

# Intraspecific behavioural variation in the lacertid lizard *Meroles cuneirostris* (Strauch, 1867) (Sauria:Lacertidae)

JACKIE L. CHILDERS<sup>1\*</sup> & DOUGLAS A. EIFLER<sup>2</sup>

<sup>1</sup>*Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA;*

<sup>2</sup>*Erell Institute, 2808 Meadow Drive, Lawrence, Kansas 66047, USA*

**Abstract.**—We characterised behavioural variation between adult male, adult female and juvenile *Meroles cuneirostris*, a diurnal lacertid lizard endemic to the Namib Desert. Variation in microhabitat preference was significant between age classes, as adults spent more time underneath vegetative cover than juveniles. Movement patterns varied between demographic classes as juveniles exhibited movements of higher average durations than adults overall, and spent a greater percentage of time moving than adult females. Juveniles turned their heads more often than adults; all individuals scan their surroundings more frequently in the open sand and near vegetation. An analysis of foraging behaviour indicates that *M. cuneirostris* exhibits relatively few movements per minute (MPM) and a wide range of percentage of time spent moving (PTM), making it difficult to categorise this species as either an ambush or active forager. Furthermore, intraspecific variation in foraging behaviour within this species exists, as adult males and juveniles exhibited higher PTM values than adult females.

**Key words.**—Lizard; Lacertidae; ontogeny; behavioural ecology; Namib Desert; foraging behaviour

## INTRODUCTION

The family Lacertidae is a diverse Old World assemblage of lizards with over 300 species distributed throughout Europe, Asia and mainland Africa (Arnold *et al.* 2007). Previous behavioural and ecological studies have revealed patterns of intraspecific behavioural variation related to ontogenetic and sexual differences. Males and females, as well as juveniles and adults, have been shown to differ in microhabitat use (Podarcis, *Lacerta*; Amat *et al.* 2003; Diego-Rasilla & Pérez-Mellado 2003; Martín & López 2003), locomotor performance (*Eremias*, *Podarcis*; Xu & Ji 2006; Brecko *et al.* 2008), and activity patterns (*Lacerta*; Amat *et al.* 2003). Species occupying desert habitats are of particular interest, as they are often faced with limited resources and harsh and constant climatic conditions. Thus individuals must either compete for shared resources or partition them by exploiting different ecological niches (Ward 2008). Both intraspecific and interspecific niche-partitioning has been documented among desert-dwelling lacertids, with the most commonly observed separations being the timing of daily or seasonal activity, and microhabitat use (Pérez-Mellado 1992; Adamopoulou & Valakos 2005; Roug *et al.* 2007; Du Plessis & Mouton 2011).

---

\*Corresponding author. Email: [jackielynnchilders@gmail.com](mailto:jackielynnchilders@gmail.com)

Here we investigate intraspecific behavioural variation within the Wedge-snouted Desert Lizard (*Meroles cuneirostris* (Strauch, 1867)), a lacertid lizard endemic to the Namib Desert of Namibia (Branch 1998). It is an ideal species for studying behavioural variation and its relation to ontogenetic and sexual differences within a desert-adapted species as its life-history traits include: (1) obvious size differences between both age classes and sexes among adult individuals; (2) small home ranges, making it easy to observe individuals in their natural habitat; and (3) dense populations. To date, previous research on *M. cuneirostris* has primarily focused on its diet and reproductive biology, while behavioural research has been limited and nothing is known about the habits of juveniles (Goldberg & Robinson 1979; Murray & Schramm 1987). In addition, a previous dietary study conducted by Murray and Schramm (1987) included observations in which they describe *M. cuneirostris* employing both active and sit-and-wait foraging tactics. However, they did not include the two standard variables used to measure foraging behaviour—movements per minute (MPM) and percentage of time spent moving (PTM)—thus the foraging mode of this species remains to be quantitatively elucidated (Cooper & Whiting 1999; McBrayer 2004; Kirchhof *et al.* 2010; Du Plessis & Mouton 2012).

The general goals of this study were to (1) identify patterns of intraspecific behavioural variation in *M. cuneirostris*, (2) investigate differences in microhabitat preference between demographic classes and (3) quantitatively assess the foraging behaviour of this species. We predicted that variation in movement patterns and habitat preference would be more pronounced between age classes than sexes due to significant size differences between adults and juveniles—a pattern that has been documented among other lacertid species (Avery *et al.* 1987; Amat *et al.* 2003; Martín & López 2003; Tang *et al.* 2013). Furthermore, considering the results of Murray and Schramm (1987), in which they observed lizards employing both ambush and active foraging tactics to acquire prey items, we hypothesised that the apparent display of both tactics indicates that intraspecific variation in foraging behaviour exists within *M. cuneirostris*.

## METHODS

This study was conducted from 12 December 2011 to 15 January 2012 at Station Dune, located 1 km south of the Gobabeb Research and Training Centre, Erongo, Namibia (23.561986° S, 15.041616° E, datum WGS84; elevation 408 m). This desert region is characterised by an extensive wind-shaped sand dune system that is largely devoid of vegetation, though a variety of grasses and shrubs sparsely inhabit the dunes at their bases. Predominant grasses include several species of Bushman's Grass (*Stipagrostis* sp.), which can be found in the sandy substrate of the dunes, and a few species of Lovegrass (*Eragrostis* sp.), which are common in the gravel plains that extend beyond the dune systems. Lizards were primarily observed using Dune Bushman's Grass (*Stipagrostis sabulicola*) and the Nara plant (*Acanthosicyos horridus*) for cover. However, for the purposes of this study plant species were not taken into account (Müller 2007; Sjöskog 2008). Rain is minimal and droughts may last 4–5 years, however moisture-rich fog rises from the Atlantic Ocean and can extend 50 km inland (Branch, 1998).

All animals were captured along a 500-m transect along the dune base. Prior to collecting behavioural data, individuals were measured (snout-to-vent length), sexed, and then marked for individual identification with unique colour codes using non-toxic paint pens. Captured individuals were processed in a facility at the Gobabeb Research and

Training Centre, and were kept overnight in separate plastic containers. They were then released at the capture site *ca.* 12–14 hours after their initial capture. We allowed 24 hours before collecting any behavioural data in order to minimise any affects from capturing and handling the animals.

Adults and juveniles were distinguished both by size and appearance. Individuals  $\leq 42$  mm snout-to-vent length (SVL) were considered juveniles; this criterion was based on the gap in size distribution observed while marking the population. Additionally in a study conducted by Goldberg and Robinson (1979) the smallest sexually mature female and male *M. cuneirostris* measured 43 and 45 mm in SVL, respectively. Adult females differ from adult males in that they possess a single, distinct, dark pink-orange lateral stripe bordered on either side by a thinner white stripe, which extends from the posterior edge of the eye to the tip of the tail. Adult males lack this striping and possess a more reticulated dorsal pattern (Branch 1998).

Surveys were conducted near the base of the dune as well as within the interdune plains during the morning (08:30–11:30) and afternoon (15:30–19:30) activity periods. These periods were selected based on our observations during preliminary surveys conducted earlier in the field season, in which we noted the time of initial and final sightings of *M. cuneirostris*. During surveys, marked individuals were located and then observed for up to 20 minutes; observations were only recorded once per marked animal. After encountering a marked individual we waited at least one minute before beginning the observation. During observations the observer kept as great a distance as possible while maintaining visual contact, which in some instances required the use of binoculars (minimum distance *ca.* 2 m; maximum distance *ca.* 4 m); all discrete behaviours were manually recorded at the time of occurrence, while continuous behaviours (i.e. time spent moving) were recorded on stopwatches and transcribed following the completion of each observation session. Observations were not done on animals that fled upon approach. Our proximity to animals did not seem to affect their behaviour. Observational data were collected from 84 individuals.

We recorded standard behaviours including head turns, total number of seconds spent immobile (S), posture during sessions of immobility, total number of seconds spent moving (M), and the total number of movements (N); microhabitat data and feeding events were also recorded (Cooper 2005; Keren-Rotem *et al.* 2006; Eifler *et al.* 2007). We also calculated the average duration per movement in seconds (AD) from our recorded data. Head turns were characterised by distinct lateral movements of the head and could be of any magnitude. Any pause or change in direction marked the end of a head turn. Bouts of immobility were recorded any time the animal remained stationary for  $>6$  s; duration and microhabitat data were collected for each bout. The posture of immobile animals was characterised as either splayed (animal is completely prostrate and venter is in contact with the substrate) or erect (animal is stationary and the ventral surface is completely raised off the substrate). Separate movements were recorded as periods of motion separated by pauses  $>4$  s. To determine foraging behaviour, two variables were calculated: the percentage of time spent moving (PTM) and the number of movements per minute (MPM). However, it is important to note that our time threshold for pauses separating movements were 2 s longer than the standard recommended by Cooper (1997), which may have resulted in slightly lower MPM and PTM values. These variables were calculated using the formulas  $PTM = 100(N \times AD)/(M + S)$  and  $MPM = 60N/(M + S)$  (Cooper 2005). The PTM and MPM of all observations were calculated in order to assess intraspecific variation in movement patterns. However, only observations in which a

feeding event was recorded were considered in the final assessment of foraging behaviour in order to ensure that analysed movements were foraging-related.

There were two primary areas in which *M. cuneirostris* allocated its time: among vegetation at the base of the sand dune, or within the gravel plain near the base of the dune. We recognised four microhabitat categories: (1) in vegetation (within cover of the plant); (2) near vegetation (beyond cover and within 0.5 m of the outermost foliage of the plant); (3) in the open (>0.5 m from the base of the plant); or (4) in the gravel plain.

Our data were tested for normality using the Kolmogorov–Smirnov test (Sokal & Rohlf 1995) and Shapiro–Wilk test (Shapiro & Wilk 1965), and we used non-parametric statistics when appropriate. All but two of the 84 animals were observed for the full 20-minute duration (two adults males were observed for 6 and 15 minutes). Thus for each observed lizard behavioural states were summarised as proportions of time, while events were summarised as rates, allowing us to adjust for the shortened observations. Microhabitat use was determined by measuring the proportion of time individuals remained stationary in each of the microhabitat categories. We tested for differences between demographic classes (adult males, adult females and juveniles) using the Kruskal–Wallis one-way analysis of variance test, with subsequent comparisons using Dunn’s test. In instances where no significant differences were found between demographic classes, the results for adult males and adult females were pooled and compared to juveniles using the Mann–Whitney *U* test. Statistical analyses were performed using the programs Minitab 15 (College Park, PA) and R version 3.0.1 (R Core Team 2013) with a significance level of  $P \leq 0.05$ .

## RESULTS

### Morphology

Adult males ( $n = 55$ ) were larger than females ( $n = 41$ ) in mean SVL (males:  $55.75 \pm 5.61$  mm, range = 45–68 mm; females:  $50.63 \pm 3.83$  mm, range = 43–58 mm; two-tailed *t*-test:  $t = 1.99$ ,  $P < 0.001$ ,  $df = 94$ ). Mean juvenile SVL was  $33.3 \pm 3.77$  mm (range = 27–42 mm,  $n = 50$ ). Interestingly, juvenile males and females also appear to be sexually dichromatic, as males possess dorsal patterning similar to adult males, and females are easily distinguished by their bright pink tails. To date, no sexual differences amongst juveniles has ever been noted in *M. cuneirostris*.

### Behavioural Variation

Juveniles turned their heads more often than adults (Mann–Whitney:  $W = 1874$ ,  $P = 0.0005$ ); there appeared to be no such variation among adult males and females (Table 1).

Table 1. Behavioural characteristics [median (range)] for adult ( $n = 49$ ) and juvenile ( $n = 35$ ) *Meroles cuneirostris* during 20-minute focal observation periods.

	Juvenile	Adult	<i>P</i>	<i>W</i>	<i>N</i>
Walking events/h	21 (0–81)	12 (0–63)	0.0635	1692.5	84
Head turns/h	45 (0–99)	24 (0–99)	0.0005	1874.0	84
Splayed sitting/h	15 (0–60)	6 (0–33)	0.0445	1709.5	84
Erect sitting/h	3 (0–24)	3 (0–27)	0.6566	1537.0	84

Among adult males, larger individuals turn their heads more frequently (simple regression analysis:  $P = 0.027$ ,  $R^2 = 20.43\%$ ; Figure 1). Juveniles sat in a splayed configuration more often than adults ( $W = 1709.5$ ,  $P = 0.0445$ ), but there was no difference in how often individual adults and juveniles sat erect (Table 1).

Lizards displayed intraspecific variation in movement patterns. Adults were more likely to have bouts of immobility than juveniles ( $\chi^2 = 4.952$ ,  $df = 1$ ,  $P = 0.026$ ). In addition, median PTM values varied significantly between demographic classes (juveniles: 19.41%, range = 0–53.92%; adult females: 10.92%, range = 0–51.58%; adult males: 11.83%, range = 0–58.33%; Kruskal–Wallis:  $W_2 = 5.89$ ,  $P = 0.0501$ ; Figure 2a) with juveniles displaying significantly higher PTM values than adult females (Dunn’s test:  $z = -2.39$ ,  $P = 0.008$ ; Figure 2c). Movements were of a greater duration in juveniles than adults, as juveniles displayed higher AD values (juveniles: median = 26.50 s, range = 0–137 s; adults: median = 18.94 s, range = 0–175 s; Mann–Whitney:  $W = 600.5$ ,  $P = 0.019$ ).

## Foraging Behaviour

Foraging behaviour was analysed based on the results from 18 separate observations, during which feeding events were recorded (juvenile:  $n = 7$ ; adult female:  $n = 5$ ; adult male:  $n = 6$ ). PTM ranged widely from 5.25 to 58.33%, with a median of 36.5%, while MPM remained relatively low, ranging from 0.05 to 1.35, with a median of 0.35 (Figure 2b). Similar to the pooled results for all observations, median PTM values varied significantly between demographic classes (juveniles: 37.5%, range = 14–53.92%; adult females: 16.25%, range = 5.25–36.17%; adult males: 43.38%, range = 16.5–58.33%; Kruskal–Wallis:  $W_2 = 6.48$ ,  $P = 0.039$ ), with adult females displaying significantly lower PTM values than both juveniles (Dunn’s test:  $z = -1.82$ ,  $P = 0.034$ ) and adult males (Dunn’s test:  $z = -2.49$ ,  $P = 0.006$ ) (Figure 2d); MPM did not appear to differ significantly between classes. Individual AD values ranged from 16.19 to 175 s, with a median of 31.84 s for all observations.

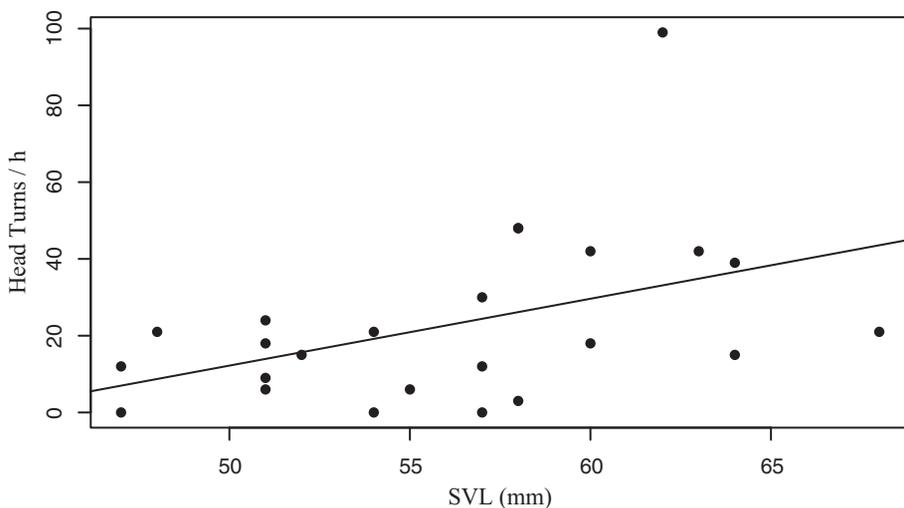


Figure 1. Head turn rates increase with body size (SVL) for adult male *Meroles cuneirostris* ( $n = 24$ ).

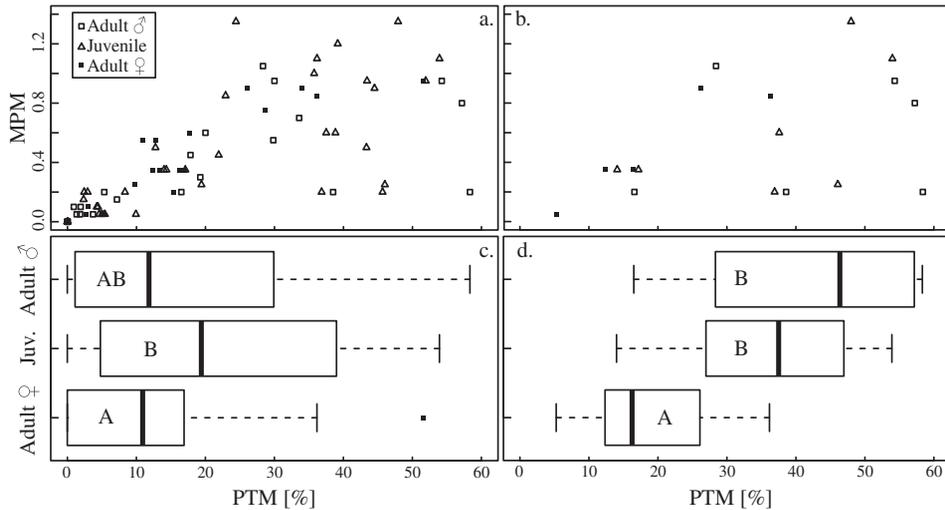


Figure 2. (Top) Scatterplots depicting adult female (■), adult male (□) and juvenile (△) median movements per minute ( $y$ -axis) and median percentage of time spent moving ( $x$ -axis) for (a) all observations,  $n = 84$  and (b) for foraging-related observations only,  $n = 18$ . (Below) Boxplots depicting percentage of time spent moving ( $x$ -axis) by demographic class ( $y$ -axis) for (c) all observations and (d) for foraging-related observations only. Differing letters indicate significant variation between groups.

## Microhabitat Preference

Adults spent more time in vegetation (Mann–Whitney:  $W = 1277.5$ ,  $P = 0.0486$ ; Figure 3), though there did not appear to be any other significant differences in microhabitat preference.

There was a positive correlation between head turn rate and proportion of time spent near vegetation (simple regression analysis:  $P = 0.034$ ,  $R^2 = 4.20\%$ ) and in the open (simple regression analysis:  $P = 0.001$ ,  $R^2 = 12.20\%$ ). Conversely there was a negative correlation between head turn rate and proportion of time spent in vegetation (simple regression analysis:  $P < 0.001$ ,  $R^2 = 17.00\%$ ). There was also a positive correlation between head turn rate and movement rate (simple regression analysis:  $P < 0.001$ ,  $R^2 = 26.20\%$ ).

## DISCUSSION

### Head Turns

Juvenile *M. cuneirostris* turn their heads more frequently than adults, this may be indicative of ontogenetic differences in predation risk within *M. cuneirostris*. Our data show that all individuals turn their heads more frequently in open areas and near vegetation than when under direct vegetative cover. Though there are predation risks associated with both open and vegetated habitats (see discussion on ambush predation below), it is possible that head turning as an anti-predator strategy may be more beneficial in exposed areas. Among lizards, smaller body size is often associated with higher predation risk as juveniles are not able to flee as fast or as far as adults, requiring them to

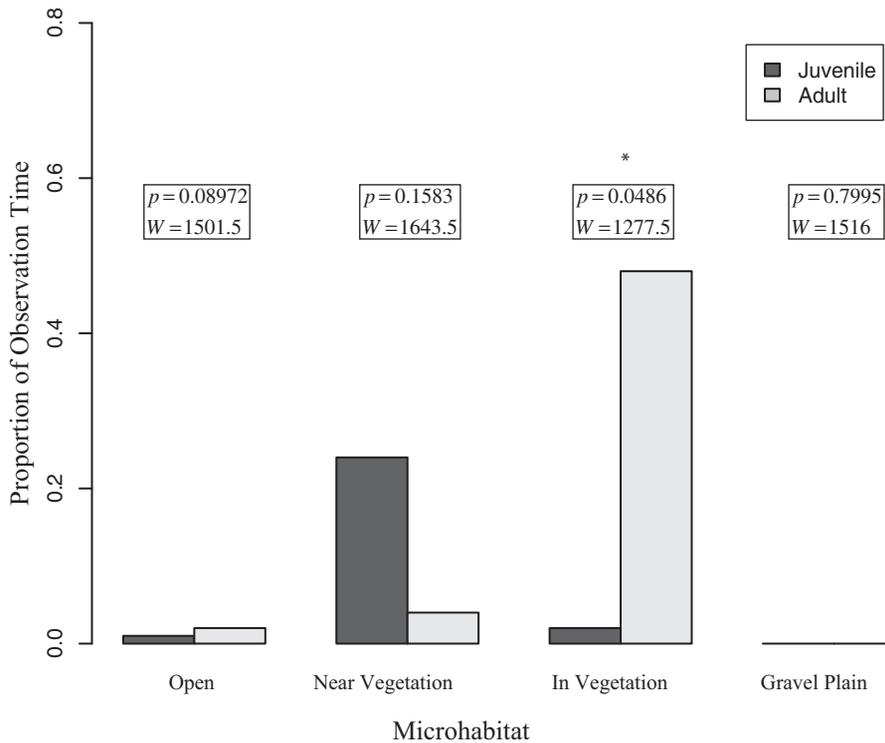


Figure 3. Median proportion of observed time in the four microhabitat categories for adult ( $n = 49$ ) and juvenile ( $n = 35$ ) *Meroles cuneirostris* during 20-minute focal observation periods.

employ different anti-predator strategies (Martín & López 1996; Irschick *et al.* 2000; Martín & López 2003). Among lacertid lizards, ontogenetic variation in anti-predator behaviour has been documented in *Lacerta monticola*, as juveniles have been shown to possess slower absolute sprint speeds, making them more vulnerable to predation (Martín & López 2003). It is possible that juvenile *M. cuneirostris* may be at a higher risk of predation due to their smaller body size and associated sprint speeds. Thus they may be scanning their surroundings more frequently than adults in order to heighten their vigilance in order to avoid predation. Additionally, we witnessed a cannibalism event in which an adult female consumed a juvenile individual (Childers & Eifler 2014). While it is presently unknown how frequently cannibalism occurs in this species, this suggests that juveniles must be wary of adult conspecifics in addition to predators of other species.

Surprisingly, we found that among adult males, larger individuals turn their heads more frequently. While it is presently unknown whether *M. cuneirostris* is territorial, larger males may be defending areas from competitors, requiring them to scan their surroundings more often. Future studies may seek to assess territorial behaviour in *M. cuneirostris* in order to test this hypothesis.

## Movement Patterns

Juveniles appear to engage in longer and more frequent bouts of movement, as the average duration per movement was higher in juveniles than adults, and juveniles are less likely to

engage in sessions of immobility than adults. However, it is interesting that the analysis of all PTM values showed that juveniles only differed significantly between adult females and not adult males. In addition, when analysing foraging-related observations only, juveniles and adult males both showed PTM values that were significantly higher than those of adult females, suggesting that intraspecific variation in foraging behaviour exists in this species (see discussion on foraging behaviour below). Consequently, it is unlikely that the differences in movement patterns between adults and juveniles are strictly due to variation in foraging mode. Other factors that could affect movement patterns include thermoregulatory and metabolic requirements that may vary between age classes. Juvenile lizards tend to have higher mass-specific metabolic rates, which can result in shifts in diet preference and thermoregulatory behaviour as they get older and larger (Pough 1973). Previous studies have identified numerous strategies by which lizards behaviourally thermoregulate, including altering of their activity times (Heatwole *et al.* 1969; Porter *et al.* 1973; Huey & Pianka 1977), moving between heat sources and sinks (Heath 1964; Hammel *et al.* 1967; Spellerberg 1972) and changing their posture (Bartholomew 1966; Barlett & Gates 1967; DeWitt 1971; Huey & Pianka 1977; Stevenson 1985b; Bauwens *et al.* 1996). Smaller animals with larger surface area to body mass ratios heat up faster in warmer environments and require less time to alter their body temperatures, resulting in higher mobility (Porter *et al.* 1973; Stevenson 1985a). Conversely, they may also lose heat faster in cooler areas, requiring cessation of movement following a return to a warmer area in order to regain heat. Juveniles appeared to maximise their heat absorption during periods of immobility by adopting a splayed posture more often than adults, allowing for direct contact with the substrate and quicker heat absorption.

Within the morning and afternoon activity periods, we did not observe intraspecific differences in activity patterns in *M. cuneirostris*. This may suggest that there is no temporal niche partitioning between different demographic classes within this species. However, we feel that this needs to be investigated further since the manner by which we collected our microhabitat data resulted in low sample sizes for this particular area of investigation. While it has been shown in some species that temporal partitioning may limit competition for resources (Pianka 1973; Simon & Middendorf 1976), other studies suggest that there are environmental and ecological constraints that can prevent such partitioning (Toft 1985; Gordon *et al.* 2010). We observed that *M. cuneirostris* activity was restricted to the early morning (08:30–11:30) and late afternoon (15:30–19:30), with a break in activity during midday due to high ambient and surface temperatures. Consequently, their activity periods may not be long enough to partition.

## Foraging Behaviour

Among lizards, foraging behaviour has historically been categorised into one of two modes: active or sit-and-wait (i.e. ambush) foraging. Active foragers are characterised by spending a significant amount of time moving in search of prey items, while sit-and-wait foragers remain stationary for long periods of time, attacking prey items once they appear within range (Cooper & Whiting 1999). Recent studies on lacertids suggest that this two-mode classification system is overly simplistic as some species exhibit MPM and PTM values that do not cluster easily into these discrete categories, and have instead opted to treat each mode as an extreme at either end of a continuum (Perry *et al.* 1990; Cooper 2005; Kirchhof *et al.* 2010; Du Plessis & Mouton 2012). Our results show that

*M. cuneirostris* displayed consistently low MPM values and relatively moderate PTM values which ranged widely, making it difficult to place this species into either foraging category. Our results corroborate previous observations by Murray & Schramm (1987) in which they described *M. cuneirostris* as displaying both an active bimodal foraging strategy, in addition to employing sit-and-wait tactics. In their study, individuals appeared to lie in wait within small tussocks for long periods of time prior to ambushing and preying upon small myrmicine ants. On rare occasions they would ambush and mob *Camponotus detritus* ants carrying food items—mainly termites—within their mandibles. In other instances, individuals were observed to actively forage for and consume termites near the sand dune surface.

Intraspecific variation in foraging behaviour appears to exist within *M. cuneirostris*. While MPM values did not appear to vary significantly between classes, adult males and juveniles exhibited higher PTM values causing them to cluster closer towards the active end of the foraging continuum, while adult females displayed significantly lower PTM values, placing them closer to the sit-and-wait end of the continuum. Ontogenetic shifts in foraging behaviour have been documented in the lacertid *Pedioplanis laticeps* as well as other lizard species (Pianka 1969; Robson & Lambert 1980; Du Plessis & Mouton 2012). Juveniles may need to actively forage more than adults because of limitations on food availability, physical limitations on the size of the food items they can consume, competition with adults and other juveniles, and limited space by which juveniles are able to forage away from predators and conspecifics (Simon & Middendorf 1976; Goldberg & Robinson 1979; Polis & Myers 1985; Liu *et al.* 2011). While ontogenetic variation in foraging behaviour has been documented numerous times, it is less clear as to why intraspecific variation exists between adult males and adult females. Similar results have been documented in the South African chameleon *Bradypodion pumilum*, in which adult females appeared to be more sedentary than adult males and juveniles (Butler 2005). Adult males may be exhibiting increased activity because they are seeking mates or because they are defending territories, a common feature of species that exhibit sexual size-dimorphism (Cox *et al.* 2003). Alternatively, it is possible that adult females may be preferentially consuming different prey items than adult males and juveniles.

Sexual differences in prey consumption have been documented in the lacertid *Podarcis melisellensis*, in which adult males consumed larger quantities of food and a higher proportion of harder prey items than adult females (Brecko *et al.* 2008). While it is known that *M. cuneirostris* consumes small arthropods such as termites and native ants, in addition to feeding opportunistically on detritus, it is unknown whether intraspecific variation in prey preference exists within this species (Murray & Schramm 1987). It is important to note, however, that our study was conducted during the breeding season of *M. cuneirostris*. Thus the possibility that some adult females may have been gravid cannot be excluded (Goldberg & Robinson 1979). Previous studies have found that gravid female lizards tend to experience reduced locomotor ability and increased predation risk. Thus they may be adopting sit-and-wait foraging tactics in order to remain inconspicuous to both prey items and potential predators (Bauwens & Thoen 1981; Cooper Jr *et al.* 1990; Sinervo *et al.* 1991).

## Microhabitat Preference

There appears to be spatial niche partitioning between adult and juvenile *M. cuneirostris* as adults spend more time in vegetation than juveniles. Juveniles may be spending less

time in vegetation due to thermoregulatory constraints inherent of small-bodied poikilotherms. The cost of fleeing to and remaining under the shade of vegetative cover may be higher in juveniles since they lose heat more rapidly than larger adults (Martin & López 2003).

Alternatively, juveniles may be actively avoiding areas where adults allocate much of their time due to predation risk (Polis & Myers 1985; Keren-Rotem *et al.* 2006). We observed several predation events in which a predator hidden within a bush or shrub ambushed prey that had been under vegetative cover. In one instance an adult Namib Sand Snake (*Psammophis namibensis*) appeared from within the centre of a *Stipagrostis sabulicola* bush and captured and consumed an adult *M. cuneirostris* that had been sitting under the foliage (JLC, personal observation). On another occasion an adult *Trachylepis occidentalis* exhibited the same strategy from within a large bush and successfully consumed an adult *M. cuneirostris* that had been walking near the base of the plant (JLC personal observation). The earlier mentioned cannibalism event on a juvenile *M. cuneirostris* by an adult female occurred under identical circumstances in which the female sat at the base of a plant and chased a juvenile that had been walking near the foliage, eventually killing and consuming it (Childers & Eifler 2014). These observations in combination with our behavioural findings suggest that ambush predation is a common strategy employed by predators in this area, and that near or under vegetative cover presents a high risk of predation.

## CONCLUSION

Our results highlight apparent behavioural differences between adult male, adult female and juvenile *M. cuneirostris*. In accordance with our predictions, behavioural differences were more pronounced between age classes as movement patterns and microhabitat preference varied between adults and juveniles, but not between adult males and adult females. Likewise, intraspecific variation in foraging behaviour was also observed. However, it is interesting that our results show that adult males and juveniles are more similar in behaviour than adult males are to adult females. Such differences may be a result of selective pressures resulting in the employment of different thermoregulatory, anti-predator and foraging strategies, as well as the occupation and utilisation of different microhabitats between demographic classes (Garland Jr & Else 1987; Garland Jr & Losos 1994). Further studies may involve fine-scale analyses of temporal habitat partitioning, as intraspecific patterns remain to be elucidated. Additionally, it is presently unclear whether intraspecific differences in prey consumption exist, as a prior dietary study on *M. cuneirostris* did not include demographic data (Murray & Schramm 1987). Finally, given that this species exhibits seasonal variation in breeding behaviour typical of species inhabiting temperate climates, it would be interesting to investigate whether seasonal variation in other associated behaviours exhibited by this species exist, such as potential shifts in prey consumption, activity and microhabitat usage (Goldberg & Robinson 1979).

## ACKNOWLEDGMENTS

We would like to thank those at the Gobabeb Research and Training Centre for operational and logistical support. Lauren White, Rheana Marchard, Jessica Evans, Kay Malela and

Luwi Nguluka provided assistance in the field. We are also grateful to Maria Eifler, Benjamin Karin, Kaitlin Allen, Sebastian Kirchof and Aaron Bauer for providing essential assistance during the production of this publication. This work was supported by the National Science Foundation [grant no. 1065532] through the International Research Experience for Students (IRES) programme. Lizards were captured and handled in accordance with taxonomically relevant animal care and use guidelines (Beaupre *et al.* 2004) under the approval of Erel Institute's Animal Care and Use Committee (IACUC proposal no. 2011-01). Finally, we thank the two anonymous reviewers whose comments greatly improved the quality of this publication.

## REFERENCES

- ADAMOPOULOU, C. & E.D. VALAKOS. 2005. Thermal ecology and activity cycle of *Podarcis milensis* in a sandy coastal area. *Isr. J. Zool.* 51: 39–52.
- AMAT, F., G.A. LLORENTE & M.A. CARRETERO. 2003. A preliminary study on thermal ecology, activity times and microhabitat use of *Lacerta agilis* (Squamata: Lacertidae) in the Pyrenees. *Folia Zool.* 52: 413–422.
- ARNOLD, E.N., Ó. ARRIBAS & S. CARRANZA. 2007. Systematics of the Palearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa* 1430: 1–86.
- AVERY, R.A., C.F. MUELLER, J.A. SMITH & D.J. BOND. 1987. The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara*. *J. Zool.* 211: 47–63.
- BARLETT, P.N. & D.M. GATES. 1967. The energy budget of a lizard on a tree trunk. *Ecology* 48: 315–322.
- BARTHOLOMEW, G.A. 1966. A field study of temperature relations in the Galápagos Marine Iguana. *Copeia* 1966: 241–250.
- BAUWENS, D. & C. THOEN. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J. Anim. Ecol.* 50: 733–743.
- BAUWENS, D., P.E. HERTZ & A.M. CASTILLA. 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 7: 1818–1830.
- BEAUPRE, S.J., E.R. JACOBSON, H.B. LILLYWHITE & K. ZAMUDIO 2004. Guidelines for use of live amphibians and reptiles in field and laboratory research, 2nd edn., American Society of Ichthyologists and Herpetologists, Miami, FL.
- BRANCH, W.R. 1998. Field guide to snakes and other reptiles of southern Africa, 3rd edn. Ralph Curtis Books Publishing, Sanibel Island.
- BRECKO, J., K. HUYGHE, B. VANHOYDONCK, A. HERREL, I. GRBAC & R. VAN DAMME. 2008. Functional and ecological relevance of intraspecific variation in body size and shape in the lizard *Podarcis melisellensis* (Lacertidae). *Biol. J. Linn. Soc.* 94: 251–264.
- BUTLER, M.A. 2005. Foraging mode of the chameleon, *Bradypodion pumilum*: a challenge to the sit-and-wait versus active forager paradigm? *Biol. J. Linn. Soc.* 84: 797–808.
- CHILDERS, J.L. & D.A. EIFLER. 2014. *Meroles cuneirostris* (Wedge-snouted Sand Lizard). *Cannibalism. Herpetol. Rev.* 44: 675–676.
- COOPER, W.E. 1997. Correlated evolution of prey chemical discrimination with foraging, lingual morphology and vomeronasal chemoreceptor abundance in lizards. *Behav. Ecol. Sociobiol.* 41: 257–265.
- COOPER, W.E. 2005. The foraging mode controversy: both continuous variation and clustering of foraging movements occur. *J. Zool.* 267: 179–190.
- COOPER, W.E. & M.J. WHITING. 1999. Foraging modes in lacertid lizards from southern Africa. *Amphibia-Reptilia* 20: 299–311.
- COOPER Jr, W.E., L.J. VITT, R. HEDGES & R.B. HUEY. 1990. Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. *Behav. Ecol. Sociobiol.* 27: 153–157.
- COX, R.M., S.L. SKELLY & H.B. JOHN-ALDER. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57: 1653–1669.

- DEWITT, C.B. 1971. Postural mechanisms in the behavioral thermoregulation of a desert lizard, *Dipsosaurus dorsalis*. J. Physiol. (Paris) 63: 242–245.
- DIEGO-RASILLA, F.J. & V. PÉREZ-MELLADO. 2003. Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in Western Spain. Folia Zool. 52: 87–98.
- DU PLESSIS, I.J. & P.L.N. MOUTON. 2011. Habitat preferences of three sympatric lacertid lizards in the arid Tankwa Karoo Basin of South Africa. Afr. Zool. 46: 88–94.
- DU PLESSIS, I.J. & P.L.N. MOUTON. 2012. Foraging strategies of coexisting lacertid lizards in the arid Tankwa Karoo Basin of South Africa. Afr. Zool. 47: 113–118.
- EIFLER, D.A., M.A. EIFLER & E.N. EIFLER. 2007. Habitat use and movement patterns in the Graceful Crag Lizard, *Pseudocordylus capensis*. Afr. Zool. 42: 152–157.
- GARLAND Jr, T. & P.L. ELSE. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. Am. J. Phys. 252: R439–R449.
- GARLAND Jr, T. & J.B. LOSOS. 1994. Ecological morphology of locomotor performance in squamate reptiles. University of Chicago Press, Chicago, IL.
- GOLDBERG, S.R. & M.D. ROBINSON. 1979. Reproduction in two Namib Desert lacertid lizards (*Aporosaura anchietae* and *Meroles cuneirostris*). Herpetologica 35: 169–175.
- GORDON, C.E., C.R. DICKMAN & M.B. THOMPSON. 2010. Partitioning of temporal activity among desert lizards in relation to prey availability and temperature. Austral Ecol. 35: 41–52.
- HAMMEL, H.T., F.T. CALDWELL & R.M. ABRAMS. 1967. Regulation of body temperature in the Blue-Tongued Lizard. Science 156: 1260–1262.
- HEATH, J.E. 1964. Head-body temperature differences in Horned Lizards. Physiol. Zool. 37: 273–279.
- HEATWOLE, H., T.-H. LIN, E. VILLALÓN, A. MUÑIZ & A. MATTA. 1969. Some aspects of the thermal ecology of Puerto Rican anoline lizards. J. Herpetol. 3: 65–77.
- HUEY, R.B. & E.R. PIANKA. 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. Ecology 58: 1066–1075.
- IRSCHICK, D.J., T.E. MACRINI, S. KORUBA & J. FORMAN. 2000. Ontogenetic differences in morphology, habitat use, behavior, and sprinting capacity in two west Indian *Anolis* lizards. J. Herpetol. 4: 444–451.
- KEREN-ROTEM, T., A. BOUSKILA & E. GEFFEN. 2006. Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behav. Ecol. Sociobiol. 59: 723–731.
- KIRCHHOF, S., J. LINDEN, D. RÖDDER & K. RICHTER. 2010. Foraging mode of *Australolacerta rupicola* (FitzSimons, 1933)(Sauria: Lacertidae): evidence of seasonal variation in an extremely active predator? J. Nat. Hist. 44: 2941–2953.
- LIU, Y., S.-Y. WANG & L. SHI. 2011. Effects of age and sex on diet composition of *Phrynocephalus grungrzimailoi*. Chinese J. Zool. 46: 111–117.
- MCBRAYER, L.D. 2004. The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. Zool. J. Linn. Soc. 140: 403–416.
- MARTÍN, J. & P. LÓPEZ. 1996. The escape response of juvenile *Psammodromus algirus* lizards. J. Comp. Psychol. 110: 187–192.
- MARTÍN, J. & P. LÓPEZ. 2003. Ontogenetic variation in antipredator behavior of Iberian rock lizards (*Lacerta monticola*): effects of body-size-dependent thermal-exchange rates and costs of refuge use. Can. J. Zool. 81: 1131–1137.
- MÜLLER, M.A.N. 2007. Grasses of Namibia, 2nd edn. Ministry of Agriculture, Water, and Forestry, Windhoek, Namibia.
- MURRAY, G.W. & D. SCHRAMM. 1987. A comparative study of the diet of the Wedge-snouted Lizard *Meroles cuneirostris* (Strauch) and the Sand-diving Lizard *Aporosaura anchietae* (Bocage), Lacertidae in the Namib Desert. Madoqua 15: 55–62.
- PÉREZ-MELLADO, V. 1992. Ecology of lacertid lizards in a desert area of eastern Morocco. J. Zool. 226: 369–386.
- PERRY, G., I. LAMPL, A. LERNER, D. ROTHENSTEIN, E. SHANI, N. SIVAN & Y.L. WERNER. 1990. Foraging mode in lacertid lizards: variation and correlates. Amphibia-Reptilia 11: 373–384.
- PIANKA, E.R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50: 1012–1030.
- PIANKA, E.R. 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4: 53–74.
- POLIS, G.A. & C.A. MYERS. 1985. A survey of intraspecific predation among reptiles and amphibians. J. Herpetol. 19: 99–107.

- PORTER, W.P., J.W. MITCHELL, W.A. BECKMAN & C.B. DEWITT. 1973. Behavioral implications of mechanistic ecology. *Oecologia* 13: 1–54.
- POUGH, F.H. 1973. Lizard energetics and diet. *Ecology* 54: 837–844.
- R Core Team. 2013. R: A language and environment for statistical computing. Vienna, Austria.
- ROBSON, G.M. & M.R.K. LAMBERT. 1980. Observations on the insect food of some semi-desert lizards in southern Morocco. *J. Arid Environ.* 3: 141–151.
- ROUAG, R., H. DJILALI, H. GUERAICHE & L. LUISELLI. 2007. Resource partitioning patterns between two sympatric lizard species from Algeria. *J. Arid Environ.* 69: 158–168.
- SHAPIRO, S.S. & M.B. WILK. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591–611.
- SIMON, C.A. & G.A. MIDDENDORF. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. *Ecology* 57: 1317–1320.
- SINERVO, B., R. HEDGES & S.C. ADOLPH. 1991. Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *J. Exp. Biol.* 155: 323–336.
- SJÖSKOG, M. 2008. Plants around Gobabeb. Unpubl. Bachelor thesis, Umeå University, Sweden.
- SOKAL, R.R. & F.J. ROHLF. 1995. *Biometry*, 3rd edn. W.H. Freeman & Company, New York.
- SPELLERBERG, I.F. 1972. Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. II. Physiological aspects of thermoregulation. *Oecologia* 9: 385–398.
- STEVENSON, R.D. 1985a. Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am. Nat.* 125: 102–117.
- STEVENSON, R.D. 1985b. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* 126: 362–386.
- TANG, X.-L., F. YUE, J.-Z. HE, N.-B. WANG, M. MA, J.-R. MO & Q. CHEN. 2013. Ontogenetic and sexual differences of thermal biology and locomotor performance in a lacertid lizard, *Eremias multiocellata*. *Zoology* 116: 331–335.
- TOFT, C.A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985: 1–21.
- WARD, D. 2008. *The Biology of Deserts (The Biology of Habitats Series)*. Oxford University Press, New York.
- XU, X.-F. & X. JI. 2006. Ontogenetic shifts in thermal tolerance, selected body temperature and thermal dependence of food assimilation and locomotor performance in a lacertid lizard *Eremias brenchleyi*. *Comp. Biochem. Physiol., Part A: Mol. Integr. Physiol.* 143: 118–124.

Received: 29 May 2014; Final acceptance: 11 December 2014