Foraging strategies of coexisting lacertid lizards in the arid Tankwa Karoo Basin of South Africa

I.J. du Plessis & P. le F.N. Mouton*

Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland, 7602 South Africa

Four lacertid lizards, *Pedioplanis laticeps, P. lineo-ocellata, Meroles knoxii* and *Nucras tessellata,* occur sympatrically on the arid plains of the Tankwa Karoo Basin in South Africa. The aim of this study was to evaluate the significance of foraging strategy in resource partitioning among the four species, allowing them to co-occur in a structurally simple system with a limited number of potential niches. Previous workers already identified *P. lineo-ocellata* and *M. knoxii* as sit-and-wait foragers and *N. tessellata* as an active forager. We recorded data on three foraging variables: movements per minute, proportion of time spent moving, and proportion of attacks on prey whilst moving, for juveniles and adults of *P. laticeps.* By comparing the foraging data obtained for *P. laticeps* to those for other lacertid species, we were able to demonstrate that adult *P. laticeps* are ambush foragers. We also noted a significant ontogenetic shift in foraging behaviour in *P. laticeps,* and, due to a significantly higher frequency of short brief movements, we classified juveniles as mixed foragers. The sharing of an ambush foraging strategy by at least three of the four lacertid species co-occurring on the Tankwa plains, suggests considerable overlap along the trophic dimension of ecological space. This overlap presumably promotes occupation of separate microhabitats by the three ambush foragers in the Tankwa Karoo Basin.

Key words: resource partitioning, foraging strategy, movements per minute, proportion of time spent moving, proportion of attacks on prey whilst moving, *Pedioplanis laticeps*

INTRODUCTION

For effective partitioning of resources and long-term coexistence, species should be well separated in ecological space defined by three main dimensions: trophic, spatial and temporal (Toft 1985). Foraging strategy is a component of the trophic dimension; species using different foraging strategies should be able to successfully partition or share the resources available to them within their communities (Pianka 1969; Pianka 1973; Hutchinson 1978; Perry *et al.* 1990). Successful resource partitioning decreases interspecific competition, increases feeding efficiency and increases the carrying capacity of an ecological system (Simon & Middendorf 1976; Toft 1985; Perry *et al.* 1990). After the spatial dimension, Toft (1985) ranked the trophic dimension as the next most important ecological dimension within which the partitioning of resources takes place among lizards.

For lizards, two main foraging strategies are ambush foraging and active foraging (Pianka 1966). Lizards that use the ambush strategy hunt by lying in wait for prey, usually mobile and often fleet prey, e.g. grasshoppers and beetles, to move within striking range (Pianka 1971; McBrayer

2004; Cooper 2005). Ambush foragers rely on a sudden short burst of speed to catch prey items (Huey & Pianka 1981). In contrast, active foragers rely more on endurance as they move through the habitat, actively searching for sedentary or patchy prey items, e.g. termites (Pianka 1971; Huey &Pianka 1981; McBrayer 2004; Cooper 2005). Active foragers depend on visual surveillance and/or frequent tongue flicking to locate chemical cues, whereas ambush foragers typically rely on visual surveillance to locate potential prey items (Huey & Pianka 1981; Cooper 1995, 1997, 2005, 2007; Cooper & Whiting 1999). The realm of foraging strategy should, however, not be regarded as a dichotomous system, but rather a continuum within which ambush and active foragers represent the two extremes of the continuum (Pianka 1973; Magnusson *et al.* 1985; Pietruzka 1986; Perry *et al.* 1990; Cooper 2005; Miles *et al.* 2007). This view is overly simplified because foraging modes may be represented by spaces of several continuous dimensions (Cooper 2005).

Most species within entire lizard genera and even families exhibit the same foraging strategy (Huey & Pianka 1981; Cooper & Whiting 1999; Perry 1999). The Lacertidae is one of few excep-

*Author for correspondence. E-mail: pnm@sun.ac.za

tions in this regard as there is evidence for at least two independent origins of ambush foraging in the family, for one of mixed foraging, and for a possible return from ambush foraging to active foraging (Cooper & Whiting 1999).

The lizard communities of the Kalahari and Namibian deserts have been the focus of a number of ecological studies and, as a result, the foraging behaviour of several southern African lacertid lizard species has been recorded (Huey & Pianka 1981; Cooper & Whiting 1999). No information is, however, available on resource partitioning among lacertid lizards inhabiting the Tankwa Karoo Basin, one of the most arid regions in South Africa. Mean annual precipitation varies between 40 and 110 mm (Rubin 1998; Mucina & Rutherford 2006) and temperatures between an average minimum of 5.7 °C during winter and an average maximum of 35.9 °C during summer (Rubin 1998).

Meyer *et al.* (2010) identified no less than seven terrestrial, diurnal lizard species occupying the Tankwa flats, four of which are lacertids. The four lacertids, *Pedioplanis laticeps, P. lineo-ocellata, Meroles knoxii* and *Nucras tessellata,* are very similar in body size and general morphology and are all classified as diurnal insectivores (Branch 1998). In studies conducted in the Kalahari and Namib desert systems, *P. lineo-ocellata* and *M. knoxii* were found to be sit-and-wait foragers and *N. tessellata* an active forager (Huey & Pianka 1981; Cooper & Whiting 1999). The aims of this study were firstly to determine the foraging strategy of *P. laticeps,* for which no information is available, and secondly to evaluate the contribution that differences in foraging strategy make to resource partitioning among the sympatric lacertid species in the Tankwa Karoo Basin.

MATERIALS & METHODS

Information on foraging behaviour of *Pedioplanis laticeps* was obtained on the farm Gansfontein (32°43′27.32″S, 19°42′55.20″E) in the southwestern parts of the Tankwa Karoo Basin, South Africa. Data were obtained during March and October 2008, on sunny days and at times and temperatures when lizards are known to be most active. The sampling procedure of Cooper & Whiting (1999) was adopted in this study. Active lizards were located and observed by walking through the different habitat types where *P. laticeps* is known to occur (Du Plessis & Mouton 2011). After the initial location of a lizard, the observer stopped to reduce any further disturbance of the lizard. If the lizard

showed signs of nervousness due to the presence of the observer, the observer waited until the lizard appeared to behave normally again before any data were recorded. The standard procedure was to record all movement and foraging behaviour on a digital voice recorder. Only recordings that lasted longer than a minute and a half were included in the data set. The maximum time per recording was 10 minutes. Behavioural aspects recorded included all movements and stops (stationary for longer than two seconds) in addition to all feeding attempts. For each feeding attempt it was noted whether the attempt was initiated from a stationary position or during movement. Postural changes in position were not recorded as foraging movements. After a successful recording, the observer moved to a different location to lower the chances of replication. Individuals were classified as adult or juvenile on the basis of size and colouration, brightly coloured individuals smaller than ~45 mm in SVL were considered to be juveniles (Nkosi *et al.* 2004).

Two traditional foraging variables were calculated, namely 'proportion of time spent moving' (PTM) and 'movements per minute' (MPM) (Huey & Pianka 1981). A third variable, 'proportion of attacks on prey whilst moving' (PAM), was included to reduce the chances of misinterpreting movement data for foraging behaviour and to increase accuracy in defining the foraging strategy used (Cooper & Whiting 1999). MPM and PTM values for juveniles and adults were compared using the Mann-Whitney test for non-parametric data.

To allow comparison of recorded foraging data for southern African lacertid lizards, a scatter plot was prepared, with MPM and PTM as axes, for juvenile and adult *P. laticeps,* three additional *Pedioplanis* species, four *Meroles* species, *Nucras tessellata* and *Heliobolus lugubris* (Huey & Pianka 1981; Cooper & Whiting 1999). In the two-dimensional foraging space represented by MPM and PTM, true ambush foragers will occupy the foraging space close to the origin where both MPM and PTM are close to zero. Active foragers on the other hand will vary greatly in their MPM values, but will have much higher PTM values. The more similar the foraging strategy used by two species the closer the two species will lie within foraging space.

RESULTS

Observations were made for six juvenile and 18 adult individuals of *P. laticeps.* Average observa-

Table 1. Foraging data for *Pedioplanis laticeps*. The table provides the mean values calculated for MPM (movements per minute), PTM (proportion of time spent moving) and PAM (proportion of attacks on prey whilst moving) for each of the age groups. The foraging data for *P. lineo-ocellata, Meroles knoxii* and *Nucras tessellata* are also included.

Species	MPM		PTM (%)		PAM (%)	
	Average	S.E.	Average	S.E.		n
P. laticeps (adults)	0.61	0.95	4.41	7.81	0	18
P. laticeps (juveniles)	2.54	1.5	21.87	13.36	100	6
P. lineo-ocellata[1]	0.49	–	5.00	–	0	4
P. lineo-ocellata[2]	1.54	–	14.30	–	–	15
M. knoxii[1]	0.61	–	7.00	–	0	27
N. tessellata[1]	0.7	–	90.00	–	100	1
N. tessellata[2]	2.9	–	50.20	–	–	11

[1]Cooper & Whiting (1999).
[2]Huey & Pianka (1981).

tion time for juveniles was 5.8 minutes and 8.8 minutes for adults (193 minutes total observation time). For adults, the mean MPM and PTM values recorded during the March ($n = 6$) and October ($n = 12$) sampling periods did not differ significantly and the two data sets were therefore combined (Mann-Whitney test: MPM: $z = -1.03$, $P = 0.303$; PTM: $z = -0.89$, $P = 0.374$). The MPM and PTM values for juveniles were significantly higher than those for adults (Mann-Whitney test: MPM: $z = 2.7$, $P = 0.0069$; PTM: $z = 2.83$, $P = 0.0047$; Table 1). In total, five feeding attempts were observed. The two attempts by adult individuals were initiated from a stationary position, from the cover of a bush (PAM: 0%), whereas the three attempts by juveniles were all made during movement (PAM: 100%). Juvenile lizards were often seen actively searching for prey items, i.e. digging under rocks. In the two-dimensional foraging space defined by MPM and PTM, adult *P. laticeps* occupied a position close to those of *P. lineo-ocellata, M. knoxii,* and *M. reticulatus,* whereas juveniles occupied a position close to that of *M. ctenodactylus* (Fig. 1).

DISCUSSION

The relatively low MPM and PTM values that we recorded for adult *P. laticeps* would place this species at the ambush end of the ambush to active foraging continuum (Perry *et al.* 1990; Perry 1995; Cooper 2005). In fact, our data would place *P. laticeps* in close proximity to *P. lineo-ocellata* and *Meroles knoxii* (Fig. 1), two lacertids that have been classified as distinct ambush foragers in previous studies (Huey & Pianka 1981; Cooper & Whiting 1999). Prior to this study, foraging data were available for only three species in the genus *Pedioplanis.*

Pedioplanis namaquensis and *P. undata* were classified as active foragers (Cooper & Whiting 1999) and *P. lineo-ocellata* as an ambush forager (Huey & Pianka 1981; Cooper & Whiting 1999). The classification of the latter species as an ambush forager is supported by its cranial morphology (McBrayer 2004), its relatively low stamina (Nagy *et al.* 1984), and its diet, which includes diurnally active prey items such as flies and beetles (Nagy *et al.* 1984). The results of our study show that ambush foraging may be more widespread in the genus.

In *Pedioplanis, P. laticeps* and *P. burchelli* form the basal clade, being the sister group to the rest of the genus (Makokha *et al.* 2007). Foraging data are presently not available for *P. burchelli,* but, with *P. laticeps* being an ambush forager, ambush foraging may well be the basal condition in *Pedioplanis,* as in *Meroles* (Huey & Pianka 1981; Arnold 1991; Cooper & Whiting 1999). The other identified ambush forager, *P. lineo-ocellata,* together with *P. breviceps,* occupies a basal position in the main *Pedioplanis* clade (Makokha *et al.* 2007), lending further support to the notion that ambush foraging may be the basal condition in the genus.

The limited PAM data that we recorded for adult *P. laticeps* seem to support the classification of this species as an ambush forager. A PAM value of 0.00% has also been recorded for *P. lineo-ocellata,* the other known ambush forager in the genus for which foraging data are available (Cooper & Whiting 1999). Theoretically, feeding attempts by active foragers should occur at a higher frequency and should therefore be observed more often than for ambush foragers. Cooper & Whiting (1999) gathered foraging data for 14 *Heliobolus lugubris* individuals during which 45 foraging attempts were observed, all of which were initiated whilst
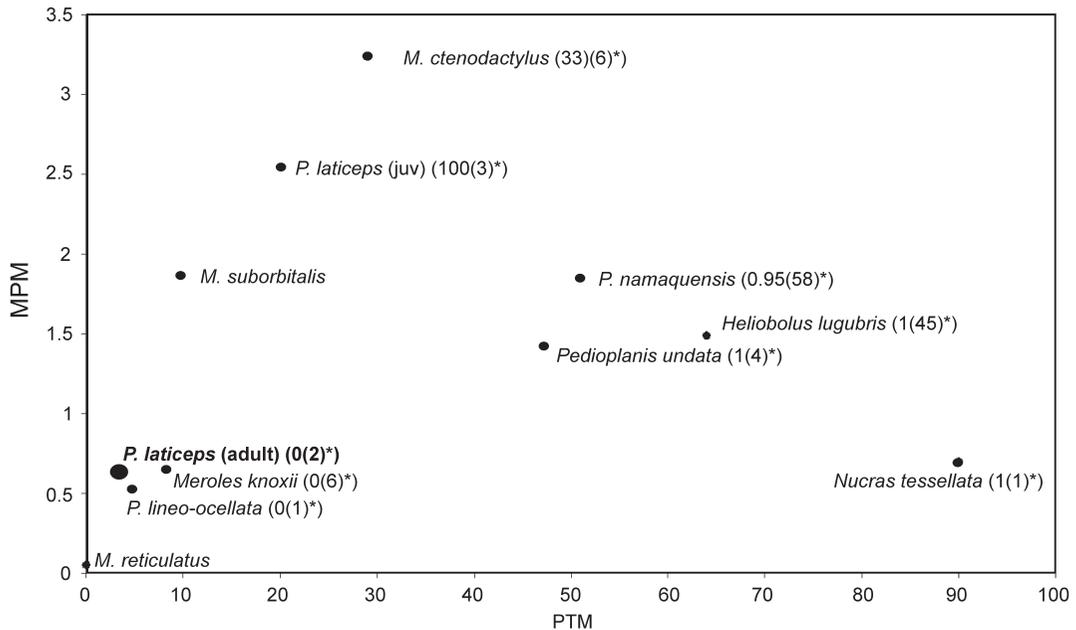
Fig. 1. Positions of juvenile and adult *Pedioplanis laticeps* relative to various other southern African lacertids (Huey & Pianka 1981; Cooper & Whiting 1999) in two-dimensional foraging space, defined by MPM and PTM. PAM (proportion of attacks on prey whilst moving) and the number of attacks witnessed (*) are provided for some species.

the specific lizard was on the move (PAM = 100%). In total, 18 *P. laticeps* adults were observed for 158 minutes, during which time only two feeding attempts were observed. This low number of feeding attempts can therefore be seen as an indication that this species uses an ambush foraging strategy, but it may also be and indication of food scarcity during the time of our survey.

The considerably higher MPM and PTM values recorded for juveniles than for adults of *P. laticeps* show that there is an ontogenetic shift in foraging strategy in this species. The values recorded for juvenile *P. laticeps,* would place them in close proximity to *M. ctenodactylus* in foraging space defined by MPM and PTM (Fig. 1). Cooper & Whiting (1999) described *M. ctenodactylus* as a mixed forager, i.e. a species displaying a high frequency of brief movements during foraging, in contrast to prolonged movement typical of active foragers or no or only a few movements typical of ambush foragers.

A difference in foraging strategy between adults and juveniles has been recorded in several other lizard species. In some Australian species, juvenile individuals tend to target smaller prey items than adult individuals (Pianka 1969). Robson & Lambert (1980) found an ontogenetic shift in food preferences in *Acanthodactylus boskianus* of southern

Morocco and stated that this could be accompanied by a similar shift in foraging strategy. Likewise Hawlena *et al.* (2006) found that juveniles of *A. beershebensis* display a more active foraging strategy than adults.

Correlating daily intake of chemical potential energy with growth rate, Nagy *et al.* (1984) found that the known active forager (*H. lugubris*) grew twice as fast during the same time as the ambush forager (*P. lineo-ocellata).* Increased energy demand might force the juveniles to adopt a more active foraging strategy, enabling them to sustain a certain required growth rate. Hawlena *et al.* (2006) suggested that the more active foraging behaviour of *A. beershebensis* juveniles could be a mechanism to sustain an increased growth rate, which results in an increase in absolute adult fitness. Juvenile foraging behaviour such as increased movements and active searching in the form of digging could be seen as a behavioural response to adapt to a limiting foraging environment.

Similar to the situation in many other lacertid species where juveniles differ from adults in colouration (Branch 1998), the colouration of juvenile *P. laticeps* is markedly different from that of adults. Juveniles are dark in colour, with yellowish dorsal stripes over the length of the trunk and a red-orange tail. Adults on the other hand, have a

much more faded appearance with spots and faint stripes. In many lacertid and teiid species, juveniles have bright tail colours combined with light longitudinal stripes on a dark skin surface that fade into more cryptic colour patterns as the individual matures (Cooper & Greenberg 1992). It has been suggested that ontogenetic colour change is a response to a change in the predator suite that preys on the different age groups of a species (Cooper & Vitt 1985). More active species tend to be striped, speckled or uniformly coloured, while ambush foragers are known to be blotchier in colouration for better concealment (Cooper & Greenberg 1992).

The finding that *P. laticeps, P. lineo-ocellata* and *M. knoxii,* three of the four lacertid species co-occurring in the arid Tankwa Karoo Basin of South Africa, are all typical ambush foragers, suggests considerable overlap along the trophic dimension of ecological space. The spatial separation of the three species due to different microhabitat preferences (Du Plessis & Mouton 2011), however, allows the narrow sympatric occurrence of the three species within the Basin. Similar results were obtained in previous studies in the Kalahari desert where as many as three out of four active foragers (*Heliobolus lugubris, Pedioplanis namaquensis, Nucras tessellata* and *N. intertexta*) are able to occur sympatrically due to different microhabitat preferences (Pianka 1971). Within other desert systems with limited microhabitat heterogeneity, a significant overlap along the trophic dimension led to the temporal separation of two sympatric species (Rouag *et al.* 2007). The fact that *P. laticeps, P. lineo-ocellata* and *M. knoxii* are spatially separated at the study site, allows them to have a similar foraging strategy.

ACKNOWLEDGEMENTS

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Responsible Editor: J.H. van Wyk