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Ecological niche separation of two sympatric insectivorous lizard species in the Namib Desert

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ABSTRACT

Individual lizard species may reduce competition within a habitat by diverging along one or more niche dimensions, such as spatial, temporal or dietary dimensions. We compared the morphology, activity patterns, microhabitat characteristics, thermal biology and feeding ecology of two species of diurnally active sympatric insectivorous lizards in the Namib Desert, the Husab sand lizard, *Pedioplanis husabensis*, and Bradfield's Namib day gecko, *Rhoptropus bradfieldi*. *Pedioplanis husabensis* and *R. bradfieldi* had similar snout-vent lengths (49–52 mm), but *P. husabensis* (2.5–3.0 g) weighed less than *R. bradfieldi* (3.1–3.9 g). The actively foraging *Pedioplanis husabensis* specialized on a termite diet (71% of all prey, found in 91% of fecal pellets), while the sedentary sit-and-wait foraging *R. bradfieldi* specialized on ants (87% of all prey, found in 100% of fecal pellets). *Pedioplanis husabensis* also had a higher active body temperature and often was found on warmer substrates than was *R. bradfieldi*. Despite occurring in the same habitat, these two lizard species do not occupy the same ecological niche space.

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1. Introduction

Lizards play critical roles in many arid ecosystems due to their high biomass and species diversity (Pianka, 1986; Mitchell et al., 1987). Individual lizard species are not distributed randomly across available habitats, nor is their diet made up of prey items that are in proportion to prey availability (Pianka, 1986; Vitt et al., 2003). Rather, species of lizards within a community tend to occupy ecological niches that are distinct from the ecological niches of other sympatric species (Pianka, 1973, 1975, 1986). Consequently, studies on lizard communities, including desert communities (Pianka, 1986; Goodyear and Pianka, 2011), have been used to better understand broader ecological and biogeographical principles about niche separation (Schoener, 1977; Pianka, 1986).

Lizard communities in southern Africa's Namib Desert have not

contributed as much as they should have to this broader understanding of niches. The Namib Desert is an ancient and hyper-arid desert, where lizards play important ecosystem roles as both consumers and prey (van Zinderen Bakker, 1975; Ward et al., 1983; Mitchell et al., 1987). Additionally, through its combination of habitat heterogeneity and isolation, the Namib Desert supports a high level of lizard endemism, particularly of gecko and lacertid species (Herrmann and Branch, 2013). We set out to investigate whether the ecological niches differ for two sympatric and similarly-sized insectivorous diurnal lizard species endemic to the Namib Desert: a lacertid, the Husab sand lizard *Pedioplanis husabensis*, and a diurnal gecko, Bradfield's Namib day gecko *Rhoptropus bradfieldi*. One way that similar species may be able to co-exist in the same environment is through a non-overlapping pattern of resource use. Consequently, we hypothesize that there may be important differences between the ecological niches of *P. husabensis* and *R. bradfieldi*. We address this hypothesis by comparing the morphology, microhabitat characteristics, daily activity patterns, thermal biology, and feeding ecology for the two species at a site where they both occur. Based on previous work highlighting ecological niche specialization within lizard

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communities (e.g., Pianka, 1986), we predict that *P. husabensis* and *R. bradfieldi* will show important differences in their ecologies which may allow these two species to coexist in sympatry.

2. Methods

2.1. Study site

We studied lizards at a site alongside the dry Swakop River, Namibia, at Hildenhof, about 40 km east of Swakopmund (22° 42.049′ S, 14° 54.890′ E; 210 m; see Murray et al., 2014, 2015 for further details). This site consists of bare rocky slopes with scattered shrubs such as *Zygophyllum stapffii* and *Lycium* sp. growing in friable substrates at their bases, as well as isolated trees including *Acacia erioloba, Tamarix usneoides*, and *Faidherbia albida* growing in the adjacent, dry river bed. Mean annual precipitation in the area is about 25 mm (Eckardt et al., 2013), and fog events, currently of unknown number, reach the site. Lizard activity may vary with season (Huey et al., 1977; Adolph and Porter, 1993), so we studied lizards during two seasons, austral summer (December 2012—January 2013) and austral autumn (May 2013). Daily mean (24 h) air temperature was 22.1 ± 1.6 °C (daily maximum temperature 30.9 ± 0.7 °C and daily mean minimum temperature 16.3 ± 0.3 °C) in December through January. In May, 24 h air mean temperature was 22.4 ± 5.0 °C (daily maximum temperature 35.3 ± 1.3 °C and daily minimum temperature 13.0 ± 1.3 °C).

2.2. Morphology, activity and temperature

We previously reported aspects of the morphology, foraging behavior, field metabolic rates, and thermal biology of *P. husabensis* (Murray et al., 2014) and *R. bradfieldi* (Murray et al., 2015). Here we compared lizard snout-vent length (SVL; ±1.0 mm) and body mass (±0.1 g; Acculab PP-250B; Goettingen, Germany) of captured individuals of the two species. Lizards of both species were active for only part of the 24 h day; at other times they were in retreats and not visible to us. We surveyed the field site for lizard activity between sunrise and sunset on 16 days in summer and 12 days in autumn. We compared the time at which we observed and captured lizards of both species to assess the timing of their activity. Finally, we compared body temperature (taken within five seconds of capture) and microhabitat temperature (air and substrate temperature at lizard locations) between the two species. We used a type T thermocouple probe and calibrated digital thermometer (±0.2 °C; Omega HH202A; Stamford, CT, USA) inserted approximately 10 mm into the cloaca to measure lizard body temperature and substrate and air temperature (10 mm above the ground) at all of the locations where lizards were observed or captured. We also recorded the substrate type (gravel, rock, sand, silt, silty-sand, gravelly-sand) at which each active lizard was located.

2.3. Diet analyses

During May 2013 we noosed a subset of observed lizards and held them overnight in clean cotton bags, and then released them the following day at their capture sites. We collected any fecal pellets that had been deposited in the bag. If the lizards defecated, it was always observed as a single pellet. We dissected each pellet in petri dishes with 70% ethanol under a binocular dissecting microscope and identified arthropods to the lowest possible phylogenetic level (usually order) using published works on southern African arthropods (Scholtz and Holm, 1985; Picker et al., 2004). We were able to identify soft-bodied prey like termites, larvae, and spiders in lizard fecal pellets from their sclerotized and indigestible portions, such as spider carapaces, head capsules, cuticle, and mandibles.

Arthropod remains generally were fragmentary, making the estimation of prey volume unreliable, but sclerotized parts could be counted using the minimum numbers criterion (Carretero and Cascio, 2010). We estimated lizard diet by calculating the abundance and frequency of occurrence of arthropod prey within the fecal pellets.

We used the inverse of Simpson's (1949) diversity measure to estimate dietary niche breadth (*B*):

$$B = 1 \left/ \sum_{i=0}^{n} p_i^2 \right.$$

where *p* is the proportional utilization of prey item *i*, and *n* is the total number of prey categories. A value of 1 indicates specialization on a single prey type, whereas a value of *n* would represent non-selective use of all prey types. We estimated symmetrical dietary niche overlap (O_{jk}) between *P. husabensis* and *R. bradfieldi* by using Pianka's similarity index (Pianka, 1973):

$$O_{kj} = O_{jk} = \sum_{i=1}^{n} P_{ij}P_{ik} \left/ \sqrt{\sum_{i=1}^{n} P_{ij}^2 \sum_{i=1}^{n} P_{ik}^2} \right.$$

where *j* and *k* are represent the two lizard species for which the overlap is computed, and *P* is the proportional utilization of prey type *i*. Niche overlap can range between 0 (no dietary overlap) to 1 (complete dietary overlap).

2.4. Statistical analyses

We used SigmaPlot 8.0 (Systat Software Inc., San Jose, CA, USA), Microsoft Excel 2007 (Microsoft Corp., Redmond, WA, USA), IBM SPSS 21.0 (SPSS Inc., Chicago, IL, USA), and Minitab 16.0 (Minitab Inc., State College, PA, USA) for all analyses. Data not normally distributed were analyzed with a Mann—Whitney test. We compared body size between species (SVL and mass) and sexes with two-way ANOVAs using species and sex as factors. The body temperature, substrate temperature, and air temperature for both species across both seasons were also compared using two-way ANOVAs that used season and species as factors, as well as partial correlation analyses to compare the relative magnitudes of the individual effects of substrate and air temperature on body temperature. Within season differences in the comparison of body temperature between species were evaluated using ANCOVAs (using substrate and air temperatures as covariates). We used a likelihood ratio χ^2 test with a Bonferroni corrected test of proportions to test for differences in the proportional use of different substrate types. Significance was accepted at $\alpha = 0.05$ and values are reported as mean ± SD.

3. Results

3.1. Morphology

Lizard SVL (Table 1) did not differ between the species (two-way ANOVA; species: $F_{1,184} = 2.66$; $P = 0.11$) but did differ significantly between sexes with males longer than females (two-way ANOVA; sex: $F_{1,184} = 11.87$; $P = 0.001$), and the sex*species interaction was significant (two-way ANOVA; sex*species: $F_{1,184} = 4.12$; $P = 0.044$).

Female *P. husabensis* were significantly longer than female *R. bradfieldi* ($P = 0.018$), while the lengths of male *R. bradfieldi* and male *P. husabensis* were similar ($P = 0.763$). Mass differed significantly between the species (two-way ANOVA; species: $F_{1,184} = 43.64$; $P < 0.001$) and sexes (two-way ANOVA; sex: $F_{1,184} = 39.09$; $P < 0.001$), but the sex*species interaction was not

Table 1
Comparison of mean *Pedioplanis husabensis* and *Rhoptropus bradfieldi* snout-vent length (SVL; mm) and body mass (g) during December–January (summer) and May (autumn) from Murray et al. (2014, 2015).

Trait	*P. husabensis*	*R. bradfieldi*
SVL – male (mm)	52 ± 4	52 ± 4
	n = 61	n = 43
SVL – female (mm)	51 ± 4	49 ± 4
	n = 48	n = 36
Body mass – male (g)	3.0 ± 0.6	3.9 ± 1.0
	n = 61	n = 43
Body mass – female (g)	2.5 ± 0.4	3.1 ± 0.8
	n = 48	n = 36

significant (two-way ANOVA; sex*species: $F_{1,184} = 2.74$; $P = 0.10$). On average, in both species, males were heavier than females at the times that they were sampled, and both male and female *R. bradfieldi* were heavier than their *P. husabensis* counterparts (Table 1).

3.2. Activity

R. bradfieldi and *P. husabensis* could be observed from the same vantage points, but the microhabitat (substrate type) at which lizards were observed differed between the two species. We always observed *R. bradfieldi* only on rock (Fig. 1). *P. husabensis* was

Fig. 1. Substrate types for active *Rhoptropus bradfieldi* (white bars; Dec.–Jan., n = 77; May, n = 98) and *Pedioplanis husabensis* (solid bars; Dec.–Jan., n = 87; May, n = 112). Data are presented as the percentage of total observations for that species in a) December–January (summer) and b) May (autumn).

observed on a variety of substrate types, predominantly rock, gravel, sand, and silt (Fig. 1).

There were significant differences in the proportional use of substrate type by *P. husabensis* during summer and autumn (likelihood ratio $\chi^2_5 = 30.0$; $P < 0.001$). This difference was driven by *P. husabensis* being sighted less often on rock, and more often on silt substrates, during May compared to December–January (z-test of column proportions; $P < 0.05$; Fig. 1). We did not quantify surface inclination at lizard locations, but made qualitative note that most *R. bradfieldi* were seen on approximately vertical rock faces, while most *P. husabensis* were seen on gently sloping rock surfaces or flat expanses of friable substrate. *P. husabensis* used crevices and fissures among broad expanses of rock exclusively as shelter, only rarely sheltering under small rocks resting superficially on the surface, and never were observed digging or using soil burrows. In the morning, *P. husabensis* moved out of their refuges and down the rocky slopes to forage amongst scattered shrubs growing in the silt and sand at the base of the rocky slopes. As temperatures increased by mid-morning, lizards moved back up into the cooler rocky slopes. We believe that *P. husabensis* is capable of scaling vertical rock faces, although we saw that happening only briefly.

R. bradfieldi were active throughout the day, and activity generally conformed to a bimodal pattern of activity in December–January as well as May (Fig. 2). Activity peaks occurred between 07:00–11:00 and at 17:00–18:00 in December–January and between 07:00–09:00 and between 14:00–17:00 in May.

P. husabensis activity conformed to a unimodal pattern of activity well before solar noon during both seasons, with peak *P. husabensis* activity between 08:00–11:00 during December–January and 09:00–11:00 in May. The peak activity occurred approximately four hours after sunrise during both periods (Fig. 2). In December–January, there were no lizards active for at least two hours after solar noon, but a few lizards emerged before sunset as they also did during May.

3.3. Temperature

Within a species there was no difference in the body temperatures of males and females so we combined them in all subsequent analyses. Lizard body temperature (Fig. 2) differed significantly across season (two-way ANOVA; season: $F_{1,202} = 45.42$; $P < 0.001$) and between species (two-way ANOVA; species: $F_{1,202} = 41.94$; $P < 0.001$).

The interaction between season and species was not significant (two-way ANOVA; season*species: $F_{1,202} = 1.87$; $P = 0.17$). In both species body temperatures of lizards active during May were higher than for lizards active during December–January (Murray et al., 2014, 2015, Fig. 3). Though lizard body temperatures differed, the average substrate temperature at lizard locations did not differ between seasons (two-way ANOVA; season: $F_{1,304} = 0.002$; $P = 0.97$) and the season*species interaction was not significant (two-way ANOVA; season*species: $F_{1,304} = 2.67$; $P = 0.10$). The relationship between *P. husabensis* body temperature and substrate temperature during December–January ($T_b = 0.09(T_{sub}) + 30.9$; $r^2 = 0.11$; $P = 0.009$) had a significantly lower slope (ANCOVA; $F_{1,128} = 21.60$; $P < 0.001$) and higher intercept (ANCOVA; $F_{1,128} = 22.34$; $P < 0.001$) than the equivalent relationship in *R. bradfieldi* ($T_b = 0.36(T_{sub}) + 21.2$; $r^2 = 0.43$; $P < 0.001$). Similarly, during May, the correlation between *P. husabensis* body temperature and substrate temperature ($T_b = 0.19(T_{sub}) + 29.0$; $r^2 = 0.19$; $P = 0.003$) had a lower slope (ANCOVA; $F_{1,68} = 6.78$; $P = 0.011$) and higher intercept (ANCOVA; $F_{1,68} = 7.42$; $P = 0.008$) than that of *R. bradfieldi* ($T_b = 0.44(T_{sub}) + 19.3$; $r^2 = 0.53$; $P < 0.001$).

The substrate temperatures recorded where lizards were captured at varied significantly between the two species (two-way
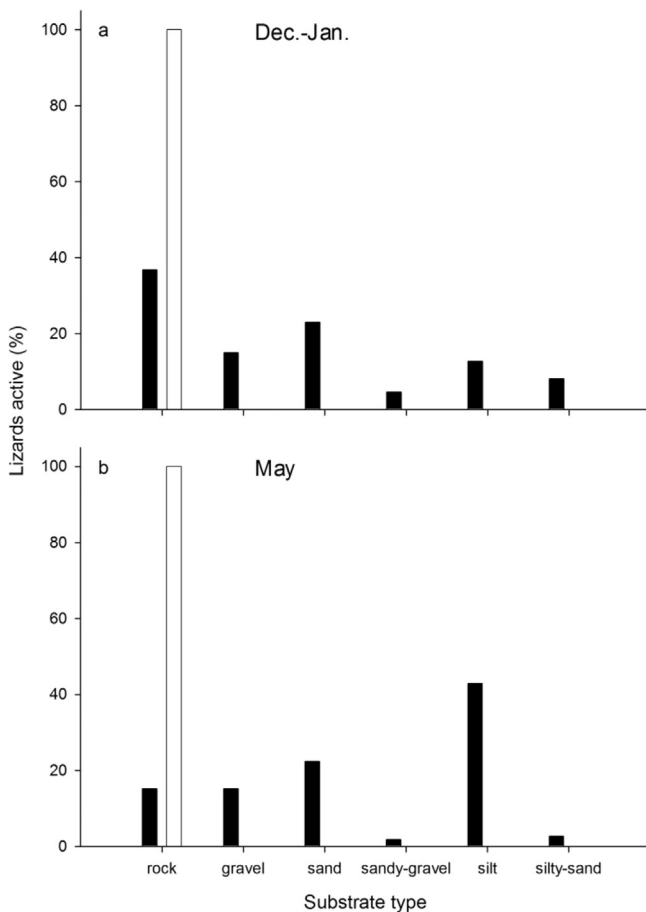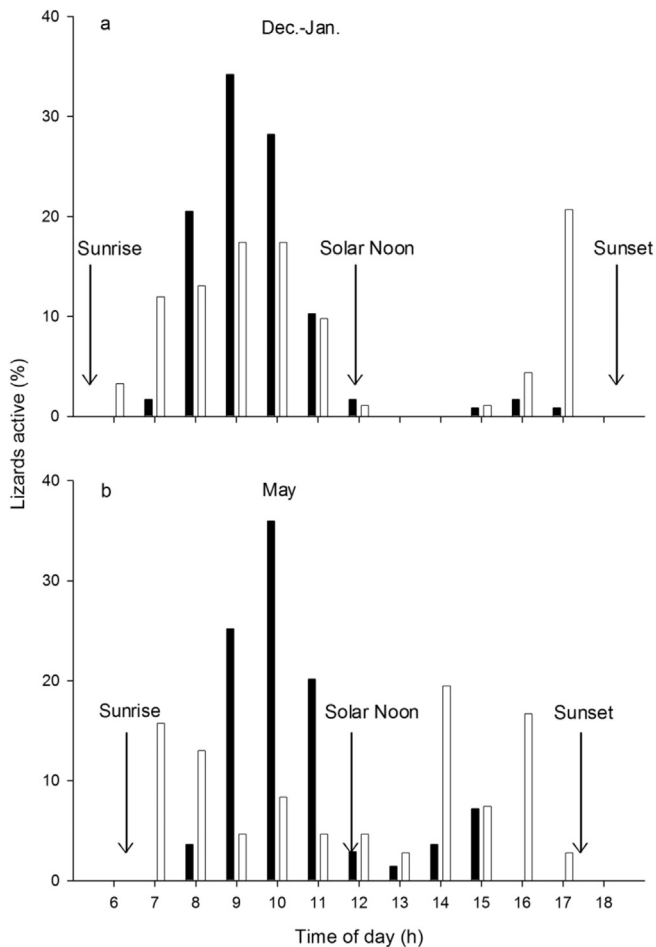
Fig. 2. Diurnal activity of *Rhoptropus bradfieldi* (white bars; Dec.–Jan., $n = 77$; May, $n = 98$) and *Pedioplanis husabensis* (solid bars; Dec.–Jan., $n = 87$; May, $n = 112$). Data are presented as the proportion of the total observed lizards across the entire respective seasonal observation periods that were active within one hour intervals during a) December–January (summer) and b) May (autumn). Average time of sunrise was 05:08 during December–January and 06:14 during May. Average time of sunset was at 18:38 during December–January and 17:21 during May. Solar noon was at 11:53 during December–January and 11:48 during May. Times of day are shown as Namibian standard time (GMT + 2). Clock time in December–January was one hour later, because of a daylight savings shift.

ANOVA; species: $F_{1,304} = 123.19$; $P < 0.001$; Fig. 3). *R. bradfieldi* were not found at substrate temperatures >45 °C, while *P. husabensis* frequently were (Fig. 3). In both seasons *P. husabensis* body temperature was above that of the substrate at cool temperatures (e.g., <30 °C) and substantially below substrate temperature at warmer temperatures (e.g., >40 °C; Fig. 3). Similarly, when found on substrate temperatures <30 °C, *R. bradfieldi* body temperatures were substantially warmer than substrate temperatures, but were slightly cooler than substrate temperatures at substrate temperatures >35 °C (Fig. 3).

Air temperatures at *P. husabensis* locations were slightly higher than air temperatures at *R. bradfieldi* locations (two-way ANOVA; species: $F_{1,305} = 26.74$; $P < 0.001$; Fig. 3), but the ranges of air temperatures for the two species were similar. Air temperatures at lizard locations also did not vary across seasons (two-way ANOVA; season: $F_{1,305} = 3.13$; $P = 0.08$), and the season*species interaction was not significant (two-way ANOVA; season*species: $F_{1,305} = 0.73$; $P = 0.40$). Across seasons, *R. bradfieldi* and *P. husabensis* body temperatures were consistently warmer than air temperatures until the highest recorded air temperatures during our study were reached, at which point body temperature was similar to air temperature

(Fig. 3). In December–January the regressions relating *P. husabensis* body temperature and air temperature ($T_b = 0.22(T_{air}) + 27.5$; $r^2 = 0.17$; $P = 0.001$) to that of *R. bradfieldi* body temperature ($T_b = 0.39(T_{air}) + 21.6$; $r^2 = 0.37$; $P < 0.001$) had similar slopes (ANCOVA; $F_{1,128} = 3.55$; $P = 0.062$), but *P. husabensis's* intercept was significantly higher (ANCOVA; $F_{1,128} = 5.02$; $P = 0.027$). During May the slope was significantly greater (ANCOVA; $F_{1,68} = 5.40$; $P = 0.023$) and the intercept significantly lower (ANCOVA; $F_{1,68} = 9.54$; $P = 0.003$) for the body temperature of *R. bradfieldi* versus air temperature ($T_b = 0.38(T_{air}) + 22.8$; $r^2 = 0.51$; $P < 0.001$) compared to that of *P. husabensis* ($T_b = 0.17(T_{air}) + 31.6$; $r^2 = 0.14$; $P = 0.011$).

Substrate and air temperatures are not independent measures of environmental temperature because they were significantly correlated for *R. bradfieldi* ($T_{substrate} = 0.79(T_{air}) + 9.8$; Pearson correlation: $r = 0.75$, $P < 0.001$) and *P. husabensis* ($T_{substrate} = 0.81(T_{air}) + 14.8$; Pearson correlation: $r = 0.51$, $P < 0.001$). Air and substrate temperatures have previously been shown to be significantly correlated with body temperatures in *R. bradfieldi* (partial correlation body temperature-substrate temperature = 0.39, $P < 0.001$, partial correlation body temperature–air temperature = 0.32, $P = 0.001$; Murray et al., 2015). However, for *P. husabensis*, substrate temperatures were only marginally correlated with body temperature, compared to the significant influence of air temperature. Relative to *R. bradfieldi*, both substrate and air temperatures were less robust in their ability to predict *P. husabensis* body temperature (partial correlation body temperature-substrate temperature = 0.20, $P = 0.051$, partial correlation body temperature–air temperature = 0.29, $P = 0.003$).

3.4. Diet

We identified 317 individual prey items from 13 arthropod orders and the order gastropoda, from 22 fecal pellets that originated from 16 female and six male *P. husabensis*. Each pellet contained an average of 15 ± 9 (range 3–33; median 10) individual prey items, and there was no difference between the number of prey items in the pellets from female (median = 9) and male *P. husabensis* (median = 11; Mann–Whitney test; U = 178.5; $P = 0.71$). We also identified 604 individual prey items from ten arthropod orders from 13 fecal pellets that originated from five male, seven female, and one unsexed *R. bradfieldi*. There were 46 ± 22 prey items per fecal pellet, and female *R. bradfieldi* had marginally fewer prey items per pellet (35 ± 12) than did males (61 ± 28; two sample t-test; $t_{10} = 2.19$; $P = 0.054$). The prey categories were divided into 14 groups for analyses of niche breadth and overlap (Table 2).

In the season that we surveyed (May), *P. husabensis* foraged primarily on termites, which made up 71% of all its prey items and were found in 91% of its fecal pellets (Table 2). Other important prey categories included beetles (8% of all prey, 55% fecal pellets), spiders (5% of all prey, 55% fecal pellets), and pseudoscorpions (4% of all prey, 23% of fecal pellets; Table 2). The dietary niche breadth (B; by frequency of occurrence) was 1.9, with a possible range of one to 14. By contrast, *R. bradfieldi* foraged primarily on ants, which accounted for 87% of all identified prey items and were found in all *R. bradfieldi* pellets (Table 2). Species in the *Lepisiota capensis* group were the ant species consumed most frequently (74% of all ants in pellets) and were in the pellets of 85% of the *R. bradfieldi* (Table 2). Beetles made up 6% of prey items and were found in 54% of the fecal pellets. Wasps and bees made up 3% of prey items and were found in 69% of the pellets (Table 2). The dietary niche breadth was 1.3 (out of a possible range of one to 14). The dietary niche overlap (O_{jk}) between *R. bradfieldi* and *P. husabensis* was 0.02.

4. Discussion

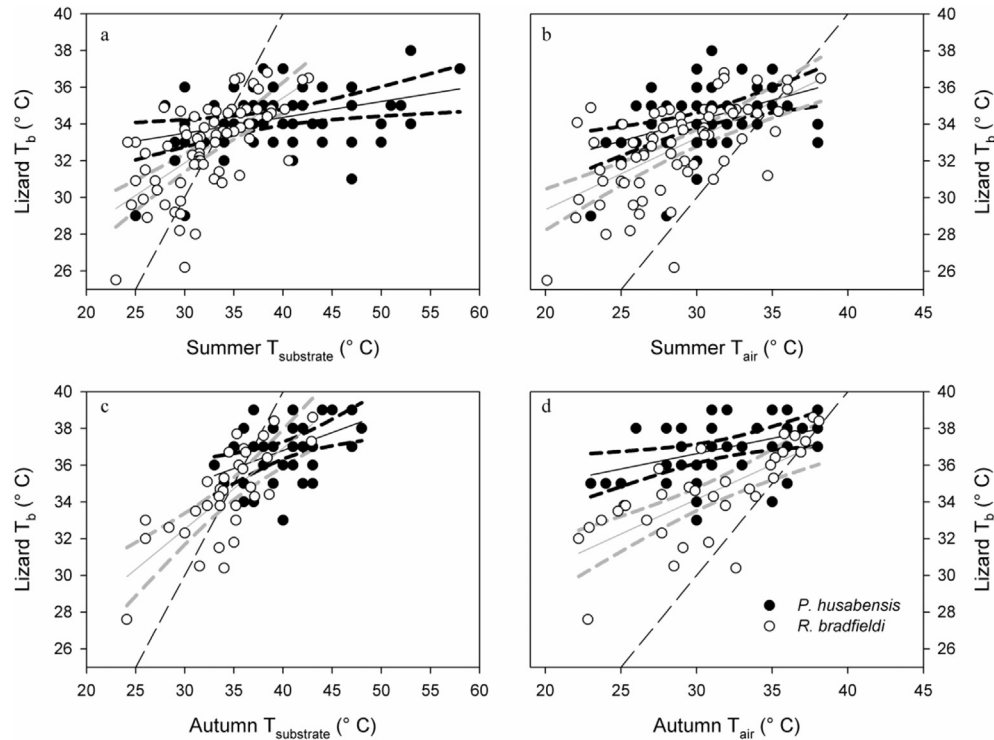We studied several aspects of the ecological niche for two

Fig. 3. The relationship between *Pedioplanis husabensis* (solid circles) and *Rhoptropus bradfieldi* (white circles) body temperature (T_b) and substrate and air temperature. December–January (summer) a) substrate temperature (T_{sub}); *P. husabensis*: $T_b = 0.09(T_{sub}) + 30.9$; $r^2 = 0.11$, $P = 0.009$; *R. bradfieldi*: $T_b = 0.36(T_{sub}) + 21.2$; $r^2 = 0.43$, $P < 0.001$, b) air temperature (T_{air}); *P. husabensis*: $T_b = 0.22(T_{air}) + 27.5$; $r^2 = 0.17$, $P = 0.001$; *R. bradfieldi*: $T_b = 0.39(T_{air}) + 21.6$; $r^2 = 0.37$, $P < 0.001$, and May (autumn) c) substrate temperature; *P. husabensis*: $T_b = 0.19(T_{sub}) + 29.0$; $r^2 = 0.19$, $P = 0.003$; *R. bradfieldi*: $T_b = 0.44(T_{sub}) + 19.3$; $r^2 = 0.53$, $P < 0.001$, and d) air temperature; *P. husabensis*: $T_b = 0.17(T_{air}) + 31.6$; $r^2 = 0.14$, $P = 0.011$; *R. bradfieldi*: $T_b = 0.38(T_{air}) + 22.8$; $r^2 = 0.51$, $P < 0.001$. Regressions are shown relative to the line of identity ($T_{body} = T_{substrate}$ or T_{air}). Dashed lines (*P. husabensis* — black; *R. bradfieldi* — gray) represent 95% confidence intervals. See Murray et al. (2015) for *R. bradfieldi* thermal data.

species of sympatric, insectivorous desert lizards living in rocky habitat of the Namib Desert. In other deserts, assemblages of lizard species occurring in similar habitats often differ in their dietary, spatial or temporal niches, which is likely to reduce interspecific competition (Pianka, 1986; Vitt et al., 2000a,b). The lizard species *R. bradfieldi* and *P. husabensis* also showed important differences in multiple niche dimensions. Their niches differed in feeding ecology, and temporal, spatial and thermal microhabitats.

R. bradfieldi and *P. husabensis* were similar in being sexually dimorphic, with males 25–30% heavier than females. For both sexes, *R. bradfieldi* were heavier than *P. husabensis*, but their SVLs were similar (Table 1), so *P. husabensis* was more gracile than the stockier *R. bradfieldi*. These differences in body form are consistent with the lighter and more gracile *P. husabensis* being an active forager (Murray et al., 2014) and the stockier *R. bradfieldi* being a sit-and-wait forager (Murray et al., 2015). Actively-foraging lizards often are active for a smaller portion of the day than are sit-and-wait foraging lizards, but their rate of energy intake can be higher (Anderson and Karasov, 1981; Nagy et al., 1984). *P. husabensis* mainly was active only during the morning, while *R. bradfieldi* were active for much of the daylight hours, showing a bimodal pattern of activity with a dip around solar noon (Fig. 2), a pattern typical of desert lizards during hot times of the year (Grant, 1990; Seely et al., 1990; Adolph and Porter, 1993). The abbreviated unimodal activity pattern of *P. husabensis* has been reported previously (Cunningham et al., 2012) and also was the activity pattern of the widely-foraging Kalahari Desert lacertids *Nucras tessellata* and *Heliobolus lugubris* (Huey et al., 1977; Nagy et al., 1984). Further work is required to assess whether the unimodal pattern of daily

activity that *P. husabensis* shows is related to thermal constraints in its environment, predation risk or prey availability. Other Namib species, such as diurnal tenebrionid beetles, generally respond to rigorous summer temperature regimes by showing a daily pattern of bimodal rather than unimodal activity (Holm and Edney, 1972; Wharton and Seely, 1981). In addition to differences in daily activity periods, the substrates upon which *P. husabensis* and *R. bradfieldi* were active were different (Fig. 1). We found *R. bradfieldi* on vertically-orientated expanses of rock, and *P. husabensis* on a variety of substrate types ranging from fine silt to gently-sloping rock surfaces. *P. husabensis* were rarely observed on vertical surfaces. We found here that the proportion of *P. husabensis* active on rock surfaces declined by half between December–January and May, while those active on a silt substrate more than tripled, and we expect these substrates to have distinct thermal properties (Fig. 1). Operative temperature models may further elucidate lizard preferences for, and use of different substrates.

Substrate differences as well as the distinct patterns of daily activity may play an important role in the significant differences seen in the thermoregulation of *R. bradfieldi* and *P. husabensis*. On average, the body temperatures of *R. bradfieldi* were two to three degrees lower than those of *P. husabensis*, and the steeper slope in the relationship between lizard body temperature and substrate temperature for *R. bradfieldi* compared to *P. husabensis* implied that substrate temperatures played a larger role in determining body temperature for *R. bradfieldi* (Fig. 3). Additionally, *R. bradfieldi* were never documented on a substrate hotter than 45 °C, while *P. husabensis* routinely were (Fig. 3). Although on average,

Table 2
Prey composition of *Pedioplanis husabensis* and *Rhoptropus bradfieldi* fecal pellets. The number of individual prey items (No.), contribution of that item expressed as a percentage of total number of prey items identified (%N), and percentage of pellets that contained a prey item (%Freq) from 22 *P. husabensis* and 13 *R. bradfieldi*.

Prey item	P. husabensis			R. bradfieldi		
	No.	%N	%Freq	No.	%N	%Freq
Arachnids[a]						
Araneae	15	5	55	8	2	31
Salticidae	6	2	23	1	<1	8
unidentified	9	3	41	7	1	23
Acari	5	2	14	1	<1	8
ticks	4	1	9	–	–	
mites	1	<1	5	1	<1	8
Pseudoscorpionidae	11	4	23	1	<1	8
Solpugidae	3	1	14	2	<1	15
Insecta						
Coleoptera[a]	25	8	55	33	6	54
adults	24	8	55	33	6	54
larvae	1	<1	5	–	–	–
Hemiptera[a]	1	<1	5	4	1	23
Homoptera[a]	–	–	–	3	1	23
Hymenoptera	9	3	27	544	90	100
Formicidae[a]	1	<1	5	527	87	100
Lepisiota sp.	–	–	–	447	74	85
Camponotus maculatus	–	–	–	5	1	39
unidentified	1	<1	5	75	12	85
Wasps/Bees[a]	8	3	23	17	3	69
Isoptera[a]	224	71	91	–	–	–
Hodotermes mossambicus	61	19	64	–	–	–
Amitermes sp. (soldier)	15	5	27	–	–	–
Psammotermes allocerus (soldier)	12	4	23	–	–	–
unidentified soldiers	12	4	68	–	–	–
unidentified workers	124	39	55	–	–	–
Lepidoptera[a]	2	1	9	–	–	–
adult	2	1	9	–	–	–
Neuroptera[a]	6	2	23	2	<1	15
adult	1	<1	5	–	–	–
larvae	5	2	18	2	<1	15
Orthoptera[a]	1	<1	5	–	–	–
grasshopper	1	<1	5	–	–	–
Thysanura[a]	–	–	–	1	<1	8
Unidentified insect[a]	5	2	23	4	1	31
Unidentified larvae[a]	9	3	41	1	<1	8
Snail[a]	1	<1	5	–	–	–
Total	**317**	**100**		**604**	**100**	
Niche breadth		**1.9**			**1.3**	

[a] Prey categories used in the analyses of dietary niche breadth and overlap.

R. bradfieldi were active at slightly lower air temperatures compared to *P. husabensis*, this difference may not be of biological importance, particularly as the species were active over a similar range of air temperatures (Fig. 3). The body temperatures of the lizards would have been determined by the balance of conductive, convective, and radiant heat transfer at their locations, as well as by their morphology. With substrate temperature higher than body temperature, radiant and conductive heat transfer would have imposed heat load on the lizards, especially if they were in direct solar radiation. With air temperature below body temperature, the lizards would have lost heat by convection, and when *P. husabensis* were active on very hot substrate temperatures above their critical thermal maximum (e.g., >44 °C; S. Kirchhof, personal communication), lizards always had access to air temperatures considerably cooler than these hot temperatures (Fig. 3). Both the gracile shape and the movement of *P. husabensis* would have increased its convective heat transfer coefficient, relative to that of *R. bradfieldi*, making *P. husabensis* better able to employ convective cooling. Indeed, when captured on the hottest substrates *P. husabensis* had body temperatures almost 20 °C less than those of the substrate

(Fig. 3). Active body temperatures of *P. husabensis* were distinct from substrate temperatures, which may be because *P. husabensis* thermoregulates more actively than does *R. bradfieldi*.

Differences in the timing of daily activity also were likely to have influenced the different microclimate temperatures experienced by the two lizard species. Consequently, it is important to compare the microhabitat temperatures for both species of lizards recorded at the same time of day. For example, for lizards active at the same time (between 08:00–09:00 during December–January; results were similar for comparisons of other times), the average substrate temperature was 40.4 ± 6.7 °C for active *P. husabensis*, but was significantly lower at 33.4 ± 6.1 °C, for active *R. bradfieldi* (t-test; $t_{26} = -2.87$; $P = 0.008$). Yet, over the same time period, the air temperatures recorded where *P. husabensis* were active (31.4 ± 4.4 °C) were not significantly higher than the air temperatures (29.3 ± 4.1 °C) where *R. bradfieldi* were active (t-test; $t_{29} = -1.36$; $P = 0.18$). These observations, together with the partial correlation analyses, imply that the substrate temperature plays a more significant role in the regulation of active body temperatures for the stockier and more sedentary *R. bradfieldi* than for the gracile and widely-ranging *P. husabensis* (Fig. 3). As a result, *R. bradfieldi* were confined to microhabitats with a more restricted thermal range than were *P. husabensis* (Fig. 3). However, deciding whether the different microhabitats were selected, or were inevitable consequences of the foraging behavior, require more detailed analyses of the thermal mosaic in the habitat.

It may well have been that access to different locations led to *P. husabensis* and *R. bradfieldi* being dietary specialists, with almost no dietary overlap between species, as our dissection of lizard fecal pellets indicated (Table 2). Estimates of dietary niche breadth (*B*) were similarly narrow for *R. bradfieldi* (1.3) and *P. husabensis* (1.9), and dietary overlap (O_{jk}) was 0.02 (on a scale of 0–1 with 0 indicating no overlap), indicating that the two species were feeding on different prey in the same habitat. Many species of actively-foraging lizards feed extensively on termites (Huey and Pianka, 1981; Pianka, 1986; van der Meer et al., 2010), and *P. husabensis* was no exception (Table 2). In contrast, *R. bradfieldi* is a sit-and-wait forager, which we now know to specialize on hymenopteran insects, particularly ants (Table 2), as do many other diurnal sit-and-wait foraging lizards such as the diurnal geckos *Lygodactylus capensis* (Pianka and Huey, 1978) and *Pristurus* sp. (Arnold, 2009). The stomachs of lizards that specialize on ants may occupy a disproportionately large part of total body volume, consistent with the large numbers of ants that must be ingested to meet total energetic requirements (Pianka, 1986). While we do not know the comparative stomach volumes of *R. bradfieldi* and *P. husabensis*, *R. bradfieldi* fecal pellets contained more than twice as many prey items than did *P. husabensis* pellets. Male and female *P. husabensis* contained similar numbers of prey per pellet, but female *R. bradfieldi* pellets contained slightly more than half of the prey items than male fecal pellets did. Examination of additional *R. bradfieldi* pellets is necessary in order to investigate if there are real sex-based differences in its feeding ecology.

Although fecal sample analyses do not necessarily reflect long-term dietary trends (Pérez-Mellado et al., 2011), the data we present here represent the first quantitative diet study for *P. husabensis* and *R. bradfieldi*. An understandable concern in examining lizard diet via fecal pellet analyses is that soft-bodied arthropod prey may be under-represented. However, past work has shown that soft-bodied arthropods are not under-represented in lizard diet as estimated from fecal pellet analysis (e.g., Pérez-Mellado et al., 2011), and we were able to identify soft-bodied prey by scrutinizing dissected pellets for characteristically hard parts of otherwise soft prey, such as termite mandibles. We examined relatively few pellets, but prior work has shown that prey diversity of lizards

may be estimated accurately from small samples (Bombi et al., 2005; Sutherland, 2011). What we do not know yet is whether the diets of these two lizard species change with season. Although in May one distinct and non-overlapping prey category formed the majority of the diet for each of the two lizard species, they regularly fed on other prey as well. Beetles, for example, occurred in more than half of the pellets of both species, but made up only 6% of total prey eaten for each species.

Lizards often are selective feeders, not simply foraging on whatever prey is most abundant (Pianka, 1986; Vitt et al., 2003). Desert lizards indeed may select their microhabitats based on the availability of preferred prey (Vitt and Pianka, 2007). We did not estimate arthropod prey availability quantitatively by microhabitat and consequently we are unable to evaluate prey availability where *P. husabensis* and *R. bradfieldi* forage. We think that *P. husabensis* may forage in different microhabitats based on where their preferred termite prey is located. For example, we noted that termite activity was most frequent and obvious among the shrubs and woody debris in loose, sandy substrates where we saw most *P. husabensis* foraging. However, relative to the more versatile *P. husabensis*, the specialized adhesive toe pad structure allowing *R. bradfieldi* to nimbly traverse vertical surfaces would probably be very inefficient for moving across loose, sandy substrates and digging up subterranean termites. Indeed, we observed *R. bradfieldi* using rock substrates exclusively (Fig. 1). Although we did not quantitatively estimate prey availabilities where geckos foraged, we observed ants most frequently on rocky slopes, and it is possible that *R. bradfieldi* were eating primarily ants because that was the arthropod most often encountered in their microhabitats. Importantly, we do not think that the geographic distributions of *R. bradfieldi* or *P. husabensis* are limited by the availability of their prey species. The ant and termite species that we found included in the diets of *R. bradfieldi* and *P. husabensis* are widespread throughout southern Africa (Uys, 2002; Picker et al., 2004).

R. bradfieldi and *P. husabensis* are both endemic to the Namib Desert. *R. bradfieldi* is broadly sympatric with *P. husabensis* across the entire range of *P. husabensis*, but in portions of its range *R. bradfieldi* does not interact with *P. husabensis* (Bauer and Good, 1996). There it may share the same habitat with other species of similarly-sized lacertid lizards like *Pedioplanis inornata* (Berger-Dell'Mour and Mayer, 1989). Our study site was typical of the specialized rocky habitats that *R. bradfieldi* and *P. husabensis* occupy sympatrically (Berger-Dell'Mour and Mayer, 1989; Cunningham et al., 2012).

We have focused on one species of diurnal gecko and one species of lacertid lizard living in sympatry, but desert lizard communities are complex assemblages, with up to 40 species coexisting at one hot desert site (Pianka, 1969), and with different species potentially occupying distinct positions within the available niche space (Pianka, 1973, 1986; Pérez-Mellado, 1992). Although *R. bradfieldi* was the only species of *Rhoptropus* gecko that occurred on our study site, in other regions of the Namib Desert several species of *Rhoptropus* gecko may occur in the same location, although they are not usually found in the same microhabitat and may not overlap in body size (Odendaal, 1979; Haacke and Odendaal, 1981; Bauer and Good, 1996). Several species of lacertid lizards (e.g., *P. inornata*, *Pedioplanis undata*, *Pedioplanis breviceps*, and *Meroles suborbitalis*) also occur within close vicinity of our study site, but we did not see any lacertid species other than *P. husabensis* during either of our study periods. Although we observed several additional species of lizards from other families on our site, this system is likely to be a less complex lizard community with significantly less species diversity than other better studied desert lizard communities (e.g., Pianka, 1969). Nonetheless, a more thorough view of lizard niche partitioning would include

data on these other species occurring on our study site.

The mechanisms that are behind the ability of a diverse assemblage of lizard species to inhabit one area include a partitioning of the trophic niche as well as variation in when and where lizard species tend to be active (Pianka, 1973; Barbault and Maury, 1981). Indeed, we found that two sympatric insectivorous lizard species in the Namib Desert use different microhabitats, forage on different arthropod resources, and have distinct patterns of activity and thermoregulation. *P. husabensis* forages mainly on termites and moves widely and often to find its prey, where it sometimes accesses very hot substrates without overheating. Termite abundance was high on friable substrates where most of the vegetation is located (Murray, personal observation) and *P. husabensis* moved across a variety of substrate types as they navigate from their rocky refuges to the silty and sandy flats where prey are located. It seems able to meet its energy needs by foraging for only a brief part of the day, perhaps because termites are such 'profitable' prey items. In comparison, *R. bradfieldi* is a sedentary sit-and-wait forager active for most of the day but apparently confined to less extreme microclimates. *Rhoptropus bradfieldi* satisfies its relatively low energy requirements by feeding on large numbers of ants, which are widespread and mobile, but 'non-profitable' prey. These sympatric lizard species are able to acquire energy through the use of distinct life strategies, and consequently do not occur in the same ecological space.

Acknowledgments

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