

**Correction**

In Perry et al., 1990, *Amphibia-Reptilia* 11: 373-384

The legends of Figures 1-3 are correct and in place but the diagrams of Figs. 1 and 3 have been exchanged (despite author's correction on the proofs).

**Foraging mode in lacertid lizards: variation and correlates\***

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**Abstract.** Foraging strategy was observed in five species of Israeli lacertid lizards in the field. *Acanthodactylus scutellatus* is a sit-and-wait strategist, whereas *A. boskianus*, *A. schreiberi*, *Lacerta laevis* and *Mesalina guttulata* forage widely. However, the actual values differed from those reported by Huey and Pianka (1981) for Kalahari lacertids, possibly indicating the existence of a continuum of foraging modes. Foraging intensity (proportion of time spent moving or frequency of moves) is positively correlated to relative tail length, and negatively correlated to relative clutch mass. Additional possible correlates are discussed, and some cautionary remarks added.

**Introduction**

Obtaining food takes up a large part of an animal's time, and is a key factor in its ecology. Because acquiring food is highly dependent on an animal's behavior, feeding strategies and foraging modes have attracted considerable research in recent decades. Lizards, among the most conspicuous vertebrates in most ecosystems, have become common models for study. Initially, a bipolar picture emerged: some lizards are sit-and-wait predators, using a perch to scan their surroundings and making swift forays to grab passing prey, whereas others forage widely, spending a considerable part of their time moving around and searching for stationary (or even hidden) food (Pianka, 1966; Rand, 1967; Schoener, 1969; Anderson and Karasov, 1981; Huey and Pianka, 1981). Recently a more complicated gradation was proposed: Regal (1978, 1983), followed by Pough (1983), suggested the existence of three discrete categories, while Magnusson et al. (1985) postulate the existence of a continuum. However,

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McLaughlin (1989) reviewed the relevant literature from a variety of climates and habitats, and concluded that the bipolar view is indeed correct.

Being so important, foraging strategy is bound to be reflected by a variety of features of the lizards' biology (Pough, 1983). Several studies have demonstrated ecological, physiological and behavioral differences between the two extreme types, although in some cases only a single species of each type was examined. Widely foraging lizards spend much less time actively searching for food than do sit-and-wait predators (Bowker, 1984; Nagy et al., 1984). They also move more rapidly while doing so (Regal, 1978; Magnusson et al., 1985) and thermoregulate more precisely (Bowker, 1984). Sit-and-wait predators have lower rates of food intake, water influx, energy expenditure, metabolism and production of biomass (Anderson and Karasov, 1981; Nagy et al., 1984; Bowker et al., 1986). Widely foraging species have better locomotor endurance than sit-and-wait strategists and are better adapted to sprinting (Huey et al., 1984). Whereas crypsis is the common predator-avoidance strategy of most "sit-and-wait" lizards, widely foraging species tend to escape predation by running.

Besides the physiological and behavioral traits associated with foraging strategy, some less-obvious, morphological and ecological ones, have been noted. The precise role of the tail in predator escape and in locomotion is still being debated (Medel et al., 1988); however, the tail is relatively longer in widely foraging species (Vitt and Congdon, 1978). Whether their rates of tail loss differ from those of sit-and-wait strategists remains unclear (Huey and Pianka, 1981; Vitt, 1983). Finally, females of widely foraging species carry smaller relative clutch masses than do "sit-and-wait" females (Huey and Pianka, 1981), thus reducing risk of predation (Shine, 1980; Brodie, 1989).

Nevertheless, we failed to find any formal definition of these terms that could serve as a yardstick for the classification of future cases. Previous workers avoided quantifying search behavior, and did not specify how the assignment to a particular mode was determined (McLaughlin, 1989). We therefore tentatively accept the terminology used by Huey and Pianka (1981), i.e. as relative terms. For further discussion of the evolution and correlates of feeding strategies in lizards, see Dunham et al. (1988).

Foraging modes have usually been regarded as characterizing high taxa of lizards—families and even infraorders. With few exceptions, the Agamidae, Chamaleonidae and Iguanidae are believed to be sit-and-wait strategists. In contrast, the Lacertidae, Teiidae and Varanidae are considered widely foraging hunters (Regal, 1978, 1983). Huey and Pianka (1981), however, found both foraging modes among the Lacertidae of the Kalahari desert.

We wanted to test the hypothesis that both foraging modes occur in the lacertid fauna of Israel. We studied feeding strategy in two desert species (*Acanthodactylus boskianus* and *A. scutellatus*) and two mesic species (*A. schreiberi* and *Lacerta laevis*). These results we integrate with data for *Mesalina* (formerly *Eremias guttulata*) (Shani, 1986) and for Kalahari lacertids (Huey and Pianka, 1981), and then discuss in relation to

other information on the same species. Movement patterns in lacertid lizards were also studied by Avery et al. (1987a,b), but their data do not lend themselves to the kind of analysis applied here.

## Material and methods

### Abbreviations

MPM	- moves per minute
PTM	- percent of time moving
ra	- rostrum-anus length (Werner, 1971)
perca	- percents of ra
RCM	- relative clutch mass
SD	- standard deviation
SW	- sit-and-wait
WF	- widely foraging

### Species and habitats

The full names, maximum sizes, geographic ranges and typical habitats of the five Israel species discussed are presented in table 1 (based on Werner 1966, 1987, 1988; and on the personal observations of the authors). Aside from *Acanthodactylus scutellatus* and *A. schreiberi*, no two of the species studied are found together. When a species was observed in more than one locality, sites were essentially similar. Observations were made between early May and mid July 1988, between 08.00 and 19.00 hours, mostly during peak activity times. Lacertid lizards have a relatively uniform morphology; illustrations of the five taxa are available in Arbel (1984), and of European congeners in Arnold et al. (1978).

Table 1. Characteristics of the species studied.

Population studied	Maximum ra mm (n)	Distribution of the species	Habitat in Israel *
<i>Acanthodactylus boskianus</i> ssp. (Daudin, 1802)	87 (103)	North Africa to Iraq and Arabia	Sands (rarely dunes) and wadi beds in the southern deserts
<i>A. schreiberi syriacus</i> Boettger, 1879	84 (33)	southern Turkey to Israel	Sandy soils in the Mediterranean region
<i>A. s. scutellatus</i> (Audouin, 1829)	66 (96)	North Africa to Iraq, Arabia	Sands in southern coastal plain and desert
<i>Lacerta l. laevis</i> Gray, 1838	78 (84)	Turkey to Israel	Tree trunks and rocks in Mediterranean maquis
<i>Mesalina g. guttulata</i> (Lichtenstein, 1823)	52 (57)	North Africa to Pakistan	Stony plains and slopes in desert regions

\* For further details, see Yom-Tov and Tchernov (1988)

### Field methods

Lizards were observed by teams of 2-3 experimenters, distributed around the subject to prevent its being hidden by bushes. To minimize "observer effect" (Regal, 1983), the watchers kept at a distance of 5-10 m from the animal, often using binoculars. One observer was the caller, describing the animals' behavior (mainly start and end of movement). Another clocked the times in seconds and put the data on paper or dictated them to a third. The lizards did not seem to respond to the human vocalizations. No interactions between the animals were seen.

In most cases, ambient temperature was recorded when observation of the lizard ceased. Ground temperature and air temperature at 2 cm above ground were measured using a quick-response mercury thermometer (Schultheis or Miller-Weber), momentarily shaded when necessary. Only adults or subadults were observed. Most lizards were not caught, and neither sex nor body temperature was normally recorded. In order not to record the same lizard twice, the observers shifted to a different location once observations of a specimen were concluded.

The temporal regime of foraging should only be measured after the lizards have ceased their basking behavior and reached their activity temperature range (Cowles and Bogert, 1944). Unfortunately, no data on temperature requirements were available for *Lacerta laevis*. Shani (1986) measured body temperatures in the *Mesalina guttulata* he observed, and these averaged 34.9°C during activity. For the three *Acanthodactylus* species, the only reports of body temperatures during activity are from enclosures. The mean activity temperatures (sensu Pough and Gans, 1982) were: *A. boskianus*, 39.2°C; *A. schreiberi*, 40.6°C; and *A. scutellatus*, 39.3°C (Duvdevani and Borut, 1974). For two species, these values somewhat exceed the respective average ground temperatures measured. Although we did not measure body temperatures in the present study, it has long been established that body temperatures are often higher than those of the surrounding habitat (Cowles and Bogert, 1944).

All species were observed in their natural habitats during peak activity hours. Our prior experience leads us to believe that all the animals were within their respective activity temperature ranges when observed. Although there were differences between habitats, the data are representative of each species' typical behavior and are thus comparable.

### Morphological data

Maximum tail lengths (table 1) were extracted from a computerized data bank of lizard biometry (Kosswig, Lavee and Werner, 1976), containing large samples from throughout the specific ranges in Israel. The material is kept in the Israel National Collections of Natural History (in the Departments of Zoology of The Hebrew University of Jerusalem and Tel Aviv University). Only data for complete, unregenerated tails were used. Relative tail length was the same for both sexes (*t* test) in all species

except *A. boskianus*, where males had longer tails than females. Since sex was unidentified in our field observations, tail lengths of the two sexes were pooled for all five species. Replacing the tail length of *A. boskianus* by that of either sex did not materially affect the resulting correlations.

The frequency of tails retained whole in the museum collections was used as a minimum estimate of tail retention in the field. The complementary percentages to Huey and Pianka's (1981) percents of tail breakage were employed to enable comparison.

RCM (clutch volume/maternal mass) was estimated from existing data on clutch volume and maternal length (Frankenberg and Werner, in press). Maternal mass was computed for each species from length, using the equations given by Perry (1990).

### Statistics

We used a computerized statistics package (SAS) for all the tests performed. Biometrical data pairs were compared by *t*-test. Temperature data and all measures of foraging were compared by both Wilcoxon and Van der Waerden non-parametric tests. All possible pairs of lizard species were compared. Both tests gave similar results for the 12 variables used; our tables give the higher *p*-values in each case. Values above 0.05 were replaced by n.s. (not significant). Measures of foraging mode were also compared by Tukey test. Correlations between various variables were tested both intra- and interspecifically, using the Spearman rank correlation. The broken lines in Figs. 2 and 3, however, represent equations derived using the parametric linear regression analysis.

### Results and comments

The observations are summarized in table 2a, which may be compared to table 1 in Huey and Pianka (1981). Although these authors presented overall average velocities for their animals, we refrained from measuring velocity, the comparison of which would necessitate relating to individual animal size (Avery et al., 1987a,b). Of all possible lizard pairs compared, only those involving *A. scutellatus* yielded any significant differences (table 2b). We measured the hitherto-ignored ground temperatures, and those differed between *L. laevis* (Jerusalem) and each of the three *Acanthodactylus* species.

Intraspecific variation in all foraging mode indices was especially high in *L. laevis*. In this species, the sample was almost equally divided between individuals which moved a lot and others which moved very little.

Table 2a also includes Shani's (1986) data for *Mesalina guttulata*. It was not included in those interspecific comparisons discussed above because of the small number of specimens observed (*n* = 3). It was, however, included in interspecific correlations of foraging intensity.

**Table 2a.** Measures of foraging mode. Species means, based on samples described or quoted in the text.

Species	n	Seconds observed		Moves/minute		% of time moving	
		x	SD	x	SD	x	SD
<i>Acanthodactylus boskianus</i>	7	425	230	2.01	1.46	28.8	25.7
<i>A. schreiberi</i>	12	315	174	1.54	0.87	30.5	20.6
<i>A. scutellatus</i>	26	354	294	1.01	0.75	7.7	7.12
<i>Lacerta laevis</i>	16	253	173	1.61	1.36	30.0	24.3
<i>Mesalina guttulata</i>	3	82 min		0.15		30.5	

**Table 2b.** Significance of the differences between species.

Species	Seconds observed	Moves/minute	% of time moving
<i>A. scutellatus-A. boskianus</i>	n.s.	n.s.	0.0239**
<i>A. scutellatus-A. schreiberi</i>	n.s.	0.0475	0.0002**
<i>A. scutellatus-L. laevis</i>	n.s.	n.s.	0.0043**

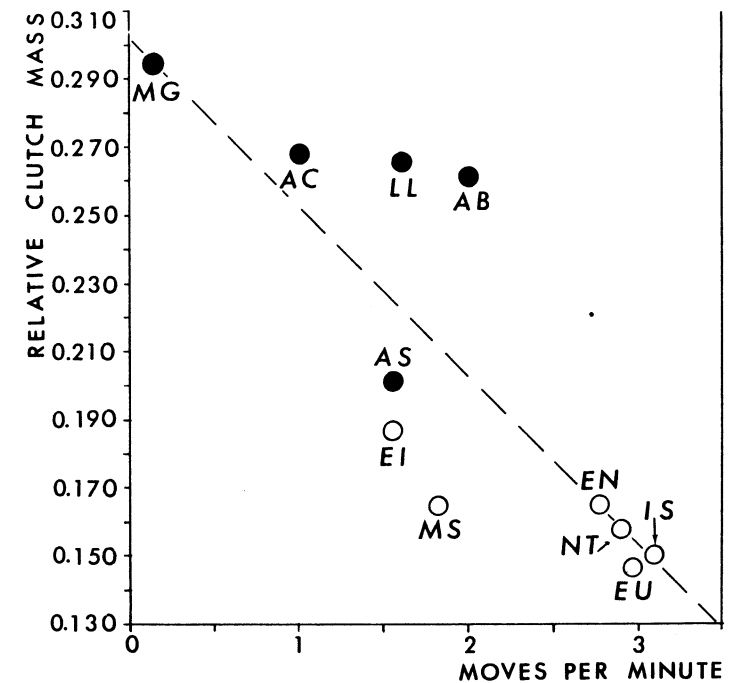
\* Data from Shani (1986)

\*\*  $p < 0.05$  by Tukey test

Fig. 1 summarizes both PTM and MPM data for the five Israeli (present study; Shani, 1986) and six Kalahari (Huey and Pianka, 1981; Pianka, 1986) species. To check whether PTM and MPM are correlated or need to be regarded separately, we correlated the two parameters within each of the four species in the current study, and among and five Israeli species. A correlation was found among the two measures within each of the four species ( $r^2$  ranged from 0.46 to 0.68,  $p$  from 0.0001 to 0.0295), but not among species ( $r^2 = 0.25$ ,  $p = 0.3910$ ). After pooling our data with those of both Shani (1986) and Huey and Pianka (1981), a significant correlation was revealed ( $r^2 = 0.61$ ,  $p = 0.0043$ ) between MPM and PTM among the 11 species.

McLaughlin (1989) used MPM as the exclusive index of foraging strategy. He based his choice both on the availability of data and on theoretical and empirical studies. We believe that PTM is of no lesser ecological significance, as demonstrated by *M. guttulata*, which spends much of its time moving around, making infrequent but protracted moves. Two Kalahari species show the reverse situation (Huey and Pianka, 1981). Until the subject is better understood, neither criterion should be omitted. Therefore, and because of the lack of quantitative criteria, we refrain for the time being from assigning our species to any of the foraging mode categories.

Huey and Pianka (1981) concluded that WF lacertids had longer tails, relative to body length, than did SW strategists. Vitt (1983) reached the same conclusion for 12 species belonging to four families from the Brazilian caatinga. Magnusson et al.



**Figure 1.** The variation of foraging mode among eleven species of lacertid lizards. Shown are the mean and one standard error, arranged in order of increasing number of moves per minute; the % of time moving is shown for comparison. Solid symbols represent Israeli species (present study; Shani, 1986); hollow symbols, Kalahari species. AB, *Acanthodactylus boskianus*; AC, *Acanthodactylus scutellatus*; AS, *Acanthodactylus schreiberi*; EI, *Eremias lineo-ocellata*; EN, *Eremias namaquensis*; EU, *Eremias lugubris*; IS, *Ichnotrophis squamulosa* juvs.; LL, *Lacerta laevis*; MG, *Mesalina guttulata*; MS, *Meroleos suborbitalis*; NS, *Nucras tessellata*.

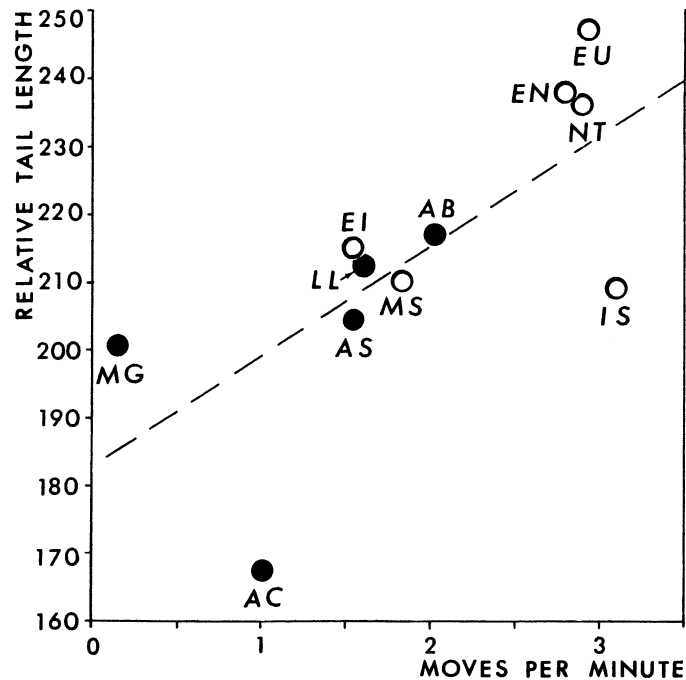
(1985), on the other hand, found that, for three Brazilian teiid species, tail length did not increase with foraging intensity. Table 3 gives the values of the foraging mode indices and their correlates. Among the five Israeli species, relative tail length was positively and significantly correlated to MPM ( $r^2 = 0.81$ ,  $p = 0.0374$ ) but not to PTM ( $r^2 = 0.36$ ,  $p = 0.2848$ ). When these data were pooled with those for the Kalahari lacertids (Huey and Pianka, 1981), relative tail length was strongly correlated to MPM ( $r^2 = 0.46$ ,  $p = 0.0229$ ) (fig. 2); the correlation to PTM was nearly significant ( $r^2 = 0.34$ ,  $p = 0.0604$ ).

Neither Huey and Pianka (1981) nor Vitt (1983) could relate the frequency of tail loss to foraging mode. Nor did we find any such correlation, even after pooling the data from Huey and Pianka (1981) with ours and Shani's (1986). Whereas all other characters we used are means of individual measurements, the percentage of tails retained is a measure of the population, rather than of the individual. Among other things, it depends on the average age of the sample (Bustard and Hughes, 1966;

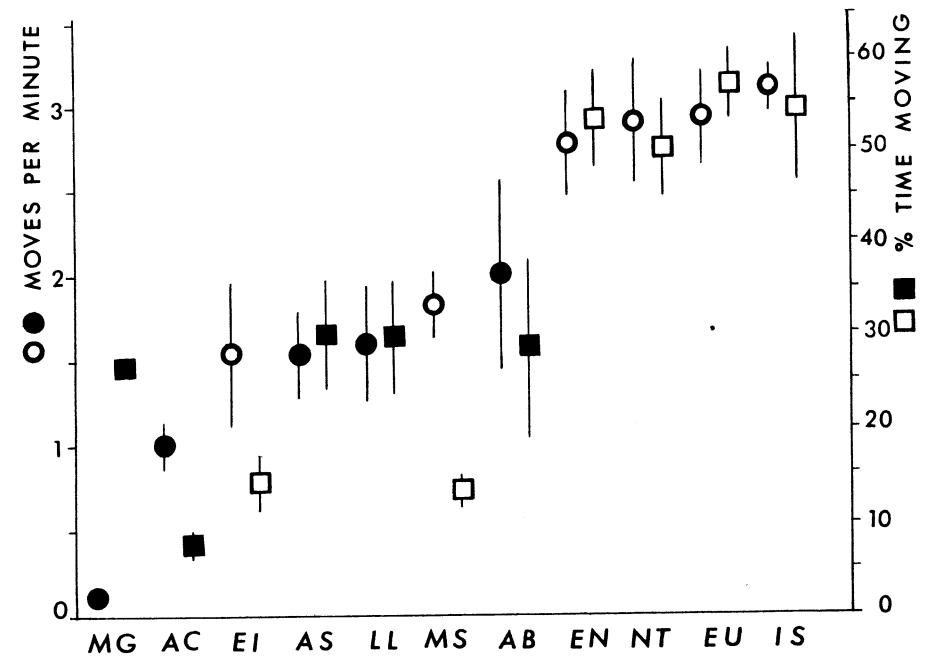
**Table 3.** Foraging mode and its correlates.

Species	Moves/minute	% of time moving	Tail <i>perca</i>	% of tails retained	Clutch volume (mm <sup>3</sup> )/maternal ra (mm)	(mm <sup>3</sup> )/maternal mass (g)
<i>Acanthodactylus boskianus</i>	2.01	28.8	216.7	37.7	21.83	0.261
<i>A. schreiberi</i>	1.54	30.5	204.5	24.2	19.97	0.201
<i>A. scutellatus</i>	1.01	7.7	167.2	59.8	16.55	0.268
<i>Lacerta laevis</i>	1.61	30.0	212.1	31.0	20.35	0.266
<i>Mesalina guttulata</i>	0.15	30.5	200.7	38.6	13.16	0.295

Tinkle and Ballinger, 1972), which may be reflected in animal body size (Calder, 1984, p. 144). Hence we tested for, and indeed found among the eleven species, a negative correlation between the percentage of tails retained by adults and the average body size ( $r^2 = 0.36$ ,  $p = 0.0510$ ). Thus, it might be fruitful to reexamine the relation of tail loss to foraging mode, using species of comparable average life span or animals of comparable age from different species.



**Figure 2.** The relation of relative tail length (*perca*) to foraging mode in eleven lacertid species. The broken line represents the parametric regression line;  $r_s^2 = 0.46$ ,  $p = 0.0229$  (Spearman rank correlation). Symbols as in fig. 1.



**Figure 3.** The variation of relative clutch mass with foraging mode. The broken line represents the parametric regression line;  $r_s^2 = 0.78$ ,  $p = 0.0003$  (Spearman rank correlation). Symbols as in fig. 1.

Vitt and Congdon (1978) and Huey and Pianka (1981) have found that WF lizards have a lower RCM than do SW strategists. This remains true even when lizards belonging to different families are compared (Dunham et al., 1988). We derived RCM data for the five Israeli species (see Material and methods), and pooled them with those of Huey and Pianka (1981) for other lacertids. Highly significant negative correlations of RCM to both MPM ( $r^2 = 0.78$ ,  $p = 0.0003$ ; fig. 3) and PTM ( $r^2 = 0.49$ ,  $p = 0.0171$ ) were obtained. Values of RCM in Israeli species were considerably higher than those reported from the Kalahari (Huey and Pianka, 1981). This is in accordance with the observations that Israeli species spend much less time foraging (fig. 1) and have considerably shorter tails (fig. 2). Apparently, Israeli lacertids are more sedentary than Kalahari ones.

We feel the following reservation must be made: any attempt to correlate foraging mode to RCM interspecifically (Vitt and Congdon, 1978; Huey and Pianka, 1981; Vitt and Price, 1982; herein) suffers from an inherent weakness. Foraging mode may be sex-dependent (Ananjeva and Tsellarius, 1986), and such correlations should only utilize data from sexed animals. Moreover, correlating foraging mode, derived from a sample of mixed sexes, with the load the clutch exerts upon the females only, might be invalid.

## General discussion

Although thermoregulation has been ruled out and no social interactions have been observed, we have no evidence that all locomotion was related to feeding. Nevertheless, we follow previous authors in assuming foraging to be the dominant factor in the activity regime of the lizards. The four species examined clearly fall into two groups (table 2a,b): *Acanthodactylus scutellatus* is relatively SW, whereas *A. boskianus*, *A. schreiberi* and *Lacerta laevis* are relatively WF. This situation parallels that discovered by Huey and Pianka (1981) in the Kalahari, but the actual MPM and PTM values are markedly different (fig. 1). It might be assumed that a dissimilarity in foraging mode between sympatric animals helps them to co-habit similar habitats. However, the only apparently sympatric species we studied, *A. scutellatus* and *A. schreiberi*, are known to utilize different microhabitats (Avital, 1981).

In each of the two studies, some species were relatively SW and some were relatively WF. In both, tail length was negatively, and RCM positively, correlated to MPM and PTM. A similar situation emerges when Israel is compared to the Kalahari: Israeli species are relatively SW, and have shorter tails and larger RCMs.

Although contrasting two discrete types has proved useful to the investigation of the "consequences" of foraging mode, some authors have recognized that these types may merely represent extremes in a gradient. Regal (1978, 1983) identified three, rather than two, types of species in this spectrum: SW predators, cruising foragers and intensive foragers. Moermond (1979) showed that in seven SW species of *Anolis*, species-specific distance and speed of locomotion varied considerably in relation to habitat structure. Recently, Magnusson et al. (1985) explicitly spoke of a continuum existing between SW and WF species.

The pooled data available for lacertids (figs. 1-3) may be interpreted as representing such a continuum, but also lend themselves to other interpretations. Lacertid lizards may indeed fall dichotomously into two foraging mode classes, with the precise measures of MPM and PTM being modulated by external factors such as food abundance. High values of MPM and PTM may be related to food scarcity (Ananjeva and Tsellarius, 1986). This may account for the situation in the Kalahari. Seasonal variations, possibly in connection with food abundance, are also a conceivable factor. Whereas Huey and Pianka (1981) collected their data during the summer, we conducted our observations from late spring to mid-summer. Finally, it is impossible to entirely rule out an artifact of differences in methodology.

Several factors may account for the considerable intraspecific variation observed in both measures of foraging mode (table 2a). Although we excluded juveniles, ontogenetic shift in food preference, as described by Robson and Lambert (1980) in Moroccan *A. boskianus*, may well also be accompanied by a change in foraging behavior and should be considered (Huey and Pianka, 1981). We did not sex the lizards we observed, and cannot exclude the possibility that some of the individual variation observed is sex-based (Ananjeva and Tsellarius, 1986). In *L. laevis*, the only

species whose habitat is 3-dimensional rather than flat, stationary individuals may have been exploiting vantage points affording better fields of view. Nevertheless, *L. laevis* differed very little in average foraging mode from the *Acanthodactylus* species.

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