

Foraging modes of cordyliform lizards

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The first quantitative data on foraging mode in the cordyliform lizards reveal different foraging behaviours between and within families. All species of cordylids studied (four *Cordylus*, two *Pseudocordylus*, and one *Platysaurus*) are ambush foragers. However, the species of *Cordylus* and *Pseudocordylus microlepidotus* are the most extreme ambushers. These species spent a significantly lower per cent time moving than did all of the other species studied and made significantly fewer movements per minute than *Platysaurus capensis* and gerrhosaurids. In addition, *P. microlepidotus* made significantly fewer movements per minute than did its congener *Pseudocordylus capensis*. Possible reasons for the high number of movements per minute in *Platysaurus capensis* are discussed. Very limited observations of two gerrhosaurid species show that *Cordylosaurus subtesselatus* is an active forager and *Gerrhosaurus validus* forages actively at least some of the time. A tentative hypothesis of the evolution of cordyliform foraging behaviour based on very limited data hints that active foraging is plesiomorphic in the Gerrhosaurini and further that gerrhosaurids may have retained active foraging from the common ancestor of Scincidae and Cordyliformes. Somewhat stronger data suggest that ambush foraging arose in the common ancestor of Cordylidae or Cordylinae. Further study is needed to trace inter- and intrageneric changes in foraging mode in cordylids.

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Foraging behaviour is of paramount importance to lizards not only in the obvious sense of finding food, but also due to its strong effects on several facets of natural history. Foraging significantly influences antipredatory behaviour (Huey & Pianka 1981; Vitt 1983), reproduction (Huey & Pianka 1981; Vitt & Congdon 1978; Vitt & Price 1982), energetics (Anderson & Karasov 1988), and chemosensory behaviour (Cooper 1994, 1995).

The cordyliform lizards include the families Cordylidae, which is endemic to southern Africa, and Gerrhosauridae, which is restricted to southern Africa and Madagascar (Lang 1991). Although ecological and behavioural information on lizards from this region has been increasing in recent years, most work on African squamates has been taxonomic. As a result, there are no published quantitative data for any of these lizards. Some cordylids have been categorized as ambush foragers based on informal observations (Branch 1988; Cooper 1994, 1995), but no published data focus on foraging of any cordylid species. The foraging behaviour of gerrhosaurids is even more poorly known, published information being inadequate to infer the foraging mode(s) of any gerrhosaurid species.

Ambush (sit-and-wait) foraging and active (wide) foraging are widely recognized discrete foraging modes (MacArthur & Pianka 1966; Huey & Pianka 1981), but there may be a continuum of degree of foraging activity (Magnusson, Junqueira De Paiva, Morcira De Rocha, Franke, Kasper & Lima 1985; Pietruszka 1986; Perry, Lampl, Lerner, Rothenstein, Shani, Sivan & Werne 1990). Foraging modes are determined empirically by measuring two variables: the number of movements per minute (MPM) and percent time spent moving (PTM). Viewed quantitatively, a dividing line between MPM and PTM values of ambush and active foragers must be determined arbitrarily. That is not necessarily unsatisfactory if there is a clear gap between values for the two modes. Perry's

(1995) criterion of < 10 PTM for ambush foraging is used here. Although lizard foraging behaviour clusters in two discrete modes (McLaughlin 1989), MPM and PTM vary substantially within modes.

Here we report the first quantitative data on foraging behaviour in cordyliform lizards. MPM and PTM were used to characterize foraging mode for seven cordylid species belonging to three genera. In addition, a few observations are described, suggesting that some gerrhosaurids are active foragers. We discuss variation in foraging behaviour among taxa and factors that may affect foraging movements, especially in *Platysaurus capensis*, and present preliminary findings about the evolution of foraging mode in Cordyliformes.

Methods

The foraging behaviour of nine species of cordylid and gerrhosaurid lizards in South Africa and Namibia was observed. Data were collected at the following sites and dates in South Africa: *Platysaurus capensis* were observed in the Northern Cape Province, all but two at Augrabies Falls National Park on 26 March 1993; the others at Ybeep (29°58'S, 17°59'E) in Namaqualand on 27 March 1993. *Pseudocordylus capensis* were observed at Papekuilsfontein (31°27'S, 19°9'E) near Nieuwoudtville, Northern Cape Province, on 4–5 March 1996. *Pseudocordylus microlepidotus* were studied in the Western Cape Province at Jonaskoop (33°58' S, 19°31'E, ca. 20 km east of Villiersdorp) on 16 March 1993 and near Hermanus (34°24'S, 19°18'E) on 6 March 1996. The holotype of *Cordylus inkae* was observed at Wolfhoek in Namaqualand (30°22'S, 18°12'E), Northern Cape Province, on 29 March 1993. *Cordylus polyzonus* were observed at various mountainous locations in the Northern Cape Province in Namaqualand at Wildeperdehoek Pass, Messelpadpas, and near Kommegas on 29 February to 2 March 1996 and on a koppie at Papendorp (31°41'S, 18°13'E) on 3 March 1996.

Cordylus cordylus were studied in the Western Cape Province at Koopman's Kloof in the Bottelary Hills of Stellenbosch (33°04'S, 18°40'E) on 12 March 1993 and at Kleinbaai (34°37'S, 19°22'E) on 6 March 1996. *Cordylus niger* were observed in the Western Cape Province at Cape Point (34°21'S, 18°30'E) on 14 April 1993. In Namibia the gerrhosaurids *Cordylus subessellatus* and *Gerrhosaurus validus* were studied on Farm Bergvellei (19°37'S, 14°40'E, 20 km west of Kamanjab) on 22 March and 20–21 March 1996, respectively. An additional observation of *C. subessellatus* was made at Augrabies Falls National Park in South Africa on 14 April 1996.

Observations were restricted to sunny days at times when the lizards were active. Prior to observations we walked slowly through the habitat, scanning the area with binoculars and unaided vision and stopping when a lizard was detected. If a lizard appeared to have been disturbed by the observer, its behaviour was not recorded at that time. We attempted to observe each individual for 10 consecutive minutes, but it was not always possible to observe the lizards continuously for the entire period. The commonest cause of abbreviated observation intervals was that a lizard moved behind a rock or into a crevice. We used data from all observations lasting at least 1.5 min. Precautions were taken to ensure that each individual was observed only once. Due to frequent human contact that might affect foraging behavior by *Platysaurus capensis* near points overlooking Augrabies Falls, specimens were observed downstream from such areas.

All data were recorded using microcassette tape recorders and were later transcribed to data sheets. For each individual we recorded the species, age category (adult vs. juvenile), location, date and time. We recorded the time moving and time stationary. No movement was recorded when lizards made non-translational movements such as postural adjustments and head or tail movements. Pauses of two or more consecutive seconds were recorded as periods of immobility. The difficulties of recording the data and simultaneously attempting to observe a lizard and keep track of time rendered analysis at shorter intervals impractical. Video-taping is more suitable for such work. For many specimens we also recorded the microhabitat such as rock or ground, qualitative aspects of

any movements, tongue-flicks, feeding attempts, and other activities.

We calculated MPM and PTM from the movement data. Differences in movement between *Platysaurus capensis* on rocks and on the ground were analysed by the Mann-Whitney U test (Zar 1984), as were differences in mean MPM and PTM between cordylid and gerrhosaurid species. Owing to non-normality of distributions of MPM and PTM, significance of differences among taxa were assessed non-parametrically by Kruskal-Wallis one-way analysis of variance. Due to the very small sample sizes of gerrhosaurids and the similarity of MPM and PTM values in all species of *Cordylus*, their data were pooled, yielding five categories: all *Cordylus* species; *Platysaurus capensis*; *Pseudocordylus capensis*; *P. microlepidotus*; and both gerrhosaurid species. Individual comparisons were conducted as outlined by Zar (1984). Alpha was 0.05 two-tailed, except where otherwise indicated.

The evolution of foraging mode for cordylid and gerrhosaurid genera was reconstructed using the TRACE routine of MacClade 3.01 (Maddison & Maddison, 1992) on Lang's (1991) generic phylogeny. Data were entered as an unordered character having two states: active foraging and ambush foraging. Genera for which no data were available were coded as having unknown foraging mode.

Results and discussion

Cordylus

The *Cordylus* species studied all are extreme ambush foragers having very low values of both MPM and PTM (Table 1). Most of the time they sat motionless, usually on the top of rocks from which they could scan relatively large areas. These lizards attempted to capture prey from ambush, rushing off the rocks to the ground to the attack and then returning to the rocks to resume visual search. Other occasional movements by *Cordylus* sp. were typically brief sorties to other vantage points on the same rock or longer movements directly to another rock. Small movements, including those by insects, often attracted the attention of *Cordylus* sp. from a distance of up to several meters, as indicated by the lizards tilting their

Table 1 Sample sizes (*N*), moves per minute (MPM), per cent time moving (PTM), and minutes observed for cordylid and gerrhosaurid lizards. Data for MPM and PTM are presented as means \pm 1.0 SE and ranges

Taxon	<i>N</i>	MPM		PTM		Minutes
		$\bar{x} \pm SE$	Range	$\bar{x} \pm SE$	Range	
<i>Cordylidae</i>						
<i>Platysaurus capensis</i>	22	1.27 \pm 0.32	0.00–6.82	6.62 \pm 1.58	0.00–24.17	205.40
<i>Pseudocordylus capensis</i>	6	0.59 \pm 0.20	0.00–1.11	6.77 \pm 2.00	0.00–14.06	51.92
<i>Pseudocordylus microlepidotus</i>	7	0.00 \pm 0.00	–	0.00 \pm 0.00	–	70.00
<i>Cordylus imkae</i>	1	0.00	–	0.00	–	10.00
<i>Cordylus polyzonus</i>	17	0.04 \pm 0.02	0.00–0.34	0.15 \pm 0.07	0.00–1.00	157.23
<i>Cordylus cordylus</i>	45	0.09 \pm 0.02	0.00–0.70	0.27 \pm 0.08	0.00–2.50	427.83
<i>Cordylus niger</i>	36	0.09 \pm 0.03	0.00–0.60	0.19 \pm 0.06	0.00–1.33	350.38
<i>Gerrhosauridae</i>						
<i>Cordylus subessellatus</i>	2	1.20 \pm 0.20	1.00–1.39	47.42 \pm 8.08	39.33–55.50	12.88
<i>Gerrhosaurus validus</i>	2	0.65 \pm 0.17	0.48–0.82	14.85 \pm 11.65	3.20–26.50	21.78

heads, changing position to afford a better view, and capture attempts.

Pseudocordylus

Sample sizes were small for both species of *Pseudocordylus* (Table 1), but sufficient to strongly suggest that they are ambush foragers. All of the *P. microlepidotus* remained motionless during the entire period of observation from distances of more than 20 m. They were all on horizontal rock surfaces, five at the tops of rocks and two on elevated horizontal surfaces below the top, but sheltered from wind.

In the limited sample, *P. capensis* moved more frequently than *P. microlepidotus* and movement varied substantially among individuals (Table 1). Movements for individuals presented as (MPM, PTM) were (0.00, 0.00), (0.10, 6.83), (0.40, 9.88), (0.90, 3.50), (1.05, 6.36), and (1.11, 14.06). *Pseudocordylus capensis* were observed stationary and moving with ease on horizontal shelves and vertical faces of the rocky cliffs. Moving individuals were sometimes difficult to observe because they moved in and out of crevices or behind rocks.

Unlike *Cordylus* sp., which made only very brief movements, *P. capensis* frequently made movements lasting five or more seconds (12 of 31 movements); three individuals each moved for 20 or more seconds in single continuous bouts. Such long, continuous movements are atypical for ambush foragers, which sometimes perform a series of movements in a bout of locomotion, but usually punctuate the movements with stops. Even the movements of active foragers such as some lacertids are discontinuous on a short time scale (Avery, Mueller, Jones, Smith & Bond 1987); those of ambushers are discontinuous over longer intervals.

Platysaurus

Platysaurus capensis moved far more frequently than the other cordylids, but their movements were brief, resulting in a low mean PTM (Table 1). Unlike the species of *Cordylus* studied, which only briefly left elevated positions on rocks, *P. capensis* at Augrabies Falls National Park foraged on elevated positions on rocks and trees, but also spent considerable time on the extensive relatively flat rock at ground level. While on rocks they searched visually, scanning the ground below like *Cordylus* sp., but they perched on vertical surfaces more frequently than *Cordylus* sp. While in elevated positions on rocks, these lizards tended to remain still, often with heads tilted down to survey the ground, and ambushed by rushing to the ground. On the ground they were more active.

Although means of MPM and PTM were much higher than in *Cordylus*, the amount of movement varied greatly among individuals (see ranges in Table 1). Among 15 individuals for which substrates were recorded, nine that remained on a rock for the entire time moved much less (MPM = 0.24 ± 0.10 , PTM = 0.38 ± 0.20) than six recorded to have spent some time on the ground, logs, or trees (MPM = 2.93 ± 0.79 , PTM = 8.60 ± 2.82). Because there was no overlap in either MPM or PTM values for these two groups, MPM and PTM were significantly lower for lizards that remained on rocks than for those that spent some time elsewhere (Mann-Whitney U = 0; $n = 5, 9$; $P < 0.001$ each).

Several factors may contribute to the greater MPM and

PTM in *Platysaurus capensis* than in *Cordylus* sp. First, the ground where the lizards were observed at Augrabies Falls National Park consists of extensive shelf rock. Although visibility is relatively unobstructed, a lizard on the ground cannot scan nearly as large an area as one on an elevated rock and would therefore have to move more frequently to cover a broad enough area to achieve a similar encounter rate with prey. Second, prey are extremely abundant in Augrabies Falls National Park because large numbers of insects come over the rim of the canyon above the Orange River. Dipterans appear to be the primary prey, but in several instances the lizards were observed to chase and capture moths and butterflies. Data on feeding attempts were not recorded consistently, but *P. capensis* moved to approach and attack prey much more frequently than the other lizards studied.

Third, prey appeared to be abundant in accumulations of litter on the ground. In large accumulations several individuals sometimes foraged simultaneously. Among individuals for which substrates were recorded, the three individuals having the highest PTM all foraged in litter accumulations. They made frequent short movements in the litter, often probing into it with their heads. Another individual moved slowly and nearly continuously for 11 seconds while probing debris with its head. Although this movement was reminiscent of the movement of actively foraging skinks in the genera *Mabuya* and *Eumeces*, the observer (WEC) was unable to ascertain whether tongue-flicking occurred. A fourth potentially important factor is phylogeny.

What is the foraging mode of *P. capensis*? By the usual yardsticks of MPM and PTM, it is clearly an ambush forager (e.g. Huey & Pianka 1981; Perry *et al.* 1990). However, the wide ranges of MPM and PTM (Table 1) indicate that some individuals moved far more frequently and spent a much higher percentage of time moving than indicated by the mean values. This could be interpreted as indicating that foraging mode varies within the population. The population might be polymorphic, but very likely the MPM and PTM vary within individuals according to factors such as distribution of patches, degree of detectability of prey by visual search, food density, and hunger.

Gerrhosauridae

The observations on gerrhosaurids are few, but are important as the first foraging data for the entire family. The PTM for the two *Cordylosaurus subtessellatus* was in the high range, even for an active forager (Table 1); MPM was fairly low because the lizards moved continuously for long intervals. Both individuals were observed foraging on rocks and crevices between rocks and both tongue-flicked frequently. While foraging in leaf litter in a crevice at the bottom of a vertical crevice between two rocks, one individual proceeded slowly, with tongue flicking frequently, and poked its head under the leaf litter.

The two juvenile *Gerrhosaurus validus* had a fairly low mean MPM (Table 1), but PTM was much higher than in the cordylids. One individual remained on top of a rock in full sun. Its movements were short changes of position lasting several seconds. The other individual was sighted while moving along a horizontal rock crevice. It moved 4.3 m in 26 s to the top of a rock 2.5 m above ground, where it basked in the

sun, part of the time with rear legs extended backwards, for most of the next seven minutes. It made only four movements of less than five seconds each and two longer movements lasting 17 and 23 s during this time. It then moved down to the ground, where it foraged very slowly, but actively in shade and filtered sun. It continued to move for all but 12 s of the next 126 s, tongue-flicking the substrate frequently. Then it climbed back onto the rock and basked for over three minutes until it moved slowly for 23 s before going out of sight into a crevice. The behaviour of the two individuals agrees with D. Broadley's observation (personal communication) that *G. validus* basks on rocks and comes down to the ground to forage.

MPM for *G. validus* is in the range considered by Perry (1995) to indicate active foraging, but is similar to that of two species of lacertids labelled ambush foragers by Huey & Pianka (1981). The foraging movements observed were much slower than those of actively foraging lacertids and teiids and considerably slower than those actively foraging skinks in the genera *Eumeces* and *Mabuya* (WEC and MJW, personal observations). The foraging behaviour of *G. validus* is therefore intermediate in mean speed and perhaps in PTM. Some investigators recognize a subtype of active foraging called cruise foraging (Regal 1978), in which food is sought actively, but the movements are slower and more deliberate than those of typical active foragers such as teiids. *Gerrhosaurus validus* may be a cruiser.

Data are needed to determine whether inclusion of individuals in the sun on rock tops in MPM and PTM calculations is appropriate. If lizards on rocks are not foraging, their inclusion would artificially deflate the foraging variables. Because the individual observed on the ground was clearly foraging actively, using vision and chemoreception, at least some of the foraging by *G. validus* involves actively searching for prey.

Preliminary comparisons of foraging behaviour

Both foraging variables differed significantly among the five taxonomic categories analysed (MPM: $H = 45.01$, $df = 4$, $P < 0.001$; PTM: $H = 29.27$, $df = 4$, $P < 0.001$). The two most extreme ambushers, *Cordylus* sp. and *Pseudocordylus microlepidotus*, had the lowest values of both MPM and PTM, which did not differ significantly. MPM were significantly fewer in *Cordylus* sp. than in *Platysaurus capensis* ($P < 0.001$ each) and the gerrhosaurids ($P < 0.05$). The only other significant differences in MPM for any taxa were the lower values in *P. microlepidotus* than in *Platysaurus capensis* ($P < 0.001$), *Pseudocordylus capensis* ($P < 0.05$) and the gerrhosaurids ($P < 0.025$). Although MPM by *Cordylus* did not differ significantly from that in the remaining taxa, they were substantially fewer than in *Pseudocordylus capensis* ($P < 0.065$). The pattern of differences for PTM was similar to that of MPM, but the statistical resolution was greater for PTM. The PTM of *Cordylus* was significantly lower than in all of the other taxa (*Platysaurus capensis*, $P < 0.001$; *Pseudocordylus capensis*, $P < 0.02$; gerrhosaurids, $P < 0.005$) except *P. microlepidotus*. PTM was significantly lower for *P. microlepidotus* than *Cordylus* (*Platysaurus capensis*, $P < 0.001$; *Pseudocordylus capensis*, $P < 0.02$; gerrhosaurids, $P < 0.005$).

Although it is premature to generalize about foraging differences between cordylids and gerrhosaurids, the seven

cordylid species all had lower PTM than the gerrhosaurid species ($U = 0$; $n = 2, 7$; $P = 0.028$, 1-tailed). Although the test suffers from lack of phylogenetic independence among taxa, especially the four species of *Cordylus*, it suggests the possibility of a biologically important difference between the families. A similar comparison for MPM is non-significant because *Platysaurus capensis* had more MPM than *G. validus* ($U = 1$; $n = 2, 7$; $P = 0.056$, 1-tailed).

The limited available data suggest that many cordylids are ambush foragers and some gerrhosaurids are active foragers. Data for more taxa in both families are essential to understanding whether there are real familial differences in MPM and PTM and how foraging behaviour has evolved in Cordyliformes.

Evolution of cordyliform foraging

Lang's (1991) hypothesis of phylogenetic relationships of cordyliform genera provides a basis for a preliminary examination of the evolution of foraging behaviour in this group (Figure 1). Lang (1991) elevated *Gerrhosaurus* and closely related genera from the subfamilial to familial level. As currently constituted, Cordyliformes consists of the families Cordylidae and Gerrhosauridae, which are sister groups (Lang, 1991). Cordyliformes in turn is the sister group of Scincidae (Estes, De Queiroz & Gauthier 1988).

The common ancestor of Scincidae and Cordyliformes was an active forager (Cooper 1995). Members of all three

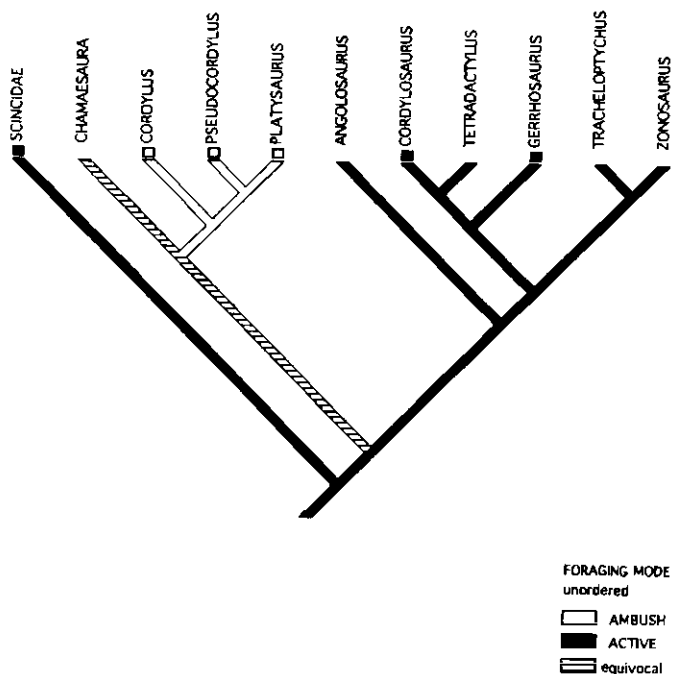


Figure 1 Preliminary hypothesis of the evolution of foraging mode in the genera of Cordyliformes plus its sister taxon, the family Scincidae. Cordyliformes has two families: Cordylidae includes the first four genera to the right of Scincidae. Gerrhosauridae includes the remaining genera. Foraging mode is unknown in most genera of gerrhosaurids (*Angolosaurus*, *Tetradactylus*, *Tracheloptychus* and *Zonosaurus*), but the most likely mode was inferred by parsimony as a first working hypothesis. Unshaded branches = ambush foraging; dark branches = active foraging; hatched branches = foraging mode equivocal.

cordylid genera studied are ambush foragers that spend a low percentage of time moving. Thus, ambush foraging is most likely to have arisen in the common ancestor of Cordylidae (*Chamaesaura*, *Cordylus*, *Pseudocordylus* and *Platysaurus*) or Cordylinae (*Cordylus*, *Pseudocordylus* and *Platysaurus*). Data on foraging mode in *Chamaesaura* are needed to help resolve this issue.

The extreme ambush foraging in the genus *Cordylus* suggests several possibilities. Further reduction in foraging movements beyond those in the common ancestor of Cordylinae may have occurred in the common ancestor of *Cordylus*. Following Lang's phylogeny, the alternative of increases in MPM and PTM in the common ancestor of Pseudocordylini (*Pseudocordylus* + *Platysaurus*) cannot be excluded. However, because there is considerable uncertainty about generic relationships within Cordylinae, it may be best to consider the three genera to form a polytomy (P. N. M. Mouton, personal communication) with several possible evolutionary changes in foraging mode. Based on the limited data showing a difference between the two species of *Pseudocordylus*, intrageneric evolutionary changes in degree of foraging movements are indicated.

Figure 1 shows the most parsimonious reconstruction of the evolution of foraging mode in Cordyliformes on Lang's (1991) phylogeny. Because observations representing only two of six gerrhosaurid genera were available, the hypothetical reconstruction is very tentative. MacClade uses available data to determine the minimum number of evolutionary steps needed to account for the observed data (Maddison & Maddison 1992). Since the only two gerrhosaurids included are active foragers and the common ancestor of Scincidae and Cordyliformes was an active forager, the simplest possible evolutionary path is retention of active foraging in all gerrhosaurids. However, although the fragmentary data on gerrhosaurid foraging show that some species engage in active foraging, the lack of data for most gerrhosaurid taxa preclude any conclusions regarding the evolution of foraging within Gerrhosauridae. Therefore, Figure 1 represents the most likely hypothesis of the evolutionary history of foraging mode based on very limited data. It is a working hypothesis to be examined in the light of more observations including the unstudied genera.

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References

- ANDERSON, R.A. & KARASOV, W.H. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecol. Monogr.* 58: 79-110.
- AVERY, R.A., MUELLER, C.F., JONES, S.M. SMITH, J.A. & BOND, D.J. 1987. The movement patterns of European lacertid lizards: a comparative study. *J. Zool. (Lond.)* 211: 324-329.
- BRANCH, B. 1988. Field guide to the snakes and other reptiles of southern Africa. Ralph Curtis Books, Sanibel Island, Florida.
- COOPER, W.E., JR. 1994. Prey chemical discrimination, foraging mode, and phylogeny. In: Lizard ecology: historical and experimental perspectives, (eds.) L.J. Vitt & E.R. Pianka. Princeton University Press, Princeton, New Jersey.
- COOPER, W.E., JR. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* 50: 973-985.
- ESTES, R., DE QUEIROZ, K. & GAUTHIER, J. 1988. Phylogenetic relationships within Squamata. In: Phylogenetic relationships of the lizard families, (eds.) R. Estes & G. Pregill. Stanford University Press, Stanford, California.
- HUIEY, R.B. & PIANKA, E.R. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991-999.
- LANG, M. 1991. Generic relationships within the Cordyliformes (Reptilia: Squamata). *Bull. Inst. r. Sci. nat. Belg.* 61: 121-188.
- MACARTHUR, R. & PIANKA, E.R. 1966. On optimal use of a patchy environment. *Am. Nat.* 100: 603-609.
- MADDISON, W.P. & MADDISON, D.R. 1992. MacClade: analysis of phylogeny and character evolution. Version 3.01. Sinauer Associates, Sunderland, Massachusetts.
- MAGNUSSON, W.E., JUNQUEIRA DE PAIVA, L., MOREIRA DE ROCHA, R., FRANKE, C.R., KASPER, L.A. & LIMA, A.P. 1985. The correlates of foraging mode in a community of Brazilian lizards. *Herpetologica* 41: 324-332.
- MCLAUGHLIN, R.L. 1989. Search modes of birds and lizards: evidence for alternate movement patterns. *Am. Nat.* 133: 654-670.
- PIERRY, G. 1995. The evolutionary ecology of lizard foraging: a comparative study. Unpubl. Ph.D. thesis, University of Texas, Austin, pp. 1-304.
- PERRY, G., LAMPL, I., LERNER, A., ROTHENSTEIN, D., SHANI, E., SIVAN, N. & WERNER, Y.I. 1990. Foraging mode in lacertid lizards: variation and correlates. *Amphibia-Reptilia* 11: 373-384.
- PIETRUSZKA, R.D. 1986. Search tactics of desert lizards: how polarized are they? *Anim. Behav.* 34: 1742-1758.
- REGAL, P.J. 1978. Behavioral differences between reptiles and mammals: an analysis of activity and mental capabilities. In: Behavior and neurology of lizards, (eds.) N. Greenberg & P. D. Maclean. NIMH, Rockville, Maryland.
- VITT, L.J. 1983. Tail loss in lizards: the significance of foraging and predator escape modes. *Herpetologica* 39: 151-162.
- VITT, L.J. & CONGDON, J.D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* 112: 595-608.
- VITT, L.J. & PRICE, H.J. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38: 237-255.
- ZAR, J.H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.