

Foraging Mode and Its Flexibility in Lacertid Lizards from Europe

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ABSTRACT.—Apart from certain species of the African clade, the lizard family Lacertidae has generally been described as consisting of active foragers. We made quantitative field observations of 14 species of lacertid lizards, mainly belonging to the more basal Eurasian clade. Our data show that sit-and-wait foraging is much more widespread in Lacertidae than previously alleged. We also investigated the influence of weather and times of day on foraging activity levels and conclude that for comparative purposes observations should be restricted to circumstances that are optimal for activity. We did not find sex differences in foraging behavior.

Classically, two types of predators are distinguished: sit-and-wait foragers remain stationary for long periods of time, waiting for mobile prey to pass into their perceptual field; active foragers spend much of their time moving actively in search for prey. Lizards have figured prominently in the development of foraging mode concepts. Since Pianka (1966) described these two alternative modes of foraging in desert lizards, they have become central to our understanding of lizard ecology and life history, with corollaries in preferred prey types and probable predators (Huey and Pianka, 1981), energy use (Anderson and Karasov, 1981, 1988), reproduction (Vitt, 1990; Colli et al., 1997), relative clutch mass (Vitt and Congdon, 1978; Vitt and Price, 1982), morphology (McBrayer, 2004), territorial behavior (Stamps, 1977), locomotor capacity (Huey et al., 1984), predator escape modes (Vitt, 1983), learning ability (Day et al., 1999), and chemosensory behavior (Cooper, 1994, 1997). In the meantime, this strict dichotomous view on foraging behaviors has been put in question and refinements to the original scheme have been proposed (Regal, 1978; Butler, 2005; Cooper, 2005a; Anderson, 2007). The accumulation of foraging data of more and more lizard species seems to suggest that a continuum in foraging activity levels exists, with classical sit-and-waiters and active foragers at the extremes, but also with intermediate species (Perry, 1999, 2007; Cooper, 2005a; but see Huey and Pianka, 2007). The combination of different foraging measures might still allow delineating distinct foraging strategies (Cooper, 2005a, 2007).

Most lizard families appear to be conservative in foraging mode and seem to fit conveniently into the traditional dichotomy (Cooper, 1994). However, other families exhibit considerable

among-species variation in moving rates and foraging behavior, for example Gekkonidae (Werner et al., 1997; Cooper et al., 1999), Scincidae (Castanzo and Bauer, 1993; Cooper and Whiting, 2000), and Lacertidae (Huey and Pianka, 1981; Perry et al., 1990; Cooper and Whiting, 1999). In the last family, active foraging is believed to be plesiomorphic (Cooper, 1994; Cooper and Whiting, 1999), and some extant species move up to 70% of their activity time. However, the family also includes much more sedentary species that move only 10–15% of the time (Huey and Pianka, 1981; Cooper and Whiting, 1999). The family Lacertidae is divided in two subfamilies (Fu, 2000): Gallotiinae, which includes the genera *Gallotia* and *Psammodromus*; and the Lacertinae, which includes all remaining lacertids. Lacertinae is further divided into two groups: an African group mainly living in Africa and Arabia, and a Eurasian group. So far, information on the foraging mode of lacertid lizards is mostly restricted to species of the African clade (Huey and Pianka, 1981; Perry et al., 1990; Cooper and Whiting, 1999). The primitive European taxa have generally been considered active foragers (e.g., Arnold, 1993; Van Damme and Vanhooydonck, 2001), but it has also been noticed that they may display considerable flexibility in foraging behavior (Arnold, 1987). The first goal of this paper is to present new foraging data for (mainly European) lacertids.

Although many studies have tacitly assumed that foraging strategy is fixed within species, several species have been observed to alter movement levels and even to switch between modes (Pietruszka, 1986; Greeff and Whiting, 2000). Both theoretical predictions (e.g., MacArthur and Pianka, 1966; Norberg, 1977; Andersson, 1981) and empirical field studies indicate that foraging behavior varies with the availability of resources. For example, lizards adapt their foraging activity or style to prevail-

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TABLE 1. Species for which observations were made are indicated by location, geographic coordinates, the prevailing habitat type, and the dates of observation.

Species	Site	Coordinates	Date	Habitat type
<i>Acanthodactylus aureus</i>	Aglou, Morocco	29°48'N 9°50'W	18–25/November/2005	dunes
<i>Acanthodactylus erythrurus</i>	Riumar, Spain	40°45'N 0°50'E	06–16/June/2005	dunes
<i>Lacerta vivipara</i>	Kalmthout, Belgium	51°25'N 4°25'E	20–30/August/2005	heath
<i>Lacerta bilineata</i>	Sant Hilari Sacalm, Spain	41°55'N 2°24'E	11–20/August/2004	bushes, meadow
<i>Lacerta monticola</i>	Plataforma de Gredos, Spain	40°20'N 5°15'W	20–27/September/2005	rocks
<i>Lacerta oxycephala</i>	Vis, Croatia	43°05'N 16°10'E	26/April–02/May/2004	walls of fortress
<i>Lacerta schreiberi</i>	Plataforma de Gredos, Spain	40°20'N 5°15'W	21–25/September/2005	waterfront, rocks
<i>Podarcis hispanica</i>	Casteldefells, Spain	41°15'N 1°58'E	15–22/August/2004	walls, pavement
<i>Podarcis melisellensis</i>	Vis, Croatia	43°05'N 16°10'E	26/April–02/May/2004	meadow
<i>Podarcis muralis</i>	El Serrat, Andorra	42°30'N 1°35'E	09–13/August/2004	rocks
<i>Podarcis peloponnesiaca</i>	Stymfalía, Greece	37°50'N 22°30'E	12–18/October/2005	rocks
<i>Podarcis tiliguerta</i>	Haut Asco, Corsica, France	42°24'N 8°57'E	06–09/June/2004	rocks
<i>Psammodromus algirus</i>	Marçá, Spain	41°08'N 0°47'E	29/05–10/June/2005	field, meadow
<i>Psammodromus hispanicus</i>	Roses, Spain	42°15'N 3°10'E	19–21/June/2005	dunes

ing conditions of prey density and distribution (Huey and Pianka, 1981; Ananjeva and Tsellaris, 1986; Eifler and Eifler, 1999; Greeff and Whiting, 2000). Temperature strongly acts upon activity of ectotherms, especially in the case of active foragers (Pietruszka, 1986; Carrascal and Díaz, 1989; Belliure et al., 1996). Sexual differences in activity levels have also been reported, especially during the reproductive season, when males are often seen to be more active than females (Pietruszka, 1986; Aragón et al., 2001; Wymann and Whiting, 2002; Butler 2005). Time of day can also affect foraging behavior (Pietruszka, 1986). All these factors may influence the quantitative measures obtained from behavioral observations that are meant to typify species' foraging behavior, posing a methodological challenge for measurements of foraging activity. To make sense in a comparative context, measures for different species should be obtained from observations in analogous circumstances. The second goal of this paper is to identify factors that change foraging activity in the field. This should allow these factors to be taken into account explicitly in developing a methodological protocol.

MATERIALS AND METHODS

We observed the foraging behavior of the following 14 species in the field: *Acanthodactylus aureus*, *Acanthodactylus erythrurus*, *Lacerta vivipara*, *Lacerta bilineata*, *Lacerta monticola*, *Lacerta*

oxycephala, *Lacerta schreiberi*, *Podarcis hispanica*, *Podarcis melisellensis*, *Podarcis muralis*, *Podarcis peloponnesiaca*, *Podarcis tiliguerta*, *Psammodromus algirus*, and *Psammodromus hispanicus* (see Table 1). Sex, locality, date, time, and weather conditions were noted. Observations were performed from late spring to autumn and at times of the day when animals were active. In four species (*Ps. hispanicus*, *L. vivipara*, *P. tiliguerta*, and *A. erythrurus*), sexes could not be discerned during the observations. Three weather conditions were distinguished: 1: sunny; 2: "veiled sun" (i.e., no fully clear sun, but with shadows projected on the ground); 3: cloudy, with no shadows projected. An observation was assigned to the category that best described the largest part of the time of the observation. Four categories of time of the day were used (following Avery, 1993): from 0900–1100 h; from 1101–1300 h; from 1301–1600 h, after 1600 h. These were not the local times but time corrected for deviations from solar noon. One of us (DV) performed observations for all but one (*P. tiliguerta*) of the species.

After having detected a lizard, the observer stopped moving and waited some time (typically around 30 sec) before starting the actual recording of behavior. Observations of animals looking in the direction of the observer or showing foot shakes or tail vibrations, which are indications of stress (Verbeek, 1972; Thoen et al., 1986), were discarded. By means of a PSION Workabout MX (Psion Teklogix, Inc.)

handheld minicomputer, on which was installed a custom written OVAL program, the beginnings and ends of movements and attacks on prey were recorded. Changes in orientation or postural changes and movements of body parts not involving displacement of the whole body were not considered as movements. Pauses of one or more seconds were considered as bouts of "immobility." Each individual was observed for 10 min if possible. Sometimes, observations had to be ended earlier because the focal animal disappeared from sight. All observations lasting at least 3 min were included in the analysis. From these observations, we calculated the number of movements per minute (MPM) and the percentage of time moving (PTM) for each individual. Observational sessions that contained movements resulting from intraspecific interactions (animals chasing each other) or predator attacks were discarded. To avoid pseudoreplication by observing the same lizard more than once, we changed location of the observation when the observation of an individual was finished. Only adult lizards were observed.

We also noted all attacks on prey, and logged whether these were launched from immobility or in the context of movements. From this, we calculated PAM-values (percentage of attacks launched while moving; see Cooper et al., 1999). No distinction was made between successful and unsuccessful feeding attempts.

Statistical Analysis.—Raw PTM and MPM data were \log_{10} -transformed prior to analysis. To include a maximum of species in the analyses, the effects of weather, sex, and time of day on PTM and MPM of the different species were examined separately by univariate analysis of variance. *Lacerta bilineata*, *L. schreiberi*, and *Ps. hispanicus* were kept out of the analyses, because of the low number of observations available for these species.

Finally, correlations between the foraging measures were calculated. The same relationships were investigated using the method of standardized independent contrasts (Felsenstein, 1985) by use of the PDTREE program/PDAP package (Garland et al., 1999; Garland and Ives, 2000). The phylogenetic tree used (Fig. 1) is based on Fu (2000) and Oliverio et al. (2000). In these analyses, all branch lengths were set to unity (see Martins and Garland, 1991; Díaz-Uriarte and Garland, 1998), and the regression of the contrasts was forced through the origin (see Garland et al., 1992).

RESULTS

For *L. monticola* and *P. tiliguerta*, only observations in full sun were available; hence,

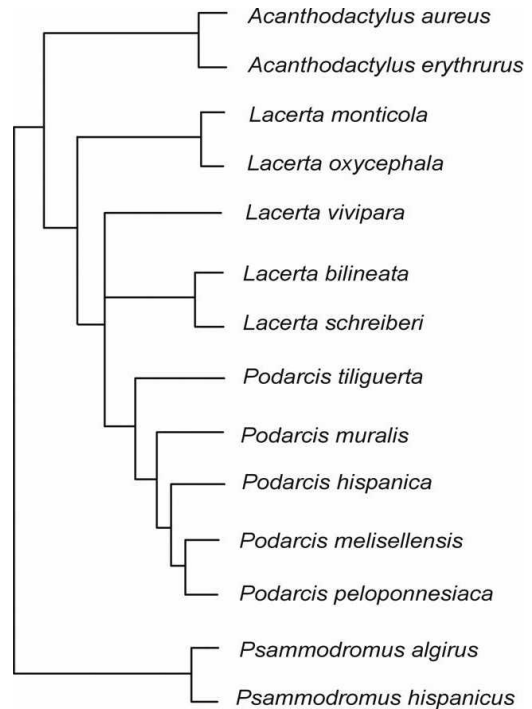


FIG. 1. Phylogeny used for the species in this study. The depicted branch lengths are not realistic; in the analyses, all branch lengths were set to unity.

these species were not included in the following analysis of the influence of weather. Mean PTM differed significantly among species ($F_{8,588} = 4.17$; $P = 0.007$), and the strong weather effect ($F_{2,588} = 30.51$; $P < 0.001$) was similar in all species (species \times weather interaction effect: $F_{16,588} = 1.32$; $P = 0.18$). Similar results were found for MPM (species effect: $F_{8,588} = 2.85$; $P = 0.04$; weather effect: $F_{2,588} = 26.80$; $P < 0.001$; species \times weather interaction effect: $F_{16,588} = 0.92$; $P = 0.54$). Both PTM and MPM decreased when the weather is cloudy, with the "veiled sun" situation showing intermediate values (see Table 2). In the following analyses only data gathered in full sun were used.

Differences between the sexes (see Table 3) in mean PTM were not significant (species-effect: $F_{7,461} = 11.35$; $P = 0.002$; sex-effect: $F_{1,461} = 0.002$; $P = 0.97$; species \times sex-effect: $F_{7,461} = 0.44$; $P = 0.88$), and the same applies to MPM (species-effect: $F_{7,461} = 5.67$; $P = 0.02$; sex-effect: $F_{1,461} = 0.65$; $P = 0.42$; species \times sex-effect: $F_{7,461} = 0.47$; $P = 0.86$).

For *P. tiliguerta*, no detailed timing of the observations was available; thus, this species was not included in the following analysis. Mean PTM changed over the course of the day (species-effect: $F_{9,504} = 4.23$; $P = 0.002$; time-effect: $F_{3,504} = 2.99$; $P = 0.03$; species \times time-

TABLE 2. Mean PTM- and MPM-values in different weather conditions for nine species lacertid lizards. *N* denotes the number of observations.

	Sunny			Veiled sun			Cloudy		
	<i>N</i>	PTM	MPM	<i>N</i>	PTM	MPM	<i>N</i>	PTM	MPM
<i>Acanthodactylus aureus</i>	36	6.13	2.1	6	3.38	1.43	4	4.23	1.52
<i>Acanthodactylus erythrurus</i>	32	15.98	2.94	5	14.06	2.87	2	9.34	1.76
<i>Lacerta oxycephala</i>	78	14.92	2.18	8	8.59	1.71	8	5.03	1.1
<i>Lacerta vivipara</i>	31	32.84	4.07	3	32.76	2.77	4	16.76	2.24
<i>Podarcis hispanica</i>	31	20.25	2.85	5	3.6	0.91	3	9.55	1.8
<i>Podarcis melisellensis</i>	77	17.16	2.41	15	12.6	1.76	13	5.74	0.97
<i>Podarcis muralis</i>	65	20.41	2.98	10	23.54	3.03	7	9.15	1.38
<i>Podarcis peloponnesiaca</i>	85	11.89	2.04	8	2.49	0.75	9	3.92	0.99
<i>Psammodromus algirus</i>	58	20.56	2.84	9	17.12	2.23	3	5.41	0.82

TABLE 3. Mean PTM- and MPM-values for males and females of eight species lacertid lizards. *N* denotes the number of observations.

	Males			Females		
	<i>N</i>	PTM	MPM	<i>N</i>	PTM	MPM
<i>Acanthodactylus aureus</i>	12	5.98	2.08	24	6.94	2.54
<i>Lacerta monticola</i>	20	22.06	3.02	31	16.74	2.95
<i>Lacerta oxycephala</i>	35	16.65	2.24	43	13.52	2.14
<i>Podarcis hispanica</i>	14	24.75	3.25	17	16.49	2.52
<i>Podarcis melisellensis</i>	34	21.09	2.49	43	14.4	2.35
<i>Podarcis muralis</i>	28	19.79	2.85	37	20.86	3.08
<i>Podarcis peloponnesiaca</i>	35	10.69	1.64	50	12.68	2.31
<i>Psammodromus algirus</i>	28	17.93	2.47	30	23.01	3.18

TABLE 4. Mean PTM- and MPM-values during different periods of the day for 10 species lacertid lizards. *N* denotes the number of observations.

	0900–1100 h			1100–1300 h			1300–1600 h			After 1600 h		
	<i>N</i>	PTM	MPM	<i>N</i>	PTM	MPM	<i>N</i>	PTM	MPM	<i>N</i>	PTM	MPM
<i>Acanthodactylus aureus</i>	4	5.56	2.24	16	7.05	2.52	14	6.26	2.29	2	5.73	2.06
<i>Acanthodactylus erythrurus</i>	3	19.14	3.98	12	18.02	2.94	15	14.85	3.34	2	5.68	1.21
<i>Lacerta monticola</i>	1	17.13	3.19	22	19.69	3.18	17	18.34	2.86	3	4.52	1.46
<i>Lacerta oxycephala</i>	9	12.25	1.98	25	19.31	2.82	31	11.73	1.74	13	13.25	2.37
<i>Lacerta vivipara</i>	7	29.68	4.28	11	26.15	3.13	10	40.96	5.38	3	26.57	3.65
<i>Podarcis hispanica</i>	4	15.86	2.36	14	22.73	3.27	8	19.05	2.86	5	17.21	2.87
<i>Podarcis melisellensis</i>	12	15.97	2.06	31	20.48	3.04	27	13.75	1.97	7	12.92	2.74
<i>Podarcis muralis</i>	10	20.24	3.14	19	18.04	2.96	28	22.24	3.11	8	9.24	1.14
<i>Podarcis peloponnesiaca</i>	7	9.81	1.48	28	10.82	1.99	35	13.58	2.19	5	6.81	1.78
<i>Psammodromus algirus</i>	5	21.55	2.98	18	22.27	3.39	25	19.54	2.63	10	16.05	2.45

effect: $F_{27,504} = 0.97$; $P = 0.50$). PTM was generally highest during the hottest hours of the day (from 1100 until 1600 h corrected time; Table 4). Mean MPM did not show such pattern (species-effect: $F_{9,504} = 2.03$; $P = 0.07$; time-effect: $F_{3,504} = 1.54$; $P = 0.20$; species \times time-effect: $F_{27,504} = 1.06$; $P = 0.39$).

Because of the influence of weather and time of day on foraging activity, we calculated mean PTM, MPM, and PAM for the species on the basis of the observations obtained in peak activity periods (from 1100 until 1600 h cor-

rected time) under sunny conditions only, pooling data for both sexes (Table 5). PTM correlated significantly with MPM ($N = 14$, $r = 0.86$, $P < 0.001$) but not with PAM ($N = 12$, $r = 0.05$, $P = 0.87$). Neither did MPM and PAM correlate ($N = 12$, $r = -0.32$, $P = 0.30$). These patterns were the same when correcting for phylogenetic relationship: PTM correlated significantly with MPM ($t_{11} = 6.99$; $r = 0.90$; $P < 0.001$) but not with PAM ($t_9 = 0.004$; $r = 0.001$; $P = 0.96$) nor did MPM and PAM correlate ($t_9 = -0.95$; $r = -0.29$; $P = 0.37$).

TABLE 5. Overview of mean PTM- and MPM-values, their standard deviations (SD), and PAM of the species studied during peak activity periods in full sun. N denotes the number of observations; tottime denotes the total time of observation; <time> denotes the mean duration of the observations; #att denotes the number of attacks on which PAM was based. Observed minimal and maximal values of PTM and MPM are reported as well (min and max).

	N	tottime	<time>	PTM	SD	min	max	MPM	SD	min	max	PAM	#att
<i>Acanthodactylus aureus</i>	30	254'51"	8'30"	6.68	6	0	25.32	2.41	1.85	0	7.6	0.19	16
<i>Acanthodactylus erythrus</i>	27	252'11"	9'20"	16.26	11.21	0	47.58	3.16	1.75	0	7.26	0.45	22
<i>Lacerta bilineata</i>	11	95'47"	8'42"	6.27	6.82	0	22.43	0.98	0.91	0	2.43	1	2
<i>Lacerta monticola</i>	39	311'31"	7'59"	19.1	11.41	0	54.87	3.04	1.33	0	6.18	0.4	15
<i>Lacerta oxycephala</i>	56	409'07"	7'19"	15.11	12.4	0	60.66	2.22	1.37	0	4.92	0.32	31
<i>Lacerta schreiberi</i>	5	44'15"	8'51"	10.75	7.65	2.32	21.1	1.86	1.35	0.38	3.67		
<i>Lacerta vivipara</i>	21	123'27"	5'53"	33.2	15.85	5.77	65.01	4.2	1.84	1.11	8.24	0.5	4
<i>Podarcis hispanica</i>	22	158'31"	7'13"	21.39	10.87	1.4	38.49	3.12	1.4	0.42	6.22	0.5	6
<i>Podarcis melisicensis</i>	58	458'03"	7'54"	17.35	12.82	0	47.26	2.54	1.51	0	6.34	0.49	39
<i>Podarcis muralis</i>	47	368'35"	7'50"	20.54	11.52	0	46.26	3.05	1.71	0	10.16	0.5	14
<i>Podarcis peloponnesiaca</i>	73	674'37"	9'14"	12.35	10.27	0	41.03	2.1	1.46	0	5.44	0.25	36
<i>Podarcis tiliguerta</i>	21	165'22"	7'52"	9.26	10.79	0	36.38	1.74	1.4	0	4.61	0.77	13
<i>Psammodromus algirus</i>	43	339'32"	7'54"	20.68	16.67	0	60.21	2.95	2.18	0	8.12	0.69	13
<i>Psammodromus hispanicus</i>	6	45'21"	7'34"	25.99	17.99	3.41	51.09	4.71	3.29	0.88	10.53		

DISCUSSION

In this paper, we report new data on foraging behavior of 14 species of lacertid lizards. Because these foraging measures are strongly influenced by some environmental conditions, first we will discuss the importance of limiting collection of foraging data to optimal circumstances. Next, we will discuss data collected in these circumstances.

Methodological Considerations.—Often, substantial intraspecific variation has been observed in the foraging behavior of lizards, but this is seldom explicitly reported in foraging mode studies (e.g., Greeff and Whiting, 2000; Persaud et al., 2003; Werner et al., 2004). Variability in MPM and PTM is mostly high (Perry, 1999, 2007), and this applies as well to the species recorded here, with some individuals sitting still during the entire observation period, whereas others move up to 60% of the time (Table 5). This type of variability may partly be the result of the methodology of observations. For example, observations for several hours instead of for only 10 min might include most of the behavioral repertoire of an individual, resulting in much more similar activity levels between individuals. Still, even with relatively short observation periods, the resulting mean PTM and MPM are quite repeatable in general (e.g., Huey and Pianka, 1981; Cooper and Whiting, 1999; Cooper et al., 2001). The length of observation periods required for generating reliable foraging measure estimates may in fact vary for different clades (Perry, 2007).

In contrast to some other authors (e.g., Perry, 1999), we did not exclude thermoregulatory behavior from our calculations, because it is mostly not feasible to isolate different motivations that can be in effect simultaneously with foraging. Attacks to prey may be launched even from a clearly thermoregulating posture (flattened body, raised legs). Inclusion of basking in our data might result in somewhat lower PTM- and MPM-values, but because the lacertids considered here only devote a very small portion of their time to the specific basking posture, especially during peak activity hours under sunny conditions (e.g., Scheers and Van Damme, 2002; DV, pers. obs.), the effect is minor. As a consequence, PTM and MPM reflect general movement behavior rather than foraging per se (Perry, 1999, suggested the term "time allocation"). For the rest, our results largely agree with the values reported for the few species already studied (e.g., *Ps. algirus*, Belliure et al., 1996; *L. monticola*, Martín and Salvador, 1997).

Part of the intraspecific variability in foraging measures has been reported to arise from

differences in environmental factors such as weather (Ellinger et al., 2001), season (Pietruszka, 1986; Lister and Aguayo, 1992; Aragón et al., 2001), time of the day (Pietruszka, 1986; Ellinger et al., 2001), or factors such as sex (Martín and Salvador, 1997; Wymann and Whiting, 2002) and prey availability (Huey and Pianka, 1981; Inoue and Matsura, 1983; Formanowicz and Bradley, 1987). Our observations also show considerable effects of weather on movement activity. The proportion of time spent basking versus foraging typically increases as temperature decreases in heliothermic lizards (e.g., Vitt et al., 1993, 1995b). Foraging success may actually be determined by body temperature (Avery et al., 1982; Díaz, 1994). Therefore, it is important to study foraging under thermally optimal conditions. Some authors report specifically that PTM- and MPM-values are based on observations under sunny conditions (e.g., Cooper and Whiting, 1999; Cooper et al., 2001; Wymann and Whiting, 2002), but others do not or take together data obtained in apparently quite different climatic conditions (e.g., Bergallo and Rocha, 1993; Vitt et al., 1995b; Perry, 1996; Butler, 2005). Admittedly, the impact of availability of solar radiation on foraging behavior of lizards may not always be equal to the one reported here for typically heliothermic lacertids.

Similar thermal effects may account for activity changes over the day, with highest activity during the hottest hours (Van Damme et al., 1990; Avery, 1993). In the early morning, lacertid lizards emerge from their overnight retreats and warm up in early sun while sitting still with only sporadic feeding. In the evening, the reverse pattern of decreasing activity may be seen, with most animals ending their day by devoting most of their time to basking (Braña, 1991). In Mediterranean regions during summer, activity may commonly show a bimodal pattern with a decline during the hottest hours of the day (e.g., Braña, 1991) when animals seek shade to avoid overheating (active foraging possibly again replaced by sit-and-waiting). We did not find such a pattern, probably because most of our observations were performed during the more temperate seasons of the year with typically a unimodal activity pattern (Foà et al., 1992).

Intersexual differences in movement behavior have been reported for some lizard species (e.g., Pietruszka, 1986; Perry, 1996; Wymann and Whiting, 2002), whereas in other species, this was not found (e.g., Pietruszka, 1986; Greeff and Whiting, 2000; Reany and Whiting, 2002; Husak and Ackland, 2003). Mostly, such differences in movement behavior were understood as reflecting differences in behavior between the sexes

during the reproductive season (see Durtsche, 1992; Aragón et al., 2001; Wymann and Whiting, 2002), with males devoting much time to territorial patrolling and mate searching rather than to foraging (e.g., Ruby, 1978; Aragón et al., 2001) and females shifting toward a more cryptic antipredation strategy (e.g., Bauwens and Thoen, 1981; Wymann and Whiting, 2002). For example, although the general PTM reported for *L. monticola* by Martín and Salvador (1997) during the mating season was comparable to ours, they found strikingly large intersexual differences in PTM not present in our data. Our observations generally took place outside the reproductive season.

For comparative use, data obtained under optimal conditions, and at peak-activity hours, after the initial warming up in the morning should be used. It is these values we have presented in Table 5 and to which we refer in the following. These PTM-values are within the range of values reported so far for lacertid species. Mostly, this is also true for MPM-values, but some species (*L. vivipara* and *Ps. hispanicus*) show the highest values reported for lizards up to now.

Foraging in Lacertidae.—Lacertidae has traditionally been typified as a family of actively foraging lizards (Cooper, 1994) but including some less active species in the derived African lineages (Huey and Pianka, 1981; Cooper and Whiting, 1999). Our data show that low activity levels are more widespread in Lacertidae than previously known. Some papers had already hinted at this: *Lacerta agilis* (Nemes, 2002) is far less active than Kalahari-species that were considered sit-and-waiters (Huey and Pianka, 1981), whereas *Ps. algirus* (Belluire et al., 1996) or *L. laevis* (Perry et al., 1990) show at most intermediate foraging activity levels.

A clear-cut classification of many lizard species as sit-and-waiters or active foragers on the basis of movement measures may not be possible, and different authors have suggested different cut-off values (Werner et al., 1997; Cooper and Whiting, 1999; Butler, 2005; Cooper, 2005a). Nevertheless, some species studied here, can be considered real sit-and-waiters (e.g., *L. bilineata*, *A. aureus*), moving considerably less than 10% of the time. More difficult to assign are the species that fall within the range of PTM-values (10–25) where very few lizard species have been positioned so far (Cooper, 2007) and that were suggested to separate more or less both foraging strategies (see Fig. 2). Only one species is substantially more active (*L. vivipara*), although still on a rather moderate level. These results warn against premature generalizations in the discussion about the existence of bimodality in foraging activity

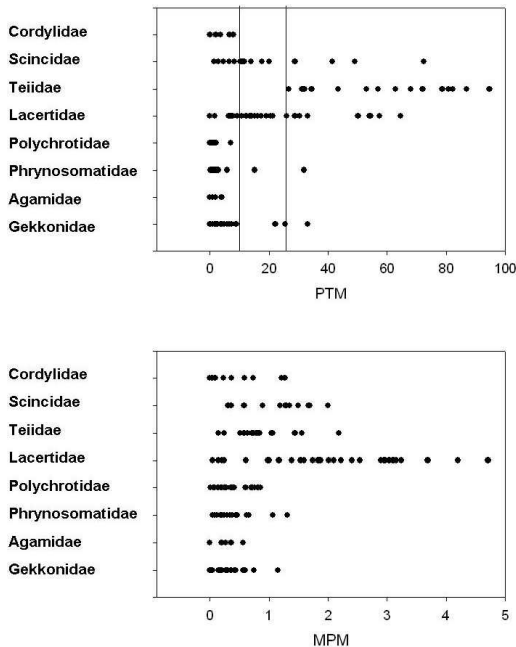


FIG. 2. Reported PTM- and MPM-values of several lizard families. Indicated as well is the zone of PTM (10–25) where the transition of sit-and-waiting to active foraging has been situated. Data are taken from the present study (Table 5); Karasov and Anderson, 1984; Bergallo and Rocha, 1993; Vitt et al., 1995a,b, 2000; Perry, 1999, 2007, and references therein; Nemes, 2002; Reany and Whiting, 2002; Lailvaux et al., 2003; McConnachie and Whiting, 2003; Persaud et al., 2003; Werner et al., 2004; Cooper, 2005b; Cooper et al., 2005.

levels in lizards (Cooper, 2005a). The finding of still more species with such intermediate foraging activity levels might further settle what remains of the controversy about bimodality in PTM and MPM in favor of a continuum (Cooper, 2005a; but see Huey and Pianka, 2007). However, the inclusion of additional foraging characteristics and the combined analysis of these might still enable us to discern distinct foraging strategies (Cooper, 2007).

PAM-values for example might help to interpret mobility measures. Low PAM-values suggest a sit-and-waiting strategy, whereas high (up to 1) values indicate active foraging. Most species reported here have PAM < 0.5. Although PAM tends to correlate positively with PTM (and to a lesser extent MPM; Cooper et al., 1999, 2001, 2005a), this was not found in our data, possibly because feeding attempts are only seldom observed and some of the resulting PAM-values are probably to be considered with some caution. In any case, they show that a considerable percentage of prey attacks are launched from a standstill, indicating sit-and-

wait behavior (Cooper et al., 1999; Cooper and Whiting, 1999).

Many of the lacertids reported here also show quite high MPM-values, suggesting that their foraging behavior may be comparable to the one described as “mixed” for *Meroles ctenodactylus* (Cooper and Whiting, 1999), containing elements of both classical sit-and-waiting and active foraging. Although a substantial portion of their time is devoted to sitting still, their activity levels are too high for sit-and-waiting. During movement bouts, periods of locomotion are alternated with frequent pauses, which contrast with nearly continuous movements of typical active foragers. Still, typical active foraging search for hidden food by digging in the soil was sometimes observed.

In conclusion, most lizard species reported here show an intermediate level of foraging activity, with some species that can be classified as sit-and-waiters. All of them show substantial flexibility in activity levels, with weather and time of the day having a clear impact. However, sexual differences were not observed. We plead for explicitly taking environmental conditions that can influence foraging behavior into account in order to obtain mean species values that can be used in a broader comparative context.

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