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Foraging mode of *Australolacerta rupicola* (FitzSimons, 1933) (Sauria: Lacertidae): evidence of seasonal variation in an extremely active predator?

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Foraging mode of the endemic Soutpansberg rock lizard (*Australolacerta rupicola*) was determined by (1) measuring the number of movements per minute (MPM) and the percentage time spent moving (PTM); and (2) analysing faecal samples. Furthermore, these criteria were related to diet composition, proportion of attacks initiated while moving and foraging substrate. The results are discussed in comparison to the foraging modes of 20 other lacertid species. Values for MPM and PTM as well as faecal analysis indicate an active foraging strategy for *A. rupicola*. Although rock living, this species mostly forages in leaf litter where it is well camouflaged while actively searching for sedentary prey. Even in comparison to other active foragers of the family Lacertidae, *A. rupicola* displays the prototypic behaviour of a widely foraging lizard with very high PTM and very low MPM.

Keywords: Soutpansberg; South Africa; foraging mode; autecology

Introduction

Traditionally, carnivorous lizards have been divided into active, widely foraging predators and ambush or sit-and-wait predators (Pianka 1966). By definition a widely foraging lizard spends considerable time moving in search of prey, using active searching actions such as digging or examination of cracks, holes and under loose bark (Cooper and Whiting 1999). This behaviour is often attended by intensive tongue-flicking to recognize prey odours (Cooper 1997; Cooper and Whiting 1999). Sit-and-wait predators on the other hand have a low frequency of movements. They remain stationary for long periods of time, scanning visually for prey which they rapidly attack when in range (Mouton et al. 2000; Du Toit et al. 2002). Chemical prey discrimination is often poorly developed in sit-and-wait predators (Huey and Pianka 1981; Mouton et al. 2000).

The foraging behaviour of lizards can be quantitatively determined by measuring two variables: the percentage time spent moving (PTM) and the number of movements per minute (MPM) (Perry et al. 1990; Cooper 2005). Additionally, the proportion of prey attacked while moving (PAM) or average foraging speed can be used as supplementary variables (Cooper 2005). In recent years various authors have suggested that the two foraging modes rather represent two extremes at either end of a continuum

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(Perry et al. 1990; Cooper and Whiting 1999; Perry 1999). A study presented by Cooper (2005) showed that frequency distributions of MPM and PTM of several species belonging to different lizard families are both continuous and unimodal. Nevertheless, cluster analysis allocated more than 98% of these species into groups corresponding to active and ambush foragers (Cooper 2005). Accordingly, ambush and active foraging are still convenient categories, but the dichotomy has limitations (Cooper 2005). Species belonging to the family Lacertidae show numerous different foraging behaviours, which do not easily fit into the two-mode foraging paradigm (Huey et al. 1984; Cooper and Whiting 1999; Cooper 2005; Verwaijen and Van Damme 2007a).

Herein, we focus on the foraging mode of *Australolacerta rupicola*, which is one of the least known lacertid species worldwide and has a distribution restricted to the Soutpansberg mountain range in north-eastern South Africa (Kirchhof et al. 2010a). To date, the ecology and biology of this species are almost completely unknown. The lifestyle of *A. rupicola* has been only vaguely described by FitzSimons (1933), Jacobsen (1989), Branch (1998), Kirchhof and Richter (2009) and Kirchhof et al. (2010b). *Australolacerta rupicola* is referred to as rock-dwelling species inhabiting scree and rocky outcrops at altitudes from 900–1600 m in dry areas of the Soutpansberg (Jacobsen 1989). Currently, *A. rupicola* is listed in the South African Red Data Book as restricted (Jacobsen 1988) and in the IUCN Red List as lower risk/near threatened (World Conservation Monitoring Centre 1996). In this study, PTM and MPM of *A. rupicola* were measured, analysed in respect of the two-variable foraging space following Cooper (2005) and compared with other lacertid lizard species. The study also highlights how diet composition, PAM and foraging substrate are related to the foraging strategy of *A. rupicola*.

Materials and methods

MPM and PTM

A total of 20 foraging specimens of *A. rupicola* were observed by SK in natural habitat at the Lajuma Research Centre property on the southern slopes of the western Soutpansberg. Data were collected at three different sample plots (SPs) during the cool dry season of 2007, from 28 April until 6 June from sunrise (06:10 h in April and 06:44 h in June) to sunset (18:02 h in April and 17:28 h in June): SP 1 (eight specimens analysed), SP 2 (five specimens analysed) and SP 3 (seven specimens analysed). All sample plots covered an area of approximately 5 ha and included the most common habitat types at Lajuma Research Centre.

SP 1 (–23.02200°dd, 29.43500°dd) was situated on the shoulder of Lajuma Mountain in Soutpansberg Summit Sourveld (following Mucina and Rutherford 2006) at an altitude of 1560–1600 m and was the highest of the three (Figure 1). It included east- and west-facing slopes with rock outcrops, bedrock and scree interspersed with areas of shallow sandy soils. The vegetation of the site was dominated by the sedge *Coleochloa setifera*. Shrubs and small trees such as *Englerophytum magalismontanum*, *Maytenus acuminata* or *Tarenna zimbabwensis* could also be found.

SP 2 (–23.04200°dd, 29.44600°dd) was a small plateau lying in Soutpansberg Mountain Bushveld (following Mucina and Rutherford 2006) at an altitude of about 1250–1260 m (Figure 2). The top of the plateau was covered by rocky bushveld, the south- and east-facing scree slopes were densely vegetated with thicket-like characteristics

Figure 1. Typical microhabitat of *Australolacerta rupicola* in Sample Plot 1. Credit: S. Kirchhof.

and consisted of mistbelt bush clumps with *Mimusops zeyheri*, *Olea capensis enervis*, *Combretum molle* and many succulents. The surveyed area also included extensions of evergreen Northern Mistbelt Forest with deeper and more developed clayey soils.

SP 3 (–23.04000°dd, 29.43000°dd) was situated at the foot of a mountain at an altitude of 1280–1340 m. The rocky outcrops were bordered by deep sand areas with *Terminalia sericea* as well as by semi-arid mountain bushveld dominated by *Acacia* species (Figure 3). A small stream ran along the eastern border which was lined by groundwater-influenced Northern Mistbelt Forest (following Mucina and Rutherford 2006) with riverine forest characteristics (with tree species like *Syzygium cordatum*, *Ilex mitis*, *Schefflera umbellifera* and *Cyathea dregei*). The whole sample plot covered altitudes of 1280–1340 m.

Focal specimens of *A. rupicola* were each observed continuously for at least 3 min (mean = 2050 s, standard deviation [SD] = 465, range = 200–2050). In total, the species was observed for 275 min. To determine foraging behaviour, only non-reproductive adult and subadult individuals were observed on sunny days during hours of activity. In conjunction with a different, ongoing study of habitat preferences of *A. rupicola* (SK unpubl. data), most individuals that were observed to determine their foraging mode had been previously caught and individually marked allowing the avoidance of pseudo-replications. In order to minimize observer effects (Regal 1983), the observer kept a minimum distance of around 3 m from the animal, remaining motionless and using a pair of binoculars when necessary. Furthermore, data recording

Figure 2. Typical microhabitat of *Australolacerta rupicola* in Sample Plot 2. Credit: S. Kirchhof.

was only started when the lizard showed no apparent reaction towards the observer. Only foraging-related movements were recorded and no data were collected when there was obvious interaction with other lizards, inter- or intraspecific, or when the individual was disturbed by a predator. Possible bias owing to reproductive activities/pregnancy can be excluded since the study was conducted outside of the breeding season (Verwaijen and Van Damme 2007b; Verwaijen and Van Damme 2008). All data were recorded by one observer only.

For each specimen, the duration of each movement and of each pause throughout the continuous observation time was measured with a stopwatch. The parameters recorded during each observation included the total time spent moving (M), the total time spent immobile (S), the total number of movements (N) and the average duration per movement (AD). Movements such as changes in body orientation or postural adjustments (e.g. during social interactions) were not recorded. Pauses had to last for at least two consecutive seconds to be noted as bouts of immobility, following Cooper et al. (1997). Furthermore, the parameters M and S were subcategorized into MR (time moving on rocks), MV (time moving in vegetation) SR (time immobile on rocks), and SV (time immobile in vegetation).

Based on these parameters, movements per minute (MPM) and the percentage time moving (PTM) were calculated using the formulae $MPM = 60N/(M + S)$ and $PTM = 100(N \times AD)/(M + S)$ as suggested by Cooper (2005). All feeding attempts were recorded including the prey item as well as whether they were initiated during active searching or while the lizard was immobile. Subsequently, the proportion of

Figure 3. Typical microhabitat of *Australolacerta rupicola* in Sample Plot 3. Credit: S. Kirchhof.

prey attacked while moving (PAM) was calculated (Cooper 2005). For each sighting, time (t_{day}) and temperature (T) were noted. Temperature was measured in degrees centigrade between 5–10 cm above the ground in the nearest shaded place to the lizard (max. 1.0 m) using a standard liquid-in-glass thermometer.

Faecal analysis

The composition of ingested prey items was studied by means of faecal analysis. Nineteen specimens of *A. rupicola* were captured in March 2006, between April and May 2007 and between September and December 2007, comprising periods within both the warm wet season (October–March) and the cool dry season (April–September). The specimens were kept in plastic boxes for four days until the intestines were empty, following Möller (1997). Faecal pellets of each specimen were put together, dried, the calculus parts removed and the samples preserved in 70% ethanol for storage. The composition of the contents of each sample was examined qualitatively under a dissection microscope. Prey types were identified to the lowest possible taxonomic category (usually order) and both different arthropod taxa as well as different developmental stages (larvae, pupae) were considered as distinct prey types. The frequency of occurrence of prey taxa found was determined.

Results

MPM and PTM

Foraging behaviour of *Australolacerta rupicola* was relatively easy to distinguish and did not vary at the different sample plots. When a lizard left its overnight refuge, it seldom spent much time basking on exposed rocks, which is quite unusual for a lacertid lizard. On the contrary, it almost immediately started to roam between rocks in the vegetation layer probing leaf litter and grass tussocks with its head. The earliest foraging behaviour was recorded at 08:45 h in the morning and the latest at 16:05 h (Table 1). Temperatures during the time of recorded foraging behaviour ranged from 16 to 24°C (mean = 20°C). PTM ranged from 44.12–80.00% with a mean of 64.55% (SD = 10.96, n = 20). The majority of the specimens (85%) spent more than 50% of the observation time moving. The average duration of all recorded moves was 86 s (SD = 38). Several individuals were observed foraging for more than three continuous

Table 1. Descriptive statistics of the parameters recorded to determine foraging mode of *Australolacerta rupicola* (n = 20) showing mean, minimum (Min.) and maximum (Max.) values as well as standard deviation (SD).

Variable	Mean	Min.	Max.	SD
Time of day (h)	11:12	8:45	16:05	2:18
Temperature (°C)	20	16	24	2
Mean observation time (s)	826	200	2050	465
Total time moving (s)	537	110	1640	342
Total time immobile in vegetation (s)	290	70	900	198
Time moving in vegetation (s)	393	0	1540	337
Time moving on rocks (s)	144	0	570	130
Time immobile in vegetation (s)	160	0	580	143
Time immobile on rocks (s)	130	0	720	165
Total number of movements	6	2	12	3
Average duration per movement (s)	86	40	183	38
Percentage of time moving (%)	64.55	44.12	80.00	10.96
Movements per minute	0.51	0.23	0.92	0.18

minutes. Accordingly, values for MPM were very low, ranging from 0.23 to 0.92 with a mean of 0.51 (SD = 0.18). With the exception of three outliers where PTM < 50%, the MPM and PTM values of the recorded individuals (*n* = 20) clustered in the lower right quadrant of the two-variable foraging space following Cooper (2005) (Figure 4).

Of the total time the lizards spent moving, an average of 69.59% (SD = 25.05) was spent moving through vegetation (MV) including leaf litter, under patches of moss, on branches lying on the ground and even up the stems of trees, where they searched for prey by lifting loose flakes of bark with their heads. Moving on rocky surfaces (MR) accounted for 30.41% on average. Although MV values ranged from 0 to 100%, 80% of all individuals spent more than 50% of the time moving in vegetation. During this time, the lizards moved their heads from left to right and up and down, lifting leaf litter while flicking their tongues frequently. The searching intervals were discontinued on average every 86 s for a mean pause of 51 s (SD = 18). The majority of bouts of immobility – 55.49% (SD = 33.52) – were spent in leaf litter, on branches and stems or at least on soft substrate like bare soil (SV). The remaining 44.51% of the periods of immobility were spent on rocks (SR).

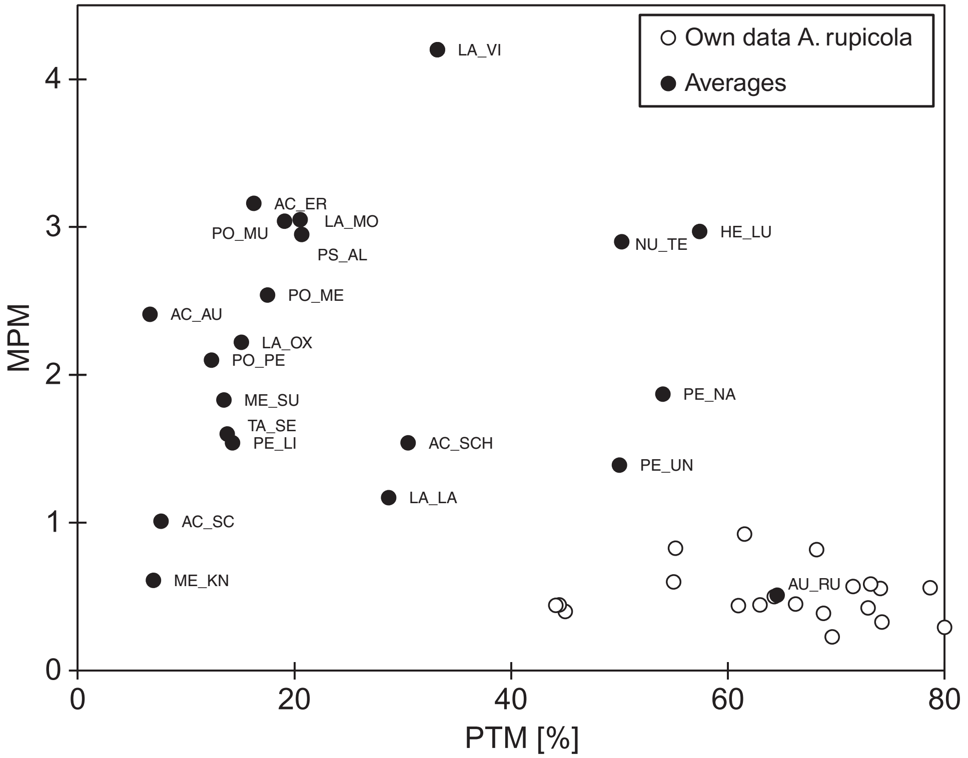

Figure 4. Mean movements per minute (MPM) and percentage time spent moving (PTM) of the analyzed lacertid species (black dots). In the case of *Australolacerta rupicola*, the absolute values for the 20 individuals sampled in the present study are also illustrated by white dots. Note: For abbreviations see Table 3.

Three specimens were observed while catching prey including one large spider of approximately 15 mm in length, a centipede (*Scutigera* sp.) and one unidentified prey item. Individuals moving on rocks probed cracks filled with leaf litter or grasses and herbs by poking the head into them whilst tongue-flicking. Bare rocks and bedrock were mostly just passed with only quick scans or a few seconds pause. One individual was observed snapping at a passing fly (Diptera: Brachycera) while the lizard was immobile. The attempt failed but was counted as an attack initiated during a bout of immobility and therefore included in the evaluation of PAM. In total, five observations of lizards attacking prey were made, four performed while the individual was actively moving and one while stationary. Accordingly, PAM was 0.80 (n = 5). Each food intake was followed by a period of immobility longer than the ones during the searching intervals, often in positions where the lizard was difficult to spot but still at least partly sun exposed.

Diet composition

Analysis of diet composition from faecal samples of 19 different specimens suggests that *A. rupicola* is completely carnivorous as no plant material was found, nor was herbivorous behaviour observed in the field. Prey items were exclusively arthropods (Arachnida, Chilopoda, Diplopoda, Crustacea and Insecta) (Figure 5). The frequency of occurrence of ingested prey items in the individual faecal samples are listed in Table 2. No predominance of certain taxa could be revealed, but especially developmental stages of butterflies and/or moths were common in the samples. Larvae and pupae together were ingested by 50% of the specimens caught during the warm wet season and in 45.45% of those caught during the cool dry season. Chilopoda and Diplopoda were only found in samples collected during the cool dry season, while Isopoda, Coleoptera, Diptera, Hymenoptera and Orthoptera were only found in samples collected during the warm wet season indicating possible seasonal effects of prey availability on diet. No adult Lepidoptera were found, only the more sedentary development stages.

Discussion

The observed specimens of *A. rupicola* all displayed very similar foraging behaviour with long periods of continuous searching accompanied by frequent tongue-flicking

Figure 5. *Australolacerta rupicola* feeding on a spider (a) and a grasshopper (b). Credit: S. Kirchhof.

Table 2. Frequencies of occurrence of ingested prey items per specimen ($n = 19$).

Prey category (CLASS, ORDER, family)	Frequency of occurence (%) Warm wet season ($n = 8$)	Frequency of occurence (%) Cool dry season ($n = 11$)
ARACHNIDA		
ARANEA	37.50	27.27
ACARI	12.50	0.00
CHILOPODA		
SCUTIGERIDA		
Scutigeridae (*Scutigera* sp.)	0.00	9.09
DIPLOPODA	0.00	27.27
CRUSTACEA		
ISOPODA	12.50	0.00
INSECTA		
COLEOPTERA		
Carabidae	12.50	0.00
Undetermined	37.50	0.00
DIPTERA (BRACHYCERA)	12.50	0.00
HEMIPTERA		
Cercopidae	0.00	9.09
Undetermined	25.00	0.00
HYMENOPTERA (NON-FORMICIDAE)	12.50	0.00
ISOPTERA	25.00	0.00
LEPIDOPTERA		
Larvae	25.00	45.45
Pupae	25.00	0.00
MANTODEA	12.50	0.00
ORTHOPTERA	25.00	0.00

and interrupted by shorter pauses. Only three individuals stood out, having PTM < 50%, but the values were still high at 44.12%, 44.44% and 45.00% respectively. The specimen characterized by the lowest PTM was the only one that spent the entire observation time (11 min 20 s) on one massive boulder. No feeding attempt was initiated during that time and its behaviour showed few signs of foraging, neither searching actively nor visually scanning the area while stationary. One might assume that thermoregulation may have been the major factor during this observation. In the second case, a lizard was observed in a sun-exposed position on the neck of Lajuma Mountain (1584 m altitude) on the east-facing slope at 10:35 h on 9 May 2007. The sky was cloudless and air temperature was 19°C. It remained motionless for four minutes and then went down into the dense grass layer. During this study, only two other individuals were observed before 11.00 h at similar altitudes on Lajuma Mountain (both at 10:20 h at 18°C and 19°C, respectively) indicating that during winter *A. rupicola* does not emerge much earlier from its overnight refuge at such high altitudes. Assuming that this specimen was using the first four observation minutes to reach its optimal body temperature and excluding them from the total observation time (27 min), PTM roses to 52.17%. The specimen with the third lowest PTM value spent the last 4 min of the total observation time (20 min) immobile following a meal. When that time

Table 3. Mean percentage time spent moving (PTM) and movements per minute (MPM) values of 21 lacertid lizard species (including *Australolacerta rupicola*). The table includes abbreviations of names (Abbr.), number of observations (#obs) and mean observation times (Ø t_{obs}) for the analyzed species. Data sources are listed below the table.

Species	Abbr.	#obs	Ø t_{obs} (s)	PTM (%)	MPM
_Acanthodactylus aureus_*	AC_AU	30	510	6.68	2.41
_Acanthodactylus erythrurus_*	AC_ER	27	560	16.26	3.16
Acanthodactylus schreiberi†	AC_SCH	12	315	30.50	1.54
Acanthodactylus scutellatus†	AC_SC	26	354	7.70	1.01
Heliobolus lugubris°	HE_LU	15	289	57.40	2.97
"Lacerta" (Phoenicolacerta) laevis†	LA_LA	16	253	28.70	1.17
_"Lacerta" (Iberolacerta) monticola_*	LA_MO	39	479	19.10	3.04
_"Lacerta" (Dalmatolacerta) oxycephala_*	LA_OX	56	531	15.11	2.22
_"Lacerta" (Zootoca) vivipara_*	LA_VI	21	600	33.20	4.20
Meroles knoxii#	ME_KN	27	491	7.00	0.61
Meroles suborbitalis°	ME_SU	15	1640	13.50	1.83
Nucras tessellata^	NU_TE	11	439	50.20	2.90
Pedioplanis lineoocellata°	PE_LI	15	548	14.30	1.54
Pedioplanis namaquensis#	PE_NA	26	448	54.00	1.87
Pedioplanis undata#	PE_UN	16	474	50.00	1.39
_Podarcis melisellensis_*	PO_ME	58	470	17.53	2.54
_Podarcis muralis_*	PO_MU	47	554	20.54	3.05
_Podarcis peloponnesiacus_*	PO_PE	73	474	12.35	2.10
_Psammodromus algirus_*	PS_AL	43	454	20.68	2.95
_Takydromus sexlineatus_*	TA_SE	37	326	13.80	1.60
Australolacerta rupicola§	AU_RU	20	826	64.55	0.51

Notes: *Values taken from Verwaijen and Van Damme (2007a); °values taken from Huey and Pianka (1981); #values taken from Cooper and Whiting (1999); †values taken from Perry et al. (1990); ^values taken from Barnea (unpubl. data; cited in Perry 1999); §own observation.

was omitted as being non-foraging behaviour, PTM rose to 56.25%. In any case, even when uncorrected values for the three outstanding individuals were included in the analysis, the high mean PTM value together with the low mean MPM value placed *A. rupicola* in the lower right quadrant of the foraging space (Figure 4).

Comparing these results with data of 20 other species of the family Lacertidae, it is apparent that the majority of species have PTM ≤ 20.68% and move 1.54–3.16 times/min (Table 3 and Figure 4). Only two species are characterized by PTM < 10% and move ≤ 1.01 times/min, thresholds which are often used in other studies to characterize ambush foragers (Du Toit et al. 2002; Cooper 2005). The largest gap in PTM values is apparent between 30.50 and 50.00% and in MPM between 3.16 and 4.20. These patterns underline the fact that species of the family Lacertidae show a variety of different foraging behaviours with continuous variation and cannot easily be placed within the two-mode foraging paradigm, as already suggested by various authors (Huey et al. 1984; Cooper and Whiting 1999; Perry 1999; Cooper 2005; Verwaijen and Van Damme 2007a).

However, among these species, *A. rupicola* holds the highest mean values for PTM and the lowest mean MPM. The other four species with PTM > 50% (*Nucras* *tessellata*, *Heliobolus lugubris*, *Pedioplanis namaquensis* and *P. undata*) have all been described as widely foraging in previous studies (Huey and Pianka 1981; Cooper and Whiting 1999; Cooper 2005) despite having higher MPM values which indicate shorter periods of continuous movement. Mean values for *A. rupicola* fall into what Cooper (2005, p. 184) defined as the region where species "match the prototypic behaviour of active foragers".

The active search mode of *A. rupicola* is further evidenced by the fact that the majority of movements and pauses were conducted in vegetation. Here, visibility is poor and lizards have to rely more on chemosensory detection of prey using tongue-flicking, which was often observed in moving specimens of *A. rupicola*. Furthermore, the colour pattern of *A. rupicola* with the distinctive longitudinal stripes also provides better camouflage in vegetation than on bare rock surfaces. The preferred utilization of vegetation as foraging substrate is even more remarkable given the structure of the habitat. Mean values for coverage of rocks, leaf litter and herb layer within the analysed lizard localities were 71.5%, 30.6% and 25.3%, respectively (S. Kirchhof, unpubl. data).

The high PAM value shows that most feeding attempts were initiated while moving; another finding that indicates an active foraging mode (Cooper and Whiting 1999; Verwaijen and Van Damme 2007b). However, it needs to be noted that the sample size for PAM is very low ($n = 5$). The components of the faecal samples especially from the cool dry season substantiate the results of the former analysis. Prey items ingested during this period comprise many arthropods of the decomposer community including nocturnal species (Diplopoda, Lepidoptera larvae) as well as other taxa inhabiting debris (spiders, *Scutigera* sp.). The number of larvae in the examined faecal samples confirms the results of other studies that widely foraging lizards consume more sedentary and hidden prey than do sit-and-wait predators owing to their active searching actions and/or well-developed prey chemical discrimination (Huey and Pianka 1981; Huey et al. 1984; Cooper 1997). The presence of Diplopoda remains in the faecal samples of *A. rupicola* is remarkable. Many millipede species are known to produce toxins, which usually results in the avoidance of these invertebrates by lizards (Vitt and Cooper 1986; Mouton et al. 2000; Van Wyk 2000). During the cool dry season arthropod abundance was low, or at least surface activity of certain prey taxa was reduced in the study area. In the case of *A. rupicola* it seems valid that prey scarcity during winter forces this species also to ingest less favourable prey like millipedes. Its active search mode is hence advantageous.

As mentioned previously, MPM and PTM data were only collected during the cool dry season, whereas the study of diet composition includes samples collected during both seasons. While sedentary and even unpalatable prey dominated the diet during winter when prey abundance is scarce, more quick-moving and flying arthropods like Orthoptera, Diptera, Hymenoptera (Apocrita) and Coleoptera appeared in samples collected in October, December and March when arthropod abundance increases (Table 2). In faecal samples from the warm wet season Diplopoda were completely absent, although they were still abundant in the sample plots (pers. obs.). Seasonal variation in stomach contents has been studied for other lizard species and several authors have suggested that even foraging mode may vary seasonally, possibly in connection with food abundance (Huey and Pianka 1981; Perry et al. 1990; Cooper 2005). However, the sample sizes in this study are too small to allow definite conclusions.

The exceptionally active foraging mode in periods of prey scarcity is demonstrated by the results of this study. Whether or not *A. rupicola* adopts a less active or even a sit-and-wait strategy in periods of increased food availability would need confirmation through further research. However, the preference of *A. rupicola* for rock-dominated habitats does offer great opportunities for the use of outcrops and rocks as perches for the visual scanning typical of sit-and-wait strategists (Cooper and Whiting 1999; Mouton et al. 2000; Du Toit et al. 2002).

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