Low field metabolic rates for geckos of the genus *Rhoptropus* may not be surprising

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ABSTRACT

Geckos of the genus *Rhoptropus* are small diurnal lizards occurring in arid regions of Namibia and Angola, and are not well studied relative to other desert lizards. *Rhoptropus afer* has a field metabolic rate significantly lower than that of other desert lizards, but comparable studies have not been carried out in any other *Rhoptropus* species. We examined the field metabolic rate, water turnover, foraging behavior, and thermal biology of Bradfield's Namib day gecko, *Rhoptropus bradfieldi*, in the Namib Desert. This species occupies rocky habitats and feeds on arthropods via a sit-and-wait strategy. We found that it has a field metabolic rate ($140 \, \mathrm{J \, d^{-1}}$) that is 26% that of a typical desert lizard of the same size ($540 \, \mathrm{J \, d^{-1}}$). We also found that *R. bradfieldi* had a relatively high water influx rate ($0.07 \, \mathrm{ml \, d^{-1}}$) for its low rate of energy turnover, and suggest that a significant proportion of this water was sourced from fog. Active body temperatures varied between summer ($32.7 \pm 2.4 \,^{\circ}\mathrm{C}$) and autumn ($34.4 \pm 2.5 \,^{\circ}\mathrm{C}$), but in both seasons *R. bradfieldi* maintained high and stable body temperatures while active. Our study supports the idea that a minimal energy requirement could be widespread within *Rhoptropus* geckos.

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1. Introduction

Geckos make up about 25% of all lizard species (McBrayer and Corbin, 2007). Although most gecko species are nocturnal, 15 of the approximately 121 gecko genera have evolved a diurnal lifestyle (Röll, 2001; Bauer, 2013) and, in many cases, occupy ecological niches similar to those occupied by other lineages of diurnal lizards (Pianka and Vitt, 2003). Geckos are primarily sit-and-wait foragers; some species, however, use a mixed foraging strategy and often move continuously while searching for prey (Cooper, 1995; Bauer, 2007). *Rhoptropus* is a genus of diurnal gecko that occupies xeric habitats in Namibia and Angola and are sit-and-wait foragers. The ecological energetics of this group is currently known from only a single species, the Common Namib day gecko, *Rhoptropus afer*. Surprisingly, its standard metabolic (SMR) and field metabolic rates are approximately ½ of that of a comparably-sized diurnal iguanid

lizard, despite *R. afer* being active for much of the day and maintaining high active body temperatures (Odendaal, 1979; Peterson, 1990; Nagy et al., 1993; Cooper et al., 1999). It is unclear whether this is a common trait among other *Rhoptropus* species; if so the energetics of *Rhoptropus* geckos may differ greatly from that of other small, diurnal, desert-dwelling lizards.

In arid ecosystems, primary productivity, which directly or indirectly underlies the requirement for energy that all organisms operate under, is directly proportional to precipitation (Polis et al., 1997). The central Namib Desert is one of the driest places in the world with infrequent and unpredictable rainfall imposing significant challenges for the maintenance of consumer biomass. However, particularly in coastal regions, moisture from fog and dew is a reliable source of water used by many species of plants and animals, and may represent the majority of annual water input into this system (Hachfeld, 2000; Henschel and Seely, 2008). Studies detailing the energy and water economy of organisms in these arid systems shed important insights into how these animals manage to meet their basic requirements for food and water and are an important part of understanding the structure and function of these ecosystems. Here we study the physiological ecology and behavior of an important consumer in this ecosystem, *Rhoptropus bradfieldi*, which represents a small step towards improving our

understanding of how animals operate and function under the challenges imposed by arid environments.

We studied the FMR, body temperatures, and foraging behavior of Bradfield's Namib day gecko, *Rhoptropus bradfieldi*, a sister species to *R. afer* (Lamb and Bauer, 2001). *R. bradfieldi* is a rock-dwelling and insectivorous diurnal gecko endemic to the Namib Desert, occurring from the Kuiseb River in the south to the area of Cape Cross *ca.* 250 km to the north, in habitats extending from the coast up to 60–70 km inland (Bauer and Good, 1996; Bauer and Lamb, 2001). Coastal populations are dark in coloration while inland populations have a lighter pattern, and small differences in scalation. Our study population resided about 50–60 km from the coast, and insufficient genetic material from inland populations has been examined to determine how divergent inland and coastal populations are (Bauer and Lamb, 2001). Even though they occur in the same areas, *R. afer* and *R. bradfieldi* do not occupy the same microhabitats, and have different morphologies and locomotor capacities (Odendaal, 1979; Bauer et al., 1996; Johnson and Russell, 2009; Higham and Russell, 2010). Because of these differences, it is not clear if the unusually low metabolic rate of *R. afer* is representative of the genus *Rhoptropus*, or is simply an artefact of *R. afer's* unique evolutionary trajectory. Although *R. afer* and *R. bradfieldi* are considered sister species and thus may not be representative of all of the genetic diversity within *Rhoptropus*, the comparison of these two species and their disparate lifestyles covers the range of *Rhoptropus* ecology reasonably well. Here we compared the FMR, active body temperatures, and foraging behavior of *R. bradfieldi*, with those of *R. afer* studied previously. Because lizard foraging strategies are closely linked with relative rates of daily energy intake and expenditure the quantification of *R. bradfieldi's* foraging mode is an important component of understanding its ecological energetics (Anderson and Karasov, 1981; Nagy et al., 1984). Specifically, we aim to assess whether the unusually low FMR found in the closely-related *R. afer* (Nagy et al., 1993) may be a trait common to diurnal geckos in the genus *Rhoptropus*. *R. afer* and several other species of *Rhoptropus* geckos examined to date all use a sedentary, sit-and-wait foraging strategy (Cooper et al., 1999). We predict that *R. bradfieldi* will also use a sit-and-wait foraging strategy similar to other species of *Rhoptropus*, and that its FMR will be similarly low as it is in its sister species *R. afer*.

2. Methods

2.1. Study site

We studied *R. bradfieldi* living in crevices on rocky outcrops in the dry Swakop River at Hildenhof, Namibia (22° 42.049′ S, 14° 54.890′ E; 210 m). Shrubs such as *Lycium* sp., *Salsola aphylla*, and *Zygophyllum stapffii* were the dominant plants growing around the rocks that geckos occupied, and scattered riparian trees also grew in the in the adjacent sandy river bed, including *Euclea pseudebenus*, *Tamarix usneoides*, *Acacia erioloba*, *Faidherbia albida*, and the non-native tree *Prosopis glandulosa*. The Swakop River area has a mean monthly maximum air temperature between 24 and 39 °C and mean monthly minimum temperature ranging from 6 to 20 °C. Mean annual precipitation is 25 mm (Eckardt et al., 2013). This inland site does not have the frequent fog events that coastal habitats receive, but some fog events do reach the site; although the number is unrecorded, approximately 25–50 fog days per year could be expected at this location given data recorded at other, similar locations (Olivier, 1995; Haensler et al., 2011) Gecko energetics and water balance were studied during austral summer (December 2012–January 2013; mean sunrise and sunset were 06:08 and 19:38, respectively) and foraging behavior was studied both during Austral summer and autumn (May 2013; mean sunrise

and sunset were 06:14 and 17:21, respectively). Mean daily air temperatures during the summer were measured on site with a Hobo data logger and temperature sensor (Mod. # S-THB-M002 and #H21-002, Bourne, MA, USA) placed 1 m above the ground in a shielded housing and averaged 22.1 ± 1.6 °C (mean maximum 30.9 ± 0.7 °C, mean minimum 16.3 ± 0.3 °C). No precipitation occurred during the December–January study period, although two mornings were noticeably foggy. Daily mean air temperatures in May were similar (22.4 ± 5.0 °C) to that in summer, but temperatures were more variable (mean maximum 35.3 ± 1.3 °C, mean minimum 13.0 ± 1.3 °C) and the site received 13 mm of precipitation (Davis Rain Collector II, # 7852M, Hayward, CA, USA; and a Hobo Pendant Event Logger, # UA-003-64, Bourne, MA, USA) on 30–31 March 2013.

2.2. Field metabolic rate

We used the single-sample method of the doubly-labelled water (DLW) technique to estimate field metabolic rates and water fluxes (Webster and Weathers, 1989). We injected 45 geckos with 0.015 ml of 98 atom% $H_2^{18}O$ (Rotem Industries, Ltd., Beer Sheva, Israel) and 99.8 atom% D_2O (Isotec, Inc., Miamisburg, OH, USA; ^{18}O:D; 4:1) intraperitoneally. Four of the labelled geckos were retained in shaded cloth bags at ambient temperature (ca. 27 °C), and a blood sample (~50 μl) was taken from the infraorbital sinus with a heparinized capillary tube (No. 2501, Chase Scientific Glass, Inc., Rockwood, TN, USA) 4 h after the injection, to estimate initial equilibrium isotope concentrations for geckos which did not have an initial blood sample taken after injection. Initial D/H and $^{18}O/^{16}O$ ratios were determined by the regression relationship between the initial equilibrium isotope concentrations and the initial body masses of the four retained geckos; these variables were strongly correlated ($r^2 > 0.91$; $p < 0.05$). Sixteen released geckos were recaptured 7–14 days post injection, measured and weighed, and a blood sample was taken from the infraorbital sinus. Sufficient blood was obtained from only 10 of the 16 recaptured geckos to allow further analyses. Additional blood samples were taken from four geckos that had not received DLW injections, to estimate mean background deuterium (2015 ± 7 ppm) and ^{18}O concentrations (160 ± 1 ppm).

We flame-sealed blood samples in heparinised capillary tubes and kept them chilled until analysis. We cryo-distilled whole blood samples in glass Pasteur pipettes under a vacuum to yield pure water, and used a liquid water isotope analyzer (Los Gatos Research Model DLT-100, No. 908-0008; Mountain View, CA, USA) at the Natural Resources and the Environment division of South Africa's Council for Scientific and Industrial Research (CSIR; Pretoria, South Africa) to measure D/H and $^{18}O/^{16}O$ ratios. The instrument employed high resolution cavity enhanced direct-absorption spectroscopy. Samples were bracketed (every five samples) by known laboratory standards calibrated previously against international standards (Vienna Standard Mean Ocean Water; VSMOW) and twelve replicate isotope measurements were made from each sample.

We used the $^{18}O/^{16}O$ ratios in the initial blood samples of the four retained geckos to calculate body water volume, as ^{18}O dilution space, and applied the resulting percentage of body mass to estimate total body water volumes for recaptured geckos, under the assumption that the percent body water did not change during the sampling period (Nagy, 1983). Rates of CO_2 production (Equation (2)) and water flux (equations (4) and (6)) were calculated using the equations listed in Nagy (1980) and Nagy and Costa (1980), assuming linear changes in body mass between sampling periods. CO_2 production was converted to energy units at 25.7 J ml^{-1} CO_2, which is typical for lizards eating an insectivorous diet (Nagy, 1983).

2.3. Morphology and body temperature

In addition to the geckos employed in the DLW study, we recorded the snout-vent length (SVL; ± 1.0 mm), body mass (± 0.1 g; Acculab PP-250B; Goettingen, Germany), and sex of additional geckos that we captured during December–January (32 male, 21 female) and May (11 male, 17 female). Before they were released at their capture site, geckos were marked with permanent marker for easy short-term field identification (until the next shed), and their toes were clipped with a unique code for long-term identification. We measured body temperature immediately after capture (Dec.–Jan. = 73, May = 33) with a calibrated type T thermocouple probe and digital thermometer (± 0.2 °C accuracy; Omega HH202A; Stamford, CT, USA) inserted approximately 10 mm into the cloaca and held in position until temperature equilibrated, generally within 10 s. We used the same thermometer and thermocouple to record substrate temperature and air temperatures (10 mm above the substrate) immediately after recording gecko temperature, at the locations for each gecko that we observed active (Dec.–Jan. = 80; May = 74), including some geckos that we did not measure or mark.

2.4. Focal animal observations

We observed active geckos for timed sessions (8–19 min), and recorded movements per minute (MPM), percent time moving (PTM), and number of prey items attacked while the gecko was moving relative to attacks occurring while the gecko was stationary (PAM; Cooper and Whiting, 2000). The sessions were between 10:31 and 13:17 in January and between 08:35 and 11:51 in May. We observed geckos from a distance of about 3 m, sufficient for them to engage in normal behavior. We made sure these sessions did not begin until all geckos under observation had changed from the darker dorsal coloration which they displayed when they first emerged from their refuges to the lighter, sandy coloration characteristic of active geckos. We could identify geckos by body size and location, and so could ensure that each gecko was observed for only one timed session. We included in analyses only geckos for which we had at least 8 min of activity data, and excluded geckos that had received DLW injections.

2.5. Statistical analyses

We used SigmaPlot version 8.0 (Systat Software, Inc., San Jose, CA, USA), SPSS version 21.0 (SPSS, Inc., Chicago, IL, USA), and Minitab version 16.0 (Minitab, Inc., State College, PA, USA) for analyses and figures. We tested data for normality with the Anderson-Darling test. We used least-squares linear regressions to estimate initial stable isotope concentrations by body mass. Gecko foraging metrics were compared between seasons with unpaired Student's t-tests. The effects of season and sex on gecko mass and SVL were compared with two-way ANOVAs, and differences in the slope and intercept describing the linear relationship between mass and SVL were compared with ANCOVAs. We used unpaired t-tests, Pearson correlation, partial correlation, least-squares linear regressions, and ANCOVAs to examine the relationship between gecko body temperature and environmental temperatures, and how the relationship varied between sexes and across seasons. Significance was accepted at $P < 0.05$, and values are reported as mean $\pm$ SD.

3. Results

3.1. Morphology

All geckos were captured on rock surfaces, and while we did not record the angle of the surface, most geckos were captured on approximately vertical rock faces. Two of the females captured in May were recaptures from December, and these individuals were removed from further May analyses. Gecko mass was significantly affected by sex (two-way ANOVA; sex: $F_{1,75} = 31.3$; $P < 0.001$), and season (two-way ANOVA; season: $F_{1,75} = 11.2$; $P < 0.001$; Table 1). Male geckos were significantly heavier than females during both capture periods (Table 1).

There also was a significant interaction of sex and season on gecko mass (two-way ANOVA; sex $\times$ season: $F_{1,75} = 6.8$; $P = 0.011$), meaning that the effect of season on mass varied by sex. Female gecko mass did not change between months, but males were significantly heavier in May relative to Dec.-Jan. (Table 1). There was no effect of season on gecko SVL (two-way ANOVA; season: $F_{1,75} = 2.5$; $P = 0.115$), but there was a significant effect of sex on SVL (two-way ANOVA; sex: $F_{1,75} = 15.5$; $P < 0.001$). Male geckos were longer than were females (Table 1). The interaction between season and sex on gecko SVL was not significant (two-way ANOVA; sex $\times$ season: $F_{1,75} = 2.2$; $P = 0.144$). Although the body mass of male geckos differed between May and Dec.–Jan., there was no difference in the slope and the intercept for the relationship between male body mass and SVL between seasons (ANCOVA; intercept: $F_{1,39} = 0.46$; $P = 0.502$; slope: $F_{1,39} = 0.71$; $P = 0.403$). The mass and SVL of female day geckos did not differ between months, but the regression lines describing male and female gecko mass and SVL were significantly different, so were plotted separately (ANCOVA; intercept: $F_{1,75} = 7.2$; $P = 0.009$; slope: $F_{1,75} = 8.3$; $P = 0.005$; Fig. 1).

3.2. Energetics and water flux

Females ($n = 5$; 3.3 g) in the DLW study were the same mass as males ($n = 5$; 3.3 g; two sample t-test; $t_8 = 0.123$; $P = 0.905$; Table 2). There was no significant difference between the water influx rates (WIR; two sample t-test; $t_8 = -1.06$; $P = 0.321$) and the field metabolic rates (FMR; two sample t-test; $t_8 = -1.93$; $P = 0.09$) of males and females, so we combined the data. Total body water volumes averaged $78 \pm 5\%$ of body mass, and mean FMR was 0.07 ml CO_2 g^{-1} h^{-1}, or 140 J d^{-1} (Table 2). The mean water influx rate was 21 ml kg^{-1} d^{-1}, and mean water efflux was 23 ml kg^{-1} d^{-1}. Daily WIR averaged 0.07 ml d^{-1} (Table 2).

On average the geckos lost body mass during the DLW study; mean difference in mass between capture and recapture ($-0.2 \pm 0.3\%$ d^{-1}; Table 2) was significantly different from zero (one sample t-test; $t = -2.61$; $P = 0.028$). However, there was no significant relationship between the rate of body mass change and gecko FMR ($F_{1,9} = 1.50$; $P = 0.256$) or WIR ($F_{1,9} = 0.47$; $P = 0.512$). Consequently, we use the mean values of FMR (0.07 ml CO_2 g^{-1} h^{-1}) and WIR (0.07 ml d^{-1}) presented in Table 2 as representative of geckos in steady state (Nagy et al., 1991). One female gecko had a noticeably higher WIR relative to the other geckos and may be an outlier (Table 2), but because our results changed very little with or without this individual (and not at all statistically), and since its values are well within parameters known for other lizard species, we chose to leave it in.

Table 1
Mass and snout-vent length (SVL) by season for male and female *Rhoptropus bradfieldi*.

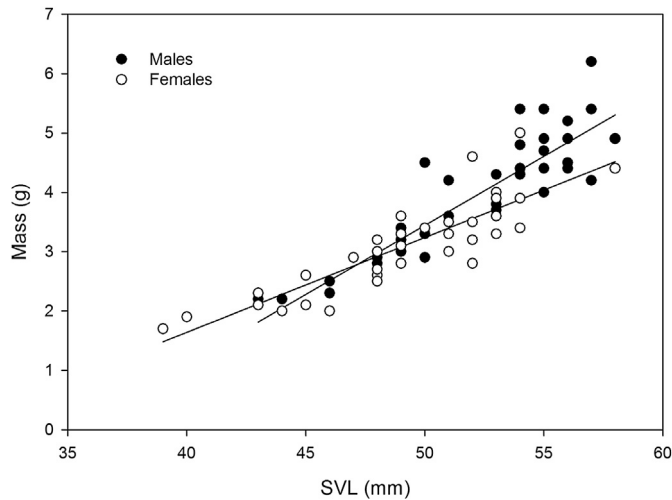| Month	Sex	Snout-vent length (SVL; mm)	Mass (g)
December–January	Female ($n = 21$)	49.0 ± 4.3	3.0 ± 0.7
December–January	Male ($n = 32$)	51.3 ± 4.0	3.6 ± 0.9
May	Female ($n = 15$)	49.1 ± 4.0	3.2 ± 0.9
May	Male ($n = 11$)	54.2 ± 2.2	4.8 ± 0.8

Fig. 1. The relationship between *Rhoptropus bradfieldi* snout-vent length (SVL) and body mass for male and female geckos combined across seasons. Regression equations are: female body mass = 0.16(SVL) − 4.76; r^2 = 0.73; $P < 0.001$, $n = 36$; male body mass = 0.23 (SVL) − 8.2; r^2 = 0.76; $P < 0.001$, $n = 43$).

3.3. Foraging behavior

We observed 11 geckos during January, and 10 geckos during May (Table 3). Lizards foraging in January and May made less than one MPM, and MPM did not vary between months (two sample *t*-test; $t_{19} = 0.47$; $P = 0.512$; Table 3). Additionally, the PTM (3%) did not differ for foraging lizards between January and May (two sample *t*-test; $t_{19} = 0.42$; $P = 0.676$; Table 3). There were no prey attacks while moving (PAM). Movement bout duration averaged 2.5 ± 1.0 s for lizards in January and 2.1 ± 0.4 s in May, durations which did not differ between months (two sample *t*-test; $t_{19} = 0.86$; $P = 0.406$).

3.4. Body temperature

The body temperatures of male and female geckos did not differ, and consequently were combined in analyses. Mean body temperature of active geckos averaged 32.7 ± 2.4 °C ($n = 73$) in Dec.-Jan., significantly lower than the mean body temperature of active geckos in May (34.4 ± 2.5 °C, $n = 33$; two sample *t*-test; $t_{104} = 3.25$; $P = 0.002$). The mean substrate temperature taken at gecko capture locations in Dec.-Jan. was 32.0 ± 4.7 °C, and was 33.1 ± 4.8 °C in May, values which did not differ between seasons (two sample *t*-test; $t_{152} = 1.34$; $P = 0.183$). Similarly, mean air

Table 3
Gecko foraging metrics: percent time moving (PTM), movements per minute (MPM), movement duration, percent prey attacked while moving (PAM), and the number of observed prey attacks for *Rhoptropus bradfieldi*, during January ($n = 11$ lizards; 9.5 ± 2.2 min per individual) and May ($n = 10$ lizards; 15.1 ± 4.0 min per individual) along the dry Swakop River in the Namib Desert.

Season	MPM	PTM (%)	Movement duration (s)	PAM (%)	# Prey attacks observed
January	0.6 ± 0.7[a]	3.0 ± 3.0[a]	2.5 ± 1.0[a]	0	7
May	0.7 ± 0.9[a]	3.0 ± 4.0[a]	2.1 ± 0.4[a]	0	4
Combined	0.7 ± 0.8	3.0 ± 4.0	2.5 ± 2.3	0	11

[a] Different letters represent significant differences between months within a column in a two sample *t*-test at a significance level of $\alpha = 0.05$. Mean ± SD.

temperature at gecko locations during Dec.-Jan. (28.5 ± 3.9 °C) was the same as that in May (28.9 ± 5.2 °C; two-sample *t*-test; $t_{152} = 0.61$; $P = 0.544$). Body temperature was positively correlated with both substrate temperature and air temperature at gecko capture locations (Fig. 2). Substrate and air temperature were highly correlated (Pearson correlation: $r = 0.67$, $P < 0.001$), and thus are not independent measures of environmental temperature, but a partial correlation analysis and multiple regression showed that both measures of environmental temperature were correlated positively with body temperature (multiple linear regression: $r^2 = 0.53$, $F_{2,104} = 58.7$, $P < 0.001$; partial correlation body temperature-substrate temperature = 0.39, $P < 0.001$, partial correlation body temperature-air temperature = 0.32, $P = 0.001$). Body temperature was correlated with substrate and air temperature in a similar fashion between seasons as the regression line slopes were indistinguishable (substrate temperature: ANCOVA; slope: $F_{1,104} = 0.92$; $P = 0.339$; air temperature: ANCOVA; slope: $F_{1,104} = 0.02$; $P = 0.889$; Fig. 2).

4. Discussion

We measured field metabolic rates, water flux, body temperature, and activity in an inland population of *R. bradfieldi* in the Namib Desert. We show that *R. bradfieldi* has exceptionally low FMRs compared to most similarly sized lizard taxa. Our work thus confirms and extends the findings of Nagy et al. (1993) who found that *R. afer* had lower than expected FMRs. Additionally, our water turnover data show that *R. bradfieldi* utilizes significant quantities of water that, given the exceptional water scarcity of the region, may come partly from fog-derived moisture. We also present some of the first quantitative data describing the thermal biology of *R. bradfieldi*.

Table 2
Mass, field metabolic rates (FMR), and water influx rates (WIR) for ten *Rhoptropus bradfieldi*, during December–January along the dry Swakop River in the Namib Desert.

| Gecko	Sex	Mass			FMR		WIR	
		Initial (g)	Final (g)	Change (% d^{-1})	ml CO$_2$ g^{-1} h^{-1}	kJ d^{-1}	ml kg^{-1} d^{-1}	ml d^{-1}
2	F	3.3	3.2	−0.2	0.06	0.13	15.5	0.05
6	F	2.7	2.5	−0.5	0.06	0.11	30.3	0.08
7	F	4.4	4.4	0	0.08	0.20	5.1	0.02
23	F	2.0	1.9	−0.7	0.14	0.17	18.1	0.04
30	F	3.9	3.9	0	0.10	0.23	63.4	0.25
5	M	3.2	3.2	0	0.06	0.11	15.0	0.05
13	M	2.9	2.9	0	0.08	0.14	14.6	0.04
20	M	3.4	3.2	−0.6	0.07	0.14	6.4	0.02
25	M	2.9	2.9	0	0.04	0.08	32.1	0.09
50	M	4.2	4.1	−0.3	0.04	0.10	5.3	0.02
Mean		3.3	3.2	−0.2	0.07	0.14	21.0	0.07
SD		0.7	0.8	0.3	0.03	0.05	18.0	0.07
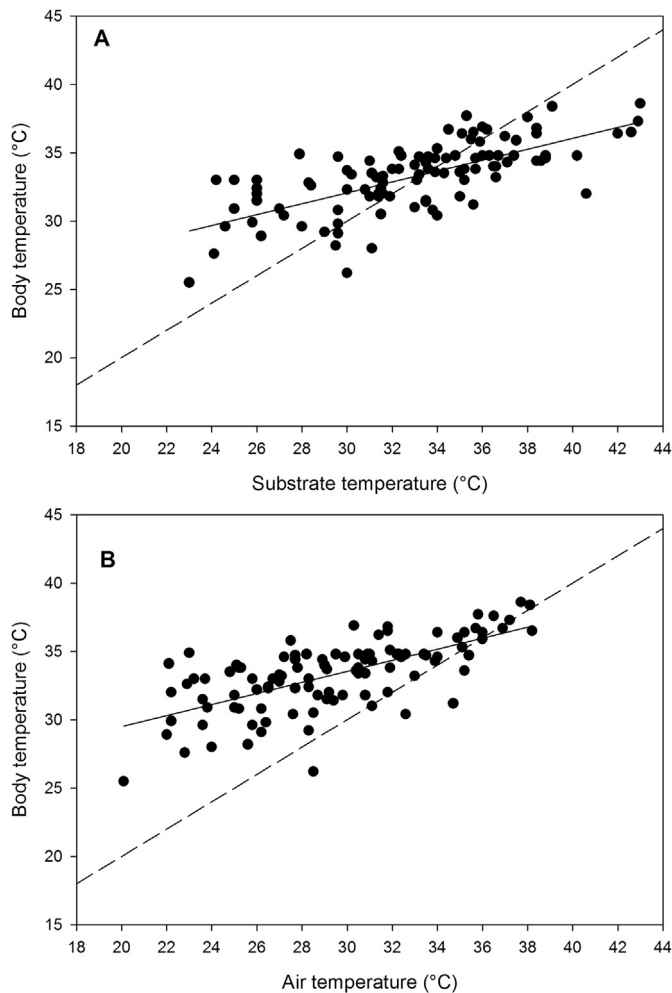
Fig. 2. The relationship between body temperature of *Rhoptropus bradfieldi* and A) substrate temperature and B) air temperature 10 mm above the substrate, at all gecko capture locations. There was no difference in the slope or intercept of the relationship between gecko body temperature and either measure of environmental temperature between December—January data and May data, and consequently we report regressions based on data combined for these two periods ($T_{body} = 0.40(T_{substrate}) + 20.1$; $r^2 = 0.48$; $P < 0.001$; $T_{body} = 0.41(T_{air}) + 21.4$; $r^2 = 0.45$; $P < 0.001$). Regressions are shown relative to the line of identity ($T_{body} = T_{substrate}/T_{air}$).

Although we were not able to obtain data from all of our validation animals, the empirical relationship between body mass and initial isotope levels were robust, and the mass range of the lizards used to predict these relationships (2.6—4.0 g) was closely enough aligned with the masses of the lizards in which we predicted initial isotope activities (2.0—4.4 g) to give us confidence in the results presented here. We are unable to examine seasonal effects on FMR and water turnover because data describing ecological energetics were collected only during the summer.

R. bradfieldi is a sexually dimorphic species with males that are heavier and longer than females (Table 1). Males were substantially heavier in May, relative to December/January, although sample size in May was small. Females, however, weighed the same across months. In addition, male and female gecko SVL did not change between the two sampling periods (Table 1). Despite the mass difference between all male and female geckos captured (male and female geckos used in the DLW analyses were the same mass), body temperature did not vary between the sexes, providing justification for combining the sexes in our subsequent analyses. Furthermore, in an analysis of a large dataset of the thermal biology of desert

lizards, sex-based differences in body temperature were almost always insignificant, and the mean difference in body temperature between male and female southern African geckos was not statistically significant at 0.23 ± 0.89 °C (*n* = 6 species; Huey and Pianka, 2007).

The foraging of *R. bradfieldi* was characterized by a sit-and-wait strategy with very little activity. On average, in both January and May, the geckos made less than one movement per minute and spent 3% of the time moving (Table 3). All of the prey attacks that we observed were initiated while the geckos were immobile. We did not witness enough prey capture attempts (*n* = 11) to permit further analyses, but we note that this low number of feeding events is not unexpected because lizards using a sit-and-wait foraging strategy generally have lower feeding rates than do actively-foraging lizards (Anderson and Karasov, 1981; Nagy et al., 1984). The metrics of foraging in our geckos conformed well to the metrics that characterize the highly-sedentary foraging of several other species of *Rhoptropus* gecko, including *R. afer, R. barnardi*, and *R. boultoni* (Cooper et al., 1999).

The foraging strategy of *R. bradfieldi* required geckos to leave the thermal refuges of their rocky habitat and remain stationary on exposed rock surfaces, which was when we captured them. Their mean body temperatures were almost 2 °C higher in May than in December—January, but the substrate and air temperatures at locations where geckos were captured did not differ during the two periods. The rate of body temperature increase with environmental temperature also was similar between months, and air and substrate temperature affected gecko body temperature equally (Fig. 2). However, air temperature and substrate temperature are just two among many factors that may influence lizard body temperature, and measuring the temperatures at a lizard's specific capture location does not identify all temperatures available to that lizard (Hertz et al., 1993). Notably, the slopes for the regressions describing body temperature versus substrate temperature (0.40 ± 0.04; 95% CI: 0.32—0.48) and air temperature (0.40 ± 0.04; 95% CI: 0.32—0.49) were similar to those found in many other species of small desert lizards which actively thermoregulate (Pianka, 1986). Although it was not our focus to describe precisely how day geckos were thermoregulating, particularly given that the slope of the regression on body temperature with ambient temperature is well known to be an incomplete index of thermoregulation (Hertz et al., 1993), it is clear that *R. bradfieldi* are able to achieve body temperatures that are significantly warmer than environmental temperatures at low air temperatures, and to achieve cooler than ambient temperature at high air temperatures (Fig. 2), presumably by adjusting solar heat gain by manipulating posture, behavior, and skin color (Walsberg and Wolf, 1995).

Our data imply that gecko thermoregulation differed between December—January and May, resulting in animals selecting for a higher body temperature in May. Indeed, during December—January *R. bradfieldi* may have selected cooler available microclimates to maintain lower body temperature as a means to enhance energy economy. During the same December—January study period, *R. afer* occurring near our study site maintained a body temperature of 35.6 °C (*n* = 54; D. Eifler, personal communication), almost 3 °C higher than the body temperatures of *R. bradfieldi*. The higher body temperatures in *R. afer* may be a reflection of higher operative temperatures present in *R. afer* habitat; they occupy flat expanses of gravel and rock where they occur, which one would expect to be more intensely heated by solar radiation throughout much of the day compared to the vertical surfaces with numerous shadows and crevices where *R. bradfieldi* resides in its rocky canyon habitat. *R. bradfieldi* maintained higher body temperatures in May than December/January; why and how remains enigmatic. Substantial precipitation several weeks before our May study may have

increased arthropod prey availability resulting in lizards feeding more and selecting higher body temperatures to process prey. However, because we do not have data on gecko FMR during May, and our observations of feeding between months were too few to allow statistical analyses, we are unable to support or deny this claim.

In lizards, body temperature and energy expenditure are considered to be proportional, however, compared to other groups of lizards, the physiology and energetics of geckos are not well studied. Some data imply that gecko standard metabolic rates (SMR) are low compared to those of other lizard groups (Dunson and Bramham, 1981; Putnam and Murphy, 1982; Peterson, 1990). However, other data claim that gecko SMR is comparable (Snyder and Weathers, 1976; Snyder, 1979; Andrews and Pough, 1985; Christian et al., 1998). There is also a controversy over the magnitude of gecko FMR. Secondarily diurnal geckos like *R. bradfieldi*, were all ancestrally nocturnal, and many nocturnal geckos operate at significantly lower active body temperatures than diurnal lizards (Huey et al., 1989). Consequently, this effect of phylogeny may be correlated with FMRs that are lower for geckos relative to other species of diurnal lizards, but the available data are equivocal. For example, the nocturnal geckos *Ptyodactylus hasselquistii* and *Chondrodactylus bibronii* have FMRs close to predicted values for diurnal lizards of the same size (Nagy and Degen, 1988; Nagy and Knight, 1989). In contrast, populations of nocturnal Australian *Oedura marmorata* geckos living in xeric habitats had lower than predicted FMR, while those living in more tropical habitats had an FMR similar to predicted values for other lizard groups (Christian et al., 1998). We show here that the diurnal *R. bradfieldi* had a low FMR, 26% of that of a typical (diurnal) desert lizard of its mass (0.540 kJ d^{-1}; 95% confidence interval 0.188 kJ d^{-1} − 1.55 kJ d^{-1}; $n = 16$ species; Nagy et al., 1999), and this value lay outside of the predicted FMR's 95% confidence interval, demonstrating its significance. The average mass-adjusted (adjusted from the allometric equation describing lizard body mass versus FMR) FMR for other species of sit-and-wait foraging lizards is 0.155 ± 0.079 kJ g$^{-0.952}$ d^{-1} (Brown and Nagy, 2007). Adjusting for mass, the FMR for *R. bradfieldi* was 0.045 kJ g$^{-0.952}$ d^{-1} which is significantly lower than that for other sit-and-wait foraging species of lizards. The previously-studied *R. afer* also had an unusually low FMR compared to other lizard species (0.227 kJ d^{-1}; Nagy et al., 1993), but its mass adjusted FMR (0.091 kJ g$^{-0.952}$ d^{-1}) lies within the confidence interval predicting the FMR in a sit-and-wait foraging lizard and is consequently not significantly different.

Like FMR, the water influx rates of *R. bradfieldi* were also lower than those observed in other desert reptiles. Our geckos had a WIR that was 70% of that expected for a desert reptile of its mass (0.10 ml d^{-1}; 95% confidence interval 0.06 ml d^{-1} − 0.17 ml d^{-1}; Nagy and Peterson, 1988), but this value was within the 95% confidence interval for the predicted WIR and thus not statistically significant. However, given their low FMRs, the WIR was surprisingly high, if the geckos were meeting their water requirements through preformed water in insects and from metabolic water production. To examine these WIR values, we can compare relative energy expenditure to water intake across species using the Water Economy Index (WEI; ml H$_2$O kJ^{-1} d^{-1}) which describes the ratio of water use to energy expenditure (Nagy and Peterson, 1988). An insectivorous reptile that does not drink free water would be expected to have a WEI between 0.075 and 0.175 (Nagy and Peterson, 1988). *R. bradfieldi* had a WEI of 0.50 ml H$_2$O kJ^{-1} (0.07 ml H$_2$O per 0.140 kJ). In contrast, *R. afer* had a WEI of 0.22 ml H$_2$O kJ^{-1} (Nagy et al., 1993), considerably less than that of *R. bradfieldi*. Two possible explanations could account for the abnormally high WEI of *R. bradfieldi*: either the geckos were drinking free water or they

were consuming prey with water content higher than that of the prey of a typical insectivorous reptile.

Rhoptropus geckos are thought to feed on ants, beetles, larvae, and moths, but no quantitative studies are available on the diet of any geckos in the genus (Branch, 1998). *Rhoptropus bradfieldi* in our population fed largely on ants, particularly ants in the genus *Lepisiota* sp. (Murray et al. unpublished data). The mean energy content in 28 species of desert ant is 26 kJ g^{-1} dry mass and the ants are 64% water (Withers and Dickman, 1995). Ants and termites have considerable amounts of undigestible chitin, and the average myrmecophagous lizard is capable of assimilating 60% of the available energy in an ant or termite based diet (Withers and Dickman, 1995; Cooper and Withers, 2004). According to these assumptions, geckos with an FMR of 0.140 kJ d^{-1} and feeding on ants should have a feeding rate of 0.009 g dry mass d^{-1}, 28% of the predicted feeding rate for an insectivorous iguanid lizard of the same size (equation (40); Nagy, 1987). *Lepisiota* sp. ants of the species that geckos eat have a dry mass of about 0.13 mg (Murray et al. unpublished data), so the geckos would be estimated to eat 69 ants per day.

R. bradfieldi feeding on the estimated number of ants would gain 0.016 ml d^{-1} of free water. Assuming that water generated from metabolic water production occurs at a rate of 0.026 ml kJ^{-1} (Schmidt-Nielsen, 1991), geckos eating such an ant-based diet would have a water influx from food and metabolic water of 0.020 ml d^{-1}, accounting for less than 30% of the WIR calculated via the DLW method. Although geckos theoretically may have selected arthropods with higher water content in order to realize a higher WIR, we did not see them doing so, and, in any case, such a source is unlikely to account for the 0.05 ml d^{-1} mismatch. Since geckos did not have access to standing water or rainfall during the study, we surmise that a significant proportion (70%) of the observed water influx in *R. bradfieldi* during the study period arose from drinking fog-derived moisture. During the course of the DLW study there were two mornings with noticeable fog, and we argue that the geckos were able to obtain that fog water, as does the Namib Desert lizard *Meroles anchietae* (Louw and Holm, 1972). In comparison, although the properties of the arthropod diet of *R. afer* are unknown, assuming that arthropods are 70% H$_2$O (Edney, 1977; Anderson and Karasov, 1988) and that 75% of the 23 kJ g^{-1} dry mass in the average arthropod is available to geckos (Harwood, 1979; Anderson and Karasov, 1988), and accounting for metabolic water production, the FMR of 0.227 kJ d^{-1} in *R. afer* corresponds to a water influx of 0.036 ml, which is lower than the isotopically-determined water influx of 0.051 ml. This difference implies that about 30% of *R. afer's* water intake could be derived from drinking free water during the two days of fog and one day of light rain recorded during Nagy et al.'s study (Nagy et al., 1993).

Differences in behavior, body temperature, and habitat may help explain the observed differences in FMR seen between the two *Rhotropus* species. Table 4 summarizes what we know about the biology of *R. bradfieldi* and *R. afer*. Although these gecko species are closely related, our measurement of FMR in *R. bradfieldi* was half that of *R. afer*. The low FMR in *R. bradfieldi* is likely related to its sedentary sit-and-wait foraging lifestyle as well as its microhabitat, morphology, and thermal biology. For example, the related species *R. afer* occurs in an open and sparse environment, has an active body temperature *ca.* 3 °C higher than *R. bradfieldi*, and sprints quickly over large distances where resources and shelters are likely widely spaced. In contrast, *R. bradfieldi* moves more slowly, and lives in a vertically-complex habitat where shelters and prey are close to one another, and rarely has to move far to thermoregulate, avoid predators, and seek prey. The morphologies of the two species also are a reflection of their disparate ecologies (Table 4). Additionally, *R. bradfieldi's* close proximity to a myriad of rock

Table 4
Summary of some known morphological and ecological features of *Rhoptropus afer* and *R. bradfieldi*.

Species	Habitat[a,b]	Body temperature (summer)[c]	Hind limb morphology[d]	Toe pad/setae morphology[e]	Maximum Speed[b]	Distance moved when fleeing[b]	Energetics/H$_2$O flux[f]
R. afer	Gravel flats/horizontal surfaces	35.6 °C ($n = 54$)	Elongated, slender	Reduced surface area/shorter setae	2.5 m s^{-1}	(>3 m)	227 J d^{-1}/0.051 ml d^{-1}
R. bradfieldi	Rock outcrops/vertical surfaces	32.7 °C ($n = 73$)	Shorter, stocky	Enlarged surface area/longer setae	1.5 m s^{-1}	(<0.5 m)	140 J d^{-1}/0.07 ml d^{-1}

[a] Odendaal 1979.
[b] Higham and Russell 2010.
[c] *R. afer*: D. Eifler, personal communication; *R. bradfieldi*: current study.
[d] Bauer et al., 1996.
[e] Johnson and Russell 2009.
[f] *R. afer*: Nagy et al., 1993; *R. bradfieldi*: current study.

crevices and the ready availability of shadows cooling its stratified habitat (IWM, pers. obs.) may be what enables this gecko to maintain lower active body temperatures relative to *R. afer*, but a more thorough investigation of available temperatures in the two habitat types, using operative temperature models, is warranted.

The low FMR we document here for *R. bradfieldi*, considered in conjunction with the FMR of the only other *Rhoptropus* species examined to date, raises the possibility that a low energy economy may be a unifying characteristic of *Rhoptropus* geckos. Surprisingly, *R. bradfieldi* had a very high water influx relative to its FMR, and that water influx could not be accounted for solely by the avenues of preformed water in their diet and metabolic water production. The geckos may be making use of drinking water available during fog events, another hypothesis requiring further testing. If the species does use fog-derived water, whether it does so simply opportunistically, or whether fog water is a critical requirement in its long-term water budgets, remains unknown. The only other data published on the FMR and WIR of *Rhoptropus* geckos implies that its sister species, *R. afer*, also uses fog/rain water when available, although free water constitutes less of its water budget (Nagy et al., 1993). Both populations of *Rhoptropus* geckos were studied close to the eastern, inland edge of their distributions. Estimating the water influxes and FMRs of gecko populations in cooler coastal habitats that receive significantly more fog events would be instructive. In Namibia, fog is recorded regularly up to 100 km inland (Hachfeld, 2000; Haensler et al., 2011), but the number of fog days per year declines progressively inland. For example, during 1981–2000 an average of about 100 fog days occurred per year in coastal areas, while areas 50–80 km inland experienced half that number (Haensler et al., 2011). The entire distribution of *R. bradfieldi* occurs within areas that receive at least some fog-derived moisture (Bauer and Good, 1996; Bauer and Lamb, 2001). Projected changes in climate may have local impacts on the pattern and extent of fog deposition, causing coastal regions to have a 10% increase in the number of annual fog days, but inland regions a decrease of 23–39% (Thuiller et al., 2006; Haensler et al., 2011). Consequently, if *R. bradfieldi* is reliant upon the availability of fog water, the species may well be constrained to near coastal habitats.

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