of the small body size (1.6–4.2 g) of *P. husabensis*, we used the single-sample method of the doubly labeled water (DLW)

technique to estimate FMRs and water fluxes, which allows animals to be bled only once following DLW injection (Webster and Weathers 1989; Nagy et al. 1993; Ochocińska and Taylor 2005). In that variation, an after injection equilibrated blood sample is not taken, but rather, the animals are released immediately after injection with DLW. A blood sample is only taken when the animals are recaptured. In separate groups of animals, a blood sample is taken as soon as isotopes have equilibrated with the body water, which generally is after a few hours for a small lizard. Isotope concentrations in these lizards, scaled for mass, are assumed to be the initial concentrations for the released lizards. The single-sample version of the DLW method has been validated and errors in calculated CO₂ production, on average, are only 4.5% higher than those inherent in the conventional DLW technique (Webster and Weathers 1989, 2000).

We used nooses on telescoping poles to capture 48 lizards, at arbitrary times during their active period. We injected (intraperitoneally) the lizards with 0.015 mL of 98 atom% H₂¹⁸O (Rotem Industries Ltd., Beer Sheva, Israel) and 99.8 atom% D₂O (Isotec, Inc., Miamisburg, Ohio, USA; 4:1 ¹⁸O:D). Eleven of those lizards were retained in shaded cloth bags at ambient temperature (approximately 27 °C), and a blood sample (approximately 50 µL) was taken with a heparinized capillary tube from the infraorbital sinus 4 h after the injection (Congdon et al. 1982; Robinson 1990). We were able to use data from only 5 of the 11 validation animals because of equipment failure (a faulty autosampler septum). The linear regression equations relating initial isotope activities to body mass were highly significant ($r^2 > 0.92$, $P < 0.05$). We recaptured 20 of the other 37 lizards 7–14 d after injection, recorded length and mass, and took a blood sample from the infraorbital sinus. In 3 of the 20 lizards, the blood sample volume was too low to allow further analysis. Additional blood samples were taken from four lizards that had not received DLW injections to establish local background blood ²H (161 ± 3 ppm) and ¹⁸O (2022 ± 7 ppm) concentrations.

All blood samples were flame-sealed in heparinized hematocrit tubes and kept cool until analysis. We cryo-distilled the whole blood samples in glass Pasteur pipettes under vacuum conditions (Nagy 1983) and used a liquid-water isotope analyzer (Los Gatos Research Model DLT-100; Los Gatos Research Inc., Mountain View, California, USA) in the stable isotope laboratory of the Natural Resources and the Environment division of South Africa's Council for Scientific and Industrial Research (CSIR; Pretoria, South Africa) to measure ²H/¹H and ¹⁸O/¹⁶O ratios, employing high-resolution cavity-enhanced direct-absorption spectroscopy. Sets of five samples were bracketed by known laboratory standards, referenced to international standards (Vienna Standard Mean Ocean Water; VSMOW). Twelve determinations of isotope concentration were made from each sample. Data from the first six injections from each sample were eliminated to reduce the risk of memory effects and the last six values were averaged to obtain unknown values. Samples and standards were positioned from least to most enriched in the sampling tray queue based on when the lizards were recaptured.

We calculated total body water volume from the equilibration samples in the retained lizards, as ¹⁸O dilution space, expressed as a percentage of body mass, and used that percentage to estimate total body water volumes for released lizards after recapture under the assumption that the percent body water had not changed during the sampling period (Nagy 1983). Rates of CO₂ production were calculated according to eq. 2 in Nagy (1980), as modified from Lifson and McClintock (1966). Rates of CO₂ production were converted from mL CO₂·g⁻¹·d⁻¹ to J·d⁻¹ using the relationship 25.7 J·(mL CO₂)⁻¹ (RQ = 0.75), which reflects the insectivorous diet typical for an insect-eating lizard (Nagy 1983). Water flux rates were calculated using eqs. 4 and 6 in Nagy and Costa (1980) assuming linear changes in body mass between sampling periods. All work was approved by the Animal Ethics Screening Commit-

tee of the University of the Witwatersrand (clearance certificate No. 2012/50/03).

Morphology and body temperature

We recorded the snout-vent length (SVL; ± 1.0 mm), body mass (± 0.1 g; Acculab (division of Sartorius AG) PP-250B; Sartorius AG, Göttingen, Germany), and sex of the lizards from the isotope study and another 77 *P. husabensis* that we captured during fieldwork. All lizards were marked with permanent marker for easy field identification until the next shed and their toes were clipped for long-term identification. We measured body temperature within seconds after capture, with a type T thermocouple probe and digital thermometer (± 0.2 °C; Omega HH202A; Omega Engineering Inc., Stamford, Connecticut USA) inserted approximately 10 mm into the cloaca and held in position until temperature equilibrated. We did not measure body temperature of lizards that had attempted to escape before capture, or if we could not obtain a measurement within a few seconds. We used the same thermometer and thermocouple to record the substrate and air temperatures (10 mm above the ground) at the locations of all the active sand lizards that we observed, even if we could not capture the lizard.

Focal animal observations

We observed actively foraging lizards for timed sessions and recorded movements per minute (MPM), percent time moving (PTM), and percent prey attacked while moving (PAM) (Cooper and Whiting 2000). Observations were carried out from a distance that allowed lizards to engage in normal behavior (approximately 3 m). Lizards were observed when temperatures were warm enough to permit foraging activity (0930–1227 in summer; 0841–1132 in autumn). Each lizard was observed once only and only those for which we had at least 2 min of data were included in analyses (in most cases, we had at least 10 min of observations per lizard). We observed two lizards that had been injected with DLW at 7 and 9 d after injection. It is unlikely that injections significantly affected lizard behavior, as we routinely observed injected lizards moving and foraging normally immediately after release. We considered lizards to be active on a given day between the times at which the first and last lizards were observed active on that particular day.

Statistical analyses

We used SigmaPlot version 8.0 and Minitab version 16.0 for all analyses and figures. The Anderson–Darling test for normality was used to ensure data were distributed normally. Non-normally distributed data were analyzed using a Mann–Whitney *U* test. We used least-squares linear regressions to analyze DLW data and estimate the initial stable isotope concentrations for recaptured sand lizards. Lizard foraging metrics were compared between months with Student's *t* tests, and lizard morphology was examined with ANCOVA (using SVL as a covariate), least-squares linear regressions, and Student's *t* tests. We estimated lizard body condition by examining the residuals of the regression of body mass on SVL for each sex during summer and autumn (Jakob et al. 1996). Significance was accepted at $\alpha < 0.05$, and values are reported as mean \pm SD.

Results

Morphology

We captured and measured 35 male, 23 female, and 3 lizards whose sex was undetermined in summer (including the initial capture masses for the 48 lizards in the DLW study) and 28 male and 32 female lizards in autumn. Six of the males and five of the females captured in autumn were recaptures from summer; these animals were not included in the analyses of mass and length. There were no significant differences between the SVL of male and female *P. husabensis* in either summer or autumn. Male lizards were significantly heavier than females in both seasons and mean

male and female lizard masses did not significantly change between seasons (Fig. 1). The slopes and intercepts for the relationship between mass and SVL of male lizards did not significantly differ seasonally (ANCOVA; intercepts: $F_{[1,54]} = 0.50$, $P = 0.49$; slopes: $F_{[1,54]} = 0.67$, $P = 0.42$), and there was no difference in body condition (residual index) during summer ($-2.5 \times 10^{-16} \pm 0.31 \times 10^{-16}$) or autumn ($-1.8 \times 10^{-15} \pm 0.22 \times 10^{-15}$) (two-sample Student's *t* test, $t_{[54]} = -0.00$, $P = 0.99$) so the data were combined in one significant regression (mass = $0.15 \times \text{SVL} - 4.88$; $r^2 = 0.79$, $P < 0.001$; Fig. 1). Although the slope for the relationship between female SVL and mass was lower in autumn than in summer (0.08 ± 0.01 vs. 0.12 ± 0.01 , respectively), there was no significant difference in either slope or intercept across seasons (ANCOVA; intercepts: $F_{[1,47]} = 2.63$, $P = 0.11$; slopes: $F_{[1,47]} = 3.37$, $P = 0.07$). Consequently, the data were combined to form one significant relationship (mass = $0.10 \times \text{SVL} - 2.59$; $r^2 = 0.66$, $P < 0.001$; Fig. 1). Female body condition did not vary between summer ($-6.5 \times 10^{-16} \pm 0.25 \times 10^{-16}$) and autumn ($-5.6 \times 10^{-16} \pm 0.20 \times 10^{-16}$) (two-sample Student's *t* test, $t_{[47]} = -0.00$, $P = 0.99$).

FMR and water flux

Females among the 17 recaptured lizards whose blood samples we could analyze for our FMR study ($n = 5$; 2.5 g) were significantly lighter than males ($n = 12$; 3.2 g) (two-sample Student's *t* test, $t_{[14]} = -2.75$, $P = 0.02$), but there was no significant difference between the mass-specific water influx rates (WIR) (two-sample Student's *t* test, $t_{[5]} = -0.66$, $P = 0.54$) and the mass-specific FMR (two-sample Student's *t* test, $t_{[8]} = -1.00$, $P = 0.35$) of males and females, so we combined the data. Mean FMR was $0.17 \text{ mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ and total body water volume averaged $75\% \pm 4\%$ of body mass. The mean WIR was $21.3 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ and the mean water efflux was $24.9 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$. Daily WIR averaged $0.06 \text{ mL} \cdot \text{d}^{-1}$ (Table 1). Lizard FMR was significantly related to lizard body mass ($F_{[1,16]} = 24.74$, $P < 0.001$, $r^2 = 0.62$; Fig. 2). Lizard mass and lizard WIR were not significantly correlated ($F_{[1,16]} = 2.21$, $P > 0.05$, $r^2 = 0.07$).

On average, recaptured lizards maintained their body mass over our study days; mean difference in mass between capture and recapture during the FMR study was not significantly different from zero (Table 1; one-sample Student's *t* test, $t = -1.55$, $P = 0.14$). There was no significant relationship between rate of mass change and lizard FMR (*F* test for regression significance, $F_{[1,16]} = 0.51$, $P = 0.49$) and we use the mean value presented in Table 1 as representative of animals in steady state. However, WIR was significantly correlated with the rate of mass change (*F* test for regression significance, $F_{[1,16]} = 5.34$, $P = 0.035$). Consequently, we regressed the mass-normalized WIR data on the rate of mass change and found that there was a marginally nonsignificant relationship ($F_{[1,16]} = 4.38$, $P = 0.054$). Despite this relationship, we consider the mean WIR as being representative of lizards maintaining constant mass because lizard body mass did not change during the study (Nagy et al. 1991).

Foraging activity

We observed 12 lizards for a total of 109 min during summer and 14 lizards for 151 min during autumn (Table 2). Lizards made about 3.0 movements per minute (MPM) while active, which did not vary between summer and autumn. The percent time moving (PTM) was also consistent for foraging lizards between the two seasons, at approximately 50%. The percent prey attacked while moving (PAM) for foraging lizards in summer was the same as during autumn (90%). Movement bout duration averaged 10.2 ± 2.3 s for lizards in summer and 8.0 ± 2.1 s during autumn. The mean movement duration was significantly shorter during autumn than summer (Table 2). Our population of lizards was active for significantly fewer hours during summer (2.6 ± 0.9 h; $n = 16$ d) than in autumn (4.3 ± 1.9 h; $n = 10$ d) (two-sample Student's *t* test, $t_{[24]} = 3.18$, $P = 0.004$).

Fig. 1. Relationship between snout–vent length (SVL) and mass of female and male Husab Sand Lizards (*Pedioplanis husabensis*). There was no significant difference between male and female SVL and mass between seasons, so male and female data were pooled (male mass = $0.15 \times \text{SVL} - 4.88$ (solid line); $r^2 = 0.79$, $P < 0.001$; female mass = $0.10 \times \text{SVL} - 2.59$ (broken line); $r^2 = 0.66$, $P < 0.001$).

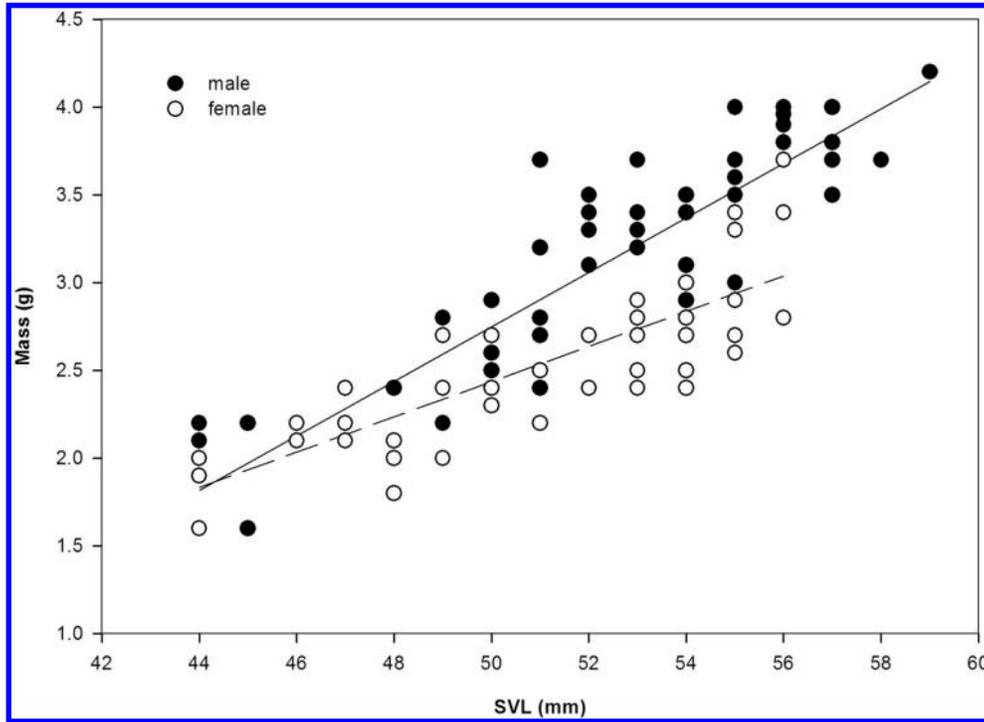


Table 1. Masses, field metabolic rates (FMR), and water influx rates (WIR) for 17 Husab Sand Lizards (*Pedioplanis husabensis*) during austral summer (December–January) along the dry Swakop River in the Namib Desert.

Lizard No.	Sex	Mass			FMR		WIR	
		Initial (g)	Final (g)	Change (%·d ⁻¹)	mL CO ₂ ·g ⁻¹ ·h ⁻¹	J·d ⁻¹	mL·kg ⁻¹ ·d ⁻¹	mL·d ⁻¹
1	F	2.1	2.3	0.7	0.14	190	53.1	0.11
12	F	2.2	2.1	-0.4	0.14	190	32.5	0.07
22	F	2.4	2.0	-1.3	0.14	210	14.5	0.04
24	F	2.9	2.8	-0.4	0.11	190	5.9	0.02
30	F	2.8	3.1	1.5	0.24	410	21.0	0.06
2	M	4.2	4.1	-0.2	0.15	390	28.4	0.12
5	M	4.0	4.4	0.7	0.22	540	22.1	0.09
11	M	2.2	1.9	-0.9	0.14	190	27.3	0.06
13	M	4.0	3.2	-2.2	0.23	560	1.8	0.01
14	M	2.6	2.4	-0.5	0.12	190	21.2	0.06
25	M	2.2	2.2	0.0	0.12	160	34.1	0.08
34	M	2.8	2.4	-1.4	0.16	280	15.6	0.04
35	M	2.5	2.5	0.0	0.23	350	20.2	0.05
40	M	3.5	3.4	-0.3	0.16	340	4.3	0.02
41	M	3.2	3.2	0.0	0.28	560	34.1	0.11
52	M	3.5	3.5	0.0	0.16	340	18.7	0.07
53	M	3.7	3.4	-0.8	0.20	460	8.0	0.03
Mean		3.0	2.9	-0.3	0.17	330	21.3	0.06
SD		0.7	0.7	0.9	0.05	140	13.0	0.03

Body temperature

Mean body temperature of actively foraging *P. husabensis* immediately after capture averaged 34.3 ± 1.7 °C ($n = 61$) during summer, significantly lower than that in autumn, 36.8 ± 1.6 °C ($n = 49$) (two-sample Student's *t* test, $t_{[108]} = 7.75$, $P < 0.001$; Fig. 3A). On average, lizards were captured 4 h and 50 min after sunrise during summer and 4 h and 40 min after sunrise in autumn. The mean substrate temperature taken at lizard capture locations during summer did not differ from that during autumn (Fig. 3B). However, mean 10 mm above ground air temperature at lizard capture

locations during summer was significantly lower than that in autumn (Fig. 3C).

Discussion

Our behavioral data for *P. husabensis* show that they are active foragers. Yet, FMR measurements were lower than expected for an actively foraging lizard and appear incongruous with its seemingly energy-intensive mode of prey acquisition. The FMR of the actively foraging *P. husabensis* ($330 \text{ J} \cdot \text{d}^{-1}$; Table 1) was similar to what would be predicted for a sit-and-wait foraging lizard of the

Fig. 2. Relationship between mass and field metabolic rate (FMR) for Husab Sand Lizards (*Pedioplanis husabensis*) (solid circles), plotted with the associated 95% confidence intervals, relative to the predicted FMR for a comparably sized active ($FMR = 0.294x^{0.875}$, where x is mass (g)) versus sit-and-wait ($FMR = 0.117x^{1.014}$, where x is mass (g)) foraging lizard (regressions from Brown and Nagy 2007). Figure appears in colour on the Web.

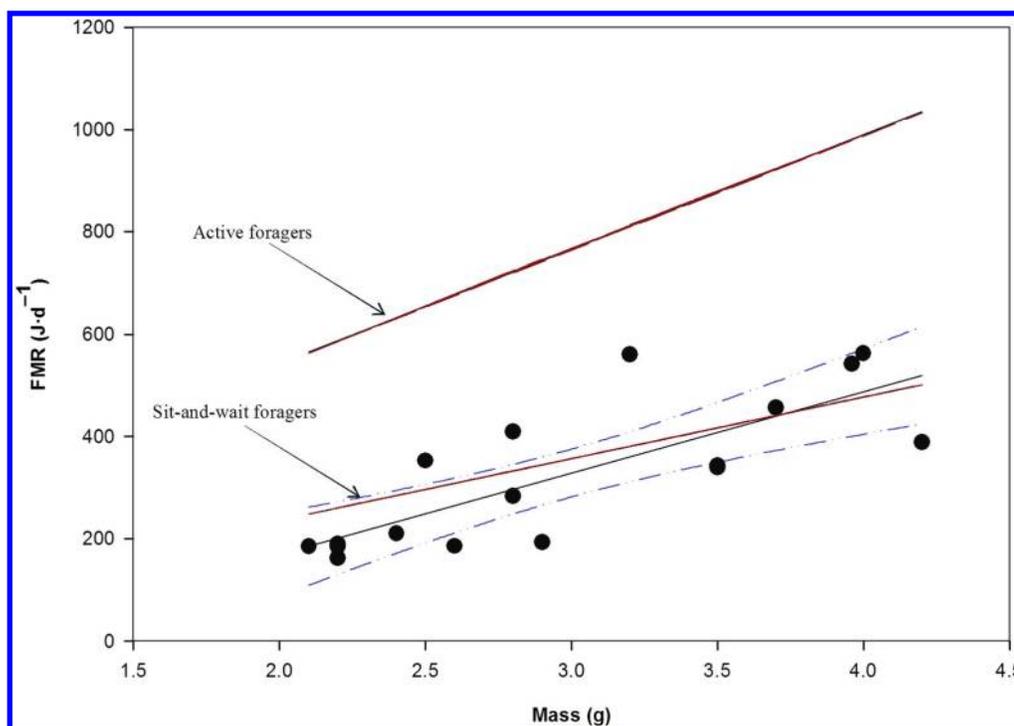


Table 2. The foraging metrics, percent time moving (PTM), movements per minute (MPM), movement duration, the percentage of prey attacked while moving (PAM), and total number of prey attacks for foraging Husab Sand Lizards (*Pedioplanis husabensis*) during austral summer (January; $n = 12$ lizards; 109 min; 31 prey attacks) and autumn (May; $n = 14$ lizards; 151 min; 74 prey attacks) along the dry Swakop River in the Namib Desert.

Season	PTM (%)	MPM	Movement duration (s)	PAM (%)	No. of prey attacks·min ⁻¹
Summer	54±20a	3.1±1.0a	10.2±2.3a	91±15a	0.25±0.2a
Autumn	44±25a	2.9±1.4a	8.0±2.1b	90±22a	0.54±0.5a

Note: Values are mean ± SD. Different letters represent significant differences between months within a column in a two-sample Student's t test at a significance level of $\alpha < 0.05$.

same size (360 J·d⁻¹; eq. 4.4 in Brown and Nagy 2007), but only 43% of the predicted value for an actively foraging lizard (770 J·d⁻¹; eq. 4.6 in Brown and Nagy 2007; Fig. 2). Adjusting for mass, the mean FMR for *P. husabensis* was 0.116 kJ·g^{-0.952}·d⁻¹, which was similar to the mean FMR for sit-and-wait foraging lizards (0.155 ± 0.079 kJ·g^{-0.952}·d⁻¹), but significantly lower (outside of the 95% confidence interval of the predicted value) than the mean value for actively foraging lizards (0.204 ± 0.069 kJ·g^{-0.952}·d⁻¹; Brown and Nagy 2007). We found that the mean WIR for *P. husabensis* (0.06 mL·d⁻¹; Table 1) was 67% of that expected for a desert reptile of the same size (0.09 mL·d⁻¹; Nagy and Peterson 1988), but this value was within the 95% confidence interval for the predicted value (0.05–0.15 mL·d⁻¹), and thus was not significantly different.

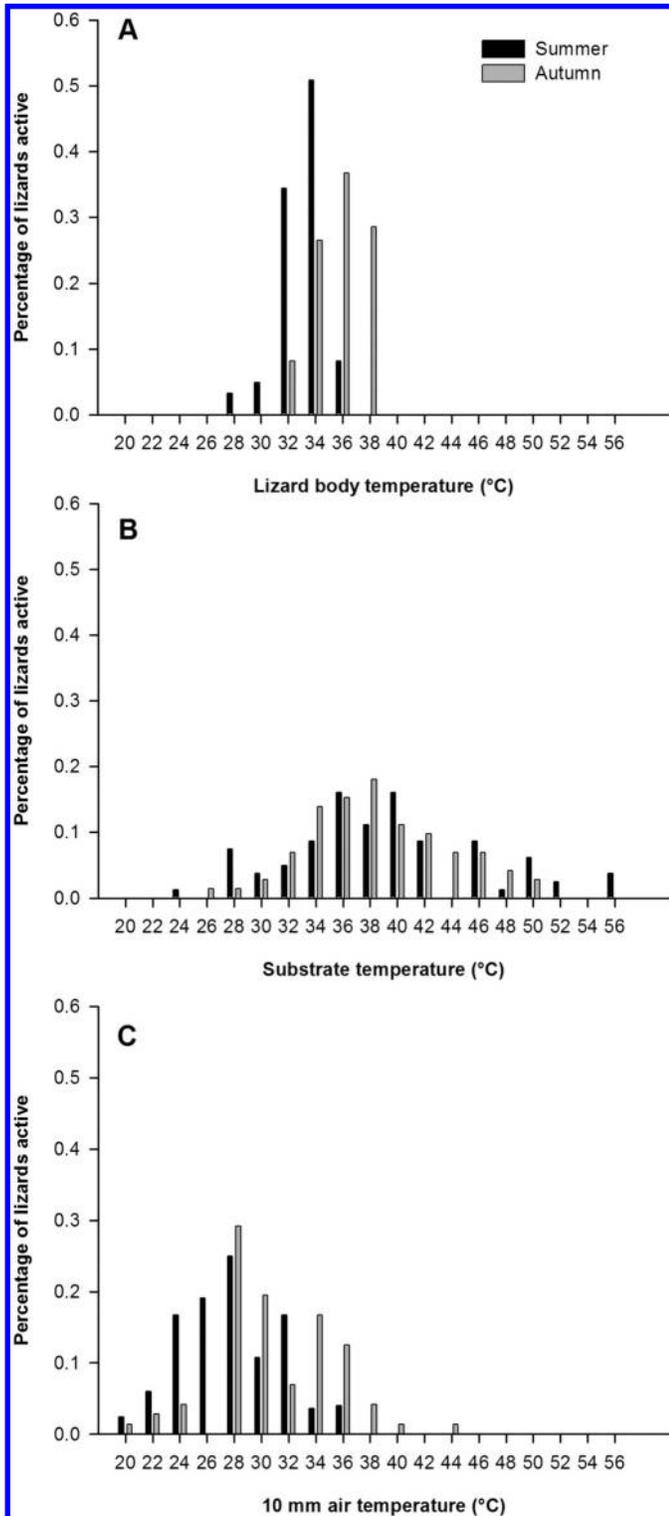
The remarkably low energy turnover of *P. husabensis* relative to other species of actively foraging lizards of the same body size are consistent with adaptations apparent in many desert organisms (Louw and Seely 1982). Although the mechanism(s) used by *P. husabensis* to realize such energy economy are unknown, we argue that this lizard may be able to reduce its energy requirements through seasonal changes in behavior and body temperature.

In the following sections, we discuss the comparative foraging ecology, field energetics, and water balance of *P. husabensis* and other desert lizards.

Foraging activity and field energetics

While actively foraging, *P. husabensis* spent about 50% of their time moving and moved, on average, three times per minute (Table 2), and the mean movement bout duration was statistically longer in summer than in autumn (10 vs. 8 s, respectively), a difference that is unlikely to be biologically significant. We observed many prey capture attempts in total (summer: $n = 31$; autumn: $n = 74$) and *P. husabensis* initiated 90% of all prey capture attempts while moving (PAM; Table 2). Because MPM in other species of foraging lizards may vary considerably, the use of PTM is a more robust metric to distinguish between foraging modes of species (Cooper et al. 2001; Verwajen and Van Damme 2007). Lizards with a PTM >10% are considered to be active foragers (Miles et al. 2007). Southern African lacertids considered to be active foragers typically spend 50%–57% of their foraging periods moving (Pianka 1979), closely matching our data. For example, the actively foraging Western Sand Lizard (*Pedioplanis undata* (Smith, 1838)) and Namaqua Sand Lizard (*Pedioplanis namaquensis* (Duméril and Bibron, 1839)) spend 50% and 54% of their active time moving, respectively, while the sit-and-wait foraging Spotted Sand Lizard (*Pedioplanis lineoocellata* (Duméril and Bibron, 1839)) spends only 5% of its active time moving (Cooper and Whiting 1999). Actively foraging lizards, however, have higher FMRs (>30% higher) compared with sit-and-wait foragers (Brown and Nagy 2007), largely because the energetic costs of movement can be significant (Huey and Slatkin 1976; Hertz et al. 1988). For example, the Bushveld Lizard (*Heliobolus lugubris* (Smith, 1838)), an actively foraging lacertid lizard in the Kalahari Desert, has a metabolic rate 12 times that of its resting metabolic rate while actively foraging; conversely, a sympatric sit-and-wait lacertid, *P. lineoocellata*, expends only 2.8 times its resting metabolic rate (resting metabolic rates do not differ between the species) while ambush foraging (Nagy

Fig. 3. (A) Cloacal temperature, (B) substrate temperature, and (C) air temperatures at 10 mm above ground level taken immediately after capture of 83 (austral summer; December–January) and 72 (autumn; May) Husab Sand Lizards (*Pedioplanis husabensis*) presented as percentage of total lizard captures in bins of 2 °C. Mean substrate temperature did not differ between summer (40.2 ± 7.0 °C) and autumn (39.1 ± 4.4 °C) (two-sample Student's *t* test, $P = 0.254$). Mean 10 mm air temperature was significantly lower in summer (30.6 ± 3.3 °C) than autumn (31.8 ± 4.1 °C) (two-sample Student's *t* test, $P = 0.036$).



et al. 1984). The example above may be an extreme case and a more representative comparison may be the sit-and-wait foraging iguanid Zebra-tailed Lizard (*Callisaurus draconoides* Blainville, 1835), which uses 1.5 times its resting metabolic rate while foraging, compared with the sympatric but active foraging teiid lizard, the Western Whiptail (*Aspidoscelis tigris* (Baird and Girard, 1852)), which uses 3.3 times its resting metabolic rate (Anderson and Karasov 1981).

Given the active foraging strategy of *P. husabensis*, we expected that its FMR would be higher than that of closely related lizard species that are not active foragers—this was not the case, and the available literature estimating FMR or daily energy expenditure of Namib lizards produced similar low values (Table 3). For example, the similarly sized sit-and-wait foraging congeneric species *P. lineoocellata* had a FMR (integrated over a similar length of time) that was 40% higher than that of actively foraging *P. husabensis*, although *P. lineoocellata* occurs in a higher rainfall region in the Kalahari Desert (mean annual rainfall of 170 vs. 25 mm at our study site), and were noted to gain mass during the study (Nagy et al. 1984). Limited activity relative to time spent in refugia is a behavior that should result in reduced FMR and is common to species such as the Desert Plated Lizard (*Gerrhosaurus skoogi* Andersson, 1916) (Mitchell et al. 1987; Nagy et al. 1991), species of Night Lizard (genus *Xantusia* Baird, 1859) (Mautz and Nagy 2000), and the Gila Monster (*Heloderma suspectum* Cope, 1869) (Beck 1990; Beck and Lowe 1994), which all have low energy requirements, and thus may help explain the low FMRs and WIRs observed in *P. husabensis*. During summer, *P. husabensis* were active for only about 50% of the time that they were active for during autumn (2.6 vs. 4.3 h) and we hypothesize that this reduction in surface activity may be a strategy to reduce energy requirements. However, further evaluation of this hypothesis requires knowledge of the body temperatures that *P. husabensis* have in their retreats, as well as estimation of lizard FMR across multiple seasons. High air and surface temperatures did not appear to potentially influence activity as substrate temperatures (Fig. 3B), and air temperatures 10 mm above the substrate at capture sites differed little between seasons (Fig. 3C), suggesting that *P. husabensis* may have been behaviorally thermoregulating during the dry summer to minimize energetic expenditure.

We hypothesize that increased lizard activity during autumn could have been driven by a combination of greater food availability in autumn relative to summer and reproductive activity after the March rainfall event. During March, the study site received two-thirds of its mean annual rainfall (13 mm) in a 2 d period and precipitation pulses in desert systems are well known to produce a spike in primary productivity and arthropod abundance (e.g., Polis et al. 1997). While we did not measure arthropod abundance in either season, lizard prey capture rates were marginally higher in autumn compared with summer (Table 2). Additionally, in autumn 38% (12/32) of the females we captured were gravid or postovipositional compared with a complete lack of reproductive activity in females during summer. These observations suggest that increased energy availability may have promoted high levels of lizard activity and initiated reproduction. However, there was no difference in male and female lizard body condition during summer and autumn, implying that lizards were capable of foraging enough to meet their nonreproductive nutritional requirements during dry periods and of replacing nutrient reserves following reproduction during more favorable periods (11 of the 12 females noted to be reproductive in autumn were postovipositional).

Lizards inactive in retreats are sheltered from high environmental temperatures and presumably would have lower body temperatures relative to when active on the surface. As body temperature increases, resting metabolism also increases resulting in higher maintenance costs and overall FMR. Alligator Lizards (*Elgaria multicarinata* (Blainville, 1835)), for example, exhibit FMRs

Table 3. Relative magnitude of field metabolic rate (FMR) and water influx rate (WIR) for lizard species in the Namib Desert relative to predicted values based on other desert reptiles.

Species	Family	Foraging mode	FMR (% expected)*	WIR (% expected)†	Reference
Anchieta's Dune Lizard, <i>Meroles anchietae</i> (Bocage, 1867)	Lacertidae	Mixed (omnivorous)	75–98	70–80	Robinson 1990
Husab Sand Lizard, <i>Pedioplanis husabensis</i>	Lacertidae	Active	63	67	This study
Namib Day Gecko, <i>Rhoptropus afer</i> Peters, 1869	Gekkonidae	Sit-and-wait	49	63	Nagy et al. 1993
Desert Plated Lizard, <i>Gerrhosaurus skoogi</i>	Gerrhosauridae	Active (herbivorous)	38	80	Nagy et al. 1991

*Predicted FMR ($\text{kJ}\cdot\text{d}^{-1}$) = $0.190x^{0.916}$, where x is mass (g); based on data for all lizards ($n = 48$ species) in Nagy et al. (1999).

†Predicted WIR ($\text{mL}\cdot\text{d}^{-1}$) = $0.038x^{0.792}$, where x is mass (g); based on data for desert reptiles in Nagy and Peterson (1988).

half the expected value of a similarly sized lizard and maintain a mean body temperature of 21 °C, which is 10–15 °C lower than the active body temperature of many other lizards (Kingsbury 1995). *Pedioplanis husabensis* exhibited a mean active body temperature during summer of 34.3 °C, which is a few degrees Celsius lower than the active body temperatures of the closely-related species *P. namaquensis* (37.8 °C) and *P. lineocellata* (36.9 °C) in the Kalahari Desert (Huey et al. 1977). During autumn, however, the active body temperatures of *P. husabensis* were significantly higher (36.8 °C) than those in summer and were closer to those expected for an actively foraging *Pedioplanis* lizard (Fig. 3A). Importantly, we did not measure the FMR of *P. husabensis* during autumn, but we suspect that higher active body temperatures during this season would be correlated with a concomitantly higher FMR. Several lizard species have been shown to reduce FMR in part through a decrease in body temperatures (via behavioral thermoregulation) and the reduction in body temperature by 2.5 °C in summer relative to autumn could translate into substantial energetic savings (Christian et al. 1996a, 1996b, 1999, 2003).

Water flux

Desert environments are known for their scarcity of water and desert animals tend to be conservative in their water usage (Louw and Seely 1982). *Pedioplanis husabensis* appears to be no exception and had an estimated WIR that was 67% of a similarly sized desert lizard. These values coupled with its low FMR gave it a water economy index (WEI) of 0.18 $\text{mL H}_2\text{O}\cdot\text{kJ}^{-1}$. The WEI is a metric that compares the millilitres of water used per kilojoules of energy expended (Nagy and Peterson 1988). Carnivorous reptiles that do not drink water are expected to have a WEI between 0.075 and 0.175 $\text{mL H}_2\text{O}\cdot\text{kJ}^{-1}$ (Nagy and Peterson 1988). *Pedioplanis husabensis* in this study had a WEI on the upper limit of the expected range for a desert reptile that was not drinking water, suggesting that *P. husabensis* could be independent of the condensing fog on which other Namib animals are known to depend (Henschel and Seely 2008). Our observations support this conjecture because on the two foggy mornings during our study, the lizards were not active until several hours after the sun had evaporated the fog.

One metric of lizard performance that is influenced by foraging mode and drives many aspects of lizard ecology is prey encounter frequencies and resultant feeding rates. We can compare lizard feeding rates calculated both from our estimates of FMR and WIR, using the mean water content and energetic yield for the diet of insectivorous lizards and the assumption that lizards were not drinking free water. We assume that arthropod prey had a mean water content of 70% (2.34 $\text{mL H}_2\text{O}\cdot(\text{g dry mass})^{-1}$) and that 75% of the available energy (23 $\text{kJ}\cdot(\text{g dry mass})^{-1}$) in an arthropod diet is metabolizable by the lizards (Edney 1977; Harwood 1979; Anderson and Karasov 1988; Karasov and Anderson 1998). We additionally assume that metabolic water production occurred at a rate of 0.026 $\text{mL}\cdot\text{kJ}^{-1}$ (Schmidt-Nielsen 1991). Using these values, we calculate that the mean *P. husabensis* FMR of 330 $\text{J}\cdot\text{d}^{-1}$ had a food intake rate of 0.019 g dry mass $\cdot\text{d}^{-1}$ and a WIR of 0.053 $\text{mL}\cdot\text{d}^{-1}$. Those values agree well with the values that we derived from our measurements of isotope turnover (0.059 $\text{mL}\cdot\text{d}^{-1}$ and 0.022 g dry mass $\cdot\text{d}^{-1}$).

The calculated feeding rate was 63% of the predicted feeding rate of 0.030 g dry mass $\cdot\text{d}^{-1}$ for a similarly sized insectivorous iguanid lizard (eq. 40 in Nagy 1987).

In arid environments, termites often represent a significant proportion of total arthropod biomass and are important drivers of plant litter removal and nutrient cycling (Polis 1991; Zaady et al. 2003). Termites are an abundant and valuable source of nutrients and water in desert food webs and are eaten by an array of consumers from frogs to raptors. The mean southern African termite worker contains 74% water (12 species; Ferrar 1982) and the mean energetic yield from two species of southern African termite is 17.8 $\text{kJ}\cdot(\text{g dry mass})^{-1}$ (Nagy et al. 1984; Williams et al. 1997). Widely foraging lizards, by virtue of their foraging strategy, should encounter and include in their diets a relatively high proportion of sedentary, clumped arthropod resources such as termites, and this pattern may be seen in desert lizard communities in Africa, North America, and Australia (Huey and Pianka 1981). Indeed, most species of widely foraging, southern African lacertid lizards rely heavily on termites (Huey and Pianka 1981; van der Meer et al. 2010) and we believe that *P. husabensis* also feed extensively on termites. We often saw *P. husabensis* excavating shallow termite worker tunnels under silt, or probing into the mud-sheeting of worker termites among dead wood. Given the mean FMR of 330 $\text{J}\cdot\text{d}^{-1}$ and assuming an assimilation efficiency of 0.75 (Harwood 1979), *P. husabensis* would have to eat 0.09 g (live mass) of termites, or 29 individual termites (mean live mass South African termites = 3.09 mg; 12 species; Ferrar 1982) to maintain energy balance. Accounting for metabolic water production, many termites would yield 0.078 $\text{mL}\cdot\text{d}^{-1}$ of water, which is significantly more than the water turnover that we estimated, and we believe this means that the lizards must include a significant proportion of arthropods with lower water content in their diet at least during summer.

This represents the first study that sketches activity patterns, foraging ecology, field energetics, and water balance of *P. husabensis*. The low FMRs that we documented in this actively foraging lizard together with data available in the literature suggest that a frugal energy economy may be widespread among lizards in the Namib Desert. The Namib Desert is one of the oldest deserts in the world. At approximately 40 million years (van Zinderen Bakker 1975; Ward et al. 1983), it is ancient in contrast with the relatively young Australian (1 million years for the sandy Simpson Desert; 2–4 million years for stony deserts; Fujioka et al. 2005, 2009) and North American (approximately 1 million years; Axelrod 1979) deserts, the lizard communities of which have been comparatively well studied. It is thus perhaps not surprising that lizard species in the Namib Desert have had ample time to develop mechanisms to maximize energy economy by molding their behavior, life history, and physiology to best suit the extreme environment that they occupy. We posit that the relatively low active body temperatures and reduced periods of daily activity factor importantly into the low energy expenditure of *P. husabensis* during summer, although further studies on the energetics of this species during periods of the year when lizards operate with higher active body temperatures (e.g., during autumn) are neces-

sary to better compare the energy requirements of *P. husabensis* to other lizard species. An understanding of how organisms budget their energy, water, and thermal requirements is the key to successfully modeling population-wide responses to future climate-change scenarios and is critical to design effective conservation activities such as assisted colonization and preservation of suitable habitat given local climate-change models (Kearney and Porter 2004; Bartelt et al. 2010; Mitchell et al. 2012; Tomlinson et al. 2014). Given that *P. husabensis* appears to manage its energetic requirements through behavioral strategies such as minimizing surface activity and reducing active body temperature, an understanding of the thermal characteristics of lizard retreats, as well as understanding how these retreats are distributed on the landscape, could prove useful for the identification of important lizard habitat. Delineating the thermal ecology of this species, including the thermal characteristics of lizard nest sites, is also crucial to understanding how projected climate change may impact the distribution of *P. husabensis* (Mitchell et al. 2008; Angilletta et al. 2009).

Acknowledgements

We thank M. Seely and T. Wassenaar of the Gobabeb Research and Training Centre in Namibia for critical research support and logistical help. We also thank S. Woodborne (iThemba Laboratories) and G. Hall (University of Pretoria) for assistance in the preparation and analysis of isotope samples. We thank J. Clarke for assistance in the field. We are grateful to Antoinette and W. Skutsch for accommodation at Hildenhof. We thank S. Tomlinson and an anonymous reviewer for their valuable comments. We acknowledge and thank Namibia's Ministry of Environment and Tourism for permission to work in the Namib Naukluft Park (research permit 1744/2012). Funding was provided by an individual Faculty Research Funding (FRF) grant to I.W.M. from the University of the Witwatersrand's Faculty of Health Sciences and a National Research Foundation (NRF) International Research Grant (Namibia-South Africa Research Cooperation Programme grant No. 89140) to D.M. The Claude Leon Foundation is thanked by I.W.M. for financial support.

References

- Anderson, R.A., and Karasov, W.H. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia*, **49**(1): 67–72. doi:10.1007/BF00376899.
- Anderson, R.A., and Karasov, W.H. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecol. Monogr.* **58**(2): 79–110. doi:10.2307/1942462.
- Angilletta, M.J., Jr., Sears, M.W., and Pringle, R.M. 2009. Spatial dynamics of nesting behavior: lizards shift microhabitats to construct nests with beneficial thermal properties. *Ecology*, **90**(10): 2933–2939. doi:10.1890/08-2224.1. PMID:19886501.
- Axelrod, D.I. 1979. Age and origin of Sonoran Desert vegetation. California Academy of Sciences, San Francisco.
- Bartelt, P.E., Klaver, R.W., and Porter, W.P. 2010. Modeling amphibian energetics, habitat suitability, and movements of western toads, *Anaxyrus (=Bufo) boreas*, across present and future landscapes. *Ecol. Model.* **221**(22): 2675–2686. doi:10.1016/j.ecolmodel.2010.07.009.
- Beck, D.D. 1990. Ecology and behavior of the Gila monster in southwestern Utah. *J. Herpetol.* **24**(1): 54–68. doi:10.2307/1564290.
- Beck, D.D., and Lowe, C.H. 1994. Resting metabolism of helodermatid lizards: allometric and ecological relationships. *J. Comp. Physiol. B*, **164**(2): 124–129. doi:10.1007/BF00301653.
- Berger-Dell'Mour, H.A.E., and Mayer, W. 1989. On the parapatric existence of two species of the *Pedioplanis undata* group (Reptilia: Sauria: Lacertidae) in the central Namib desert (Southwest Africa) with description of the new species *Pedioplanis husabensis*. *Herpetozoa*, **1**(3–4): 83–95.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. 2004. Toward a metabolic theory of ecology. *Ecology*, **85**(7): 1771–1789. doi:10.1890/03-9000.
- Brown, T.K., and Nagy, K.A. 2007. Lizard energetics and the sit-and-wait vs. wide-foraging paradigm. In *Lizard ecology*. Edited by S.M. Reilly, L.B. McBrayer, and D.B. Miles. Cambridge University Press, Cambridge. pp. 120–140.
- Christian, K., Green, B., Bedford, G., and Newgrain, K. 1996a. Seasonal metabolism of a small, arboreal monitor lizard, *Varanus scalaris*, in tropical Australia. *J. Zool. (Lond.)*, **240**(2): 383–396. doi:10.1111/j.1469-7998.1996.tb05293.x.
- Christian, K.A., Griffiths, A.D., and Bedford, G.S. 1996b. Physiological ecology of fruitneck lizards in a seasonal tropical environment. *Oecologia*, **106**(1): 49–56.
- Christian, K., Bedford, G., Green, B., Griffiths, A., Newgrain, K., and Schultz, T. 1999. Physiological ecology of a tropical dragon, *Lophognathus temporalis*. *Aust. J. Ecol.* **24**: 171–181. doi:10.1046/j.1442-9993.1999.241960.x.
- Christian, K.A., Webb, J.K., and Schultz, T.J. 2003. Energetics of bluetongue lizards (*Tiliqua scincoides*) in a seasonal tropical environment. *Oecologia*, **136**(4): 515–523. doi:10.1007/s00442-003-1301-9. PMID:12774225.
- Congdon, J.D., Vitt, L.J., van Loben Sels, R.C., and Ohmart, R.D. 1982. The ecological significance of water flux rates in arboreal desert lizards of the genus *Urosaurus*. *Physiol. Zool.* **55**(3): 317–322.
- Cooper, W.E., Jr., and Whiting, M.J. 1999. Foraging modes in lacertid lizards from southern Africa. *Amphib.-Reptilia*, **20**(3): 299–311. doi:10.1163/156853899X00312.
- Cooper, W.E., Jr., and Whiting, M.J. 2000. Ambush and active foraging modes both occur in the scincid genus *Mabuya*. *Copeia*, **2000**(1): 112–118. doi:10.1643/0045-8511(2000)2000[0112:AAAFMB]2.0.CO;2.
- Cooper, W.E., Jr., Vitt, L.J., Caldwell, J.P., and Fox, S.F. 2001. Foraging modes of some American lizards: relationships among measurement variables and discreteness of modes. *Herpetologica*, **57**(1): 65–76.
- Cunningham, P., Wassenaar, T., and Henschel, J. 2012. Notes on some aspects of the ecology of the Husab Sand Lizard, *Pedioplanis husabensis*, from Namibia. *African Herp News*, **56**: 1–11.
- Eckardt, F.D., Soderberg, K., Coop, L.J., Muller, A.A., Vickery, K.J., Grandin, R.D., Jack, C., Kapalanga, T.S., and Henschel, J. 2013. The nature of moisture at Gobabeb, in the central Namib Desert. *J. Arid Environ.* **93**: 7–19. doi:10.1016/j.jaridenv.2012.01.011.
- Edney, E.B. 1977. Water balance in land arthropods. Springer-Verlag, Berlin and New York.
- Ferrar, P. 1982. Termites of a South African savanna. IV. Subterranean populations, mass determinations and biomass estimations. *Oecologia*, **52**(1): 147–151. doi:10.1007/BF00349024.
- Fujioka, T., Chappell, J., Honda, M., Yatsevich, I., Fifield, K., and Fabel, D. 2005. Global cooling initiated stony deserts in central Australia 2–4 ma, dated by cosmogenic ²¹Ne–¹⁰Be. *Geology*, **33**(12): 993–996. doi:10.1130/G21746.1.
- Fujioka, T., Chappell, J., Fifield, L.K., and Rhodes, E.J. 2009. Australian desert dune fields initiated with Pliocene–Pleistocene global climatic shift. *Geology*, **37**(1): 51–54. doi:10.1130/G25042A.1.
- Haensler, A., Cermak, J., Hagemann, S., and Jacob, D. 2011. Will the southern African west coast fog be affected by future climate change? Results of an initial fog projection using a regional climate model. *Erdkunde*, **65**(3): 261–275. doi:10.3112/erdkunde.2011.03.04.
- Harwood, R.H. 1979. The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicarinatus* and *Sceloporus occidentalis*. *Comp. Biochem. Physiol. A*, **63**(3): 417–433.
- Henschel, J.R., and Seely, M.K. 2008. Ecophysiology of atmospheric moisture in the Namib Desert. *Atmos. Res.* **87**(3–4): 362–368. doi:10.1016/j.atmosres.2007.11.015.
- Hertz, P.E., Huey, R.B., and Garland, T., Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles Olympians or boy scouts? *Am. Zool.* **28**(3): 927–938. doi:10.1093/icb/28.3.927.
- Huey, R.B., and Bennett, A.F. 1986. A comparative approach to field and laboratory studies in evolutionary ecology. In *Predator–prey relationships in lower vertebrates*. Edited by M.E. Feder and G. Lauder. University of Chicago Press, Chicago. pp. 82–98.
- Huey, R.B., and Pianka, E.R. 1981. Ecological consequences of foraging mode. *Ecology*, **62**(4): 991–999. doi:10.2307/1936998.
- Huey, R.B., and Slatkin, M. 1976. Cost and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**(3): 363–384. doi:10.1086/409470. PMID:981504.
- Huey, R.B., Pianka, E.R., and Hoffman, J.A. 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology*, **58**(5): 1066–1075. doi:10.2307/1936926.
- Jakob, E.M., Marshall, S.D., and Uetz, G.W. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*, **77**(1): 61–67. doi:10.2307/3545585.
- Karasov, W.H., and Anderson, R.A. 1998. Correlates of average daily metabolism of field-active zebra-tailed lizards (*Callisaurus draconoides*). *Physiol. Zool.* **71**(1): 93–105. PMID:9472817.
- Kearney, M., and Porter, W.P. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, **85**(11): 3119–3131. doi:10.1890/03-0820.
- Kingsbury, B.A. 1995. Field metabolic rates of a eurythermic lizard. *Herpetologica*, **51**(2): 155–159.
- Lifson, N., and McClintock, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* **12**(1): 46–74. doi:10.1016/0022-5193(66)90185-8. PMID:6015431.
- Louw, G.N. 1972. The role of advective fog in the water economy of certain Namib Desert animals. *Symp. Zool. Soc. (Lond.)*, **31**: 297–314.
- Louw, G.N., and Seely, M.K. 1982. Ecology of desert organisms. Longman, London and New York.
- Mautz, W.J., and Nagy, K.A. 2000. Xantusiid lizards have low energy, water, and food requirements. *Physiol. Biochem. Zool.* **73**(4): 480–487. doi:10.1086/317742. PMID:11009401.
- Miles, D.B., Losos, J.B., and Irschick, D.J. 2007. Morphology, performance, and foraging mode. In *Lizard ecology: the evolutionary consequences of foraging mode*. Edited by S.M. Reilly, L.B. McBrayer, and D.B. Miles. Cambridge University Press, Cambridge. pp. 49–93.

- Mitchell, D., Seely, M.K., Roberts, C.S., Pietruszka, R.D., McClain, E., Criffin, M., and Yeaton, R.I. 1987. On the biology of the lizard *Angolosaurus skoogi* in the Namib Desert. *Madoqua*, **15**: 201–216.
- Mitchell, N.J., Kearney, M.R., Nelson, N.J., and Porter, W.P. 2008. Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? *Proc. R. Soc. B Biol. Sci.* **275**(1648): 2185–2193. doi:10.1098/rspb.2008.0438. PMID:18595840.
- Mitchell, N., Hipsey, M.R., Arnall, S., McGrath, G., Tareque, H.B., Kuchling, G., Vogwill, R., Sivapalan, M., Porter, W.P., and Kearney, M.R. 2012. Linking eco-energetics and eco-hydrology to select sites for the assisted colonization of Australia's rarest reptile. *Biology*, **2**(1): 1–25. doi:10.3390/biology2010001. PMID:24832649.
- Nagy, K.A. 1980. CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* **238**(5): R466–R473. PMID:6769345.
- Nagy, K.A. 1983. The doubly labeled water (3HH18O) method: a guide to its use. University of California, Los Angeles, Publ. No. 12-1417.
- Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**(2): 111–128. doi:10.2307/1942620.
- Nagy, K.A., and Costa, D.P. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* **238**(5): R454–R465. PMID:6990797.
- Nagy, K.A., and Peterson, C.C. 1988. Scaling of water flux rate in animals. *Univ. Calif. Publ. Zool.* **120**: 1–172.
- Nagy, K.A., Huey, R.B., and Bennett, A.F. 1984. Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology*, **65**(2): 588–596. doi:10.2307/1941421.
- Nagy, K.A., Clarke, B.C., Seely, M.K., Mitchell, D., and Lighton, J.R.B. 1991. Water and energy balance in Namibian desert sand-dune lizards *Angolosaurus skoogi* (Andersson, 1916). *Funct. Ecol.* **5**(6): 731–739. doi:10.2307/2389535.
- Nagy, K.A., Seely, M.K., and Buffenstein, R. 1993. Surprisingly low field metabolic rate of a diurnal desert gecko, *Rhoptropus afer*. *Copeia*, **1993**(1): 216–219. doi:10.2307/1446313.
- Nagy, K.A., Girard, I.A., and Brown, T.K. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.* **19**: 247–277. doi:10.1146/annurev.nutr.19.1.247. PMID:10448524.
- Ochocińska, D., and Taylor, J.R.E. 2005. Living at the physiological limits: field and maximum metabolic rates of the common shrew (*Sorex araneus*). *Physiol. Biochem. Zool.* **78**(5): 808–818. doi:10.1086/431190. PMID:16096983.
- Pianka, E.R. 1979. Diversity and niche structure in desert communities. In *Aridland ecosystems: structure, function, and management*. Edited by R. Perry and D. Goodall. Cambridge University Press, Cambridge. pp. 321–341.
- Polis, G.A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* **138**(1): 123–155. doi:10.1086/285208.
- Polis, G.A., Hurd, S.D., Jackson, C.T., and Piñero, F.S. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology*, **78**(6): 1884–1897. doi:10.1890/0012-9658(1997)078[1884:ENOEOT]2.0.CO;2.
- Robinson, M.D. 1990. Summer field energetics of the Namib desert dune lizard *Aporosaura anchietae* (Lacertidae), and its relation to reproduction. *J. Arid Environ.* **18**(2): 207–215.
- Schmidt-Nielsen, K. 1991. *Animal physiology: adaptation and environment*. 5th ed. Cambridge University Press, Cambridge.
- Soderberg, K.S. 2010. The role of fog in the ecohydrology and biogeochemistry of the Namib Desert. Ph.D. dissertation, University of Virginia, Charlottesville.
- Thuiller, W., Midgley, G.F., Hughes, G.O., Bomhard, B., Drew, G., Rutherford, M.C., and Woodward, F. 2006. Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biol.* **12**: 759–776. doi:10.1111/j.1365-2486.2006.01140.x.
- Tomlinson, S., Arnall, S.G., Munn, A., Bradshaw, S.D., Maloney, S.K., Dixon, K.W., and Didham, R.K. 2014. Applications and implications of ecological energetics. *Trends Ecol. Evol.* **29**(5): 280–290. doi:10.1016/j.tree.2014.03.003. PMID:24725438.
- Tracy, C.R., Nussear, K.E., Esque, T.C., Dean-Bradley, K., Tracy, C.R., DeFalco, L.A., Castle, K.T., Zimmerman, L.C., Espinoza, R.E., and Barber, A.M. 2006. The importance of physiological ecology in conservation biology. *Integr. Comp. Biol.* **46**(6): 1191–1205. doi:10.1093/icb/icl054. PMID:21672817.
- van der Meer, M.H., Whiting, M.J., and Branch, W.R. 2010. Ecology of Southern African Sandveld lizards (Lacertidae, *Nucras*). *Copeia*, **2010**(4): 568–577. doi:10.1643/CE-09-134.
- van Zinderen Bakker, E.M. 1975. The origin and palaeoenvironment of the Namib Desert biome. *J. Biogeogr.* **2**: 65–73. doi:10.2307/3038074.
- Verwajen, D., and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. *J. Therm. Biol.* **32**(7–8): 388–395. doi:10.1016/j.jtherbio.2007.05.005.
- Verwajen, D., and Van Damme, R. 2008. Foraging mode and its flexibility in lacertid lizards from Europe. *J. Herpetol.* **42**(1):124–133. doi:10.1670/07-136R1.1.
- Ward, J.D., Seely, M.K., and Lancaster, N. 1983. On the antiquity of the Namib. *S. Afr. J. Sci.* **79**(5): 175–183.
- Webster, M.D., and Weathers, W.W. 1989. Validation of single-sample doubly labeled water method. *Am. J. Physiol.* **256**(2): R572–R576. PMID:2492774.
- Webster, M.D., and Weathers, W.W. 2000. Seasonal changes in energy and water use by verdins, *Auriparus flaviceps*. *J. Exp. Biol.* **203**(21): 3333–3344. PMID:11023853.
- Williams, J.B., Anderson, M.D., and Richardson, P.R.K. 1997. Seasonal differences in field metabolism, water requirements, and foraging behavior of free-living aardwolves. *Ecology*, **78**(8): 2588–2602. doi:10.1890/0012-9658(1997)078[2588:SDIFMW]2.0.CO;2.
- Zaady, E., Groffman, P.M., Shachak, M., and Wilby, A. 2003. Consumption and release of nitrogen by the harvester termite *Anacanthotermes ubachi navas* in the northern Negev Desert, Israel. *Soil Biol. Biochem.* **35**(10): 1299–1303. doi:10.1016/S0038-0717(03)00200-1.