

Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards

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Abstract

1. We investigated the association between field body temperatures (T_b), field air temperatures (T_a), and their differences (Δ) with measurements of foraging activity (percentage of time moving (PTM), number of movements per minute (MPM) and proportion of prey attacked while moving (PAM)) for 25 species of lacertid lizards.
2. Lizards active at relatively high field body temperatures tended to have higher PTM and PAM values. We found no association between temperatures and MPM. The difference Δ did not co-vary with PTM and MPM, but showed a positive trend with PAM.
3. Our results seem robust with regard to the assumptions of different models of evolution and to the phylogenetic trees used.

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1. Introduction

In many animals, acquiring food is a risky, time-consuming and energetically demanding activity. At the same time, it is a prerequisite for survival and reproduction. In consequence, foraging efficiency can be expected to be under strong selective pressure. Since food gathering is typically a whole-animal function, it seems likely that this selection pressure will affect the whole of an animal's morphology, physiology, behaviour and life history (McLaughlin, 1989).

Lizards have proved to be excellent model organisms in studies on the correlates of foraging styles (Reilly et al., 2006). Pianka (1966) recognised two modes of foraging in lizards: sit-and-wait foraging (SW) and active foraging (AF). SW foragers remain sedentary for most of their activity period, waiting in ambush for suitable prey. Movements are limited to short, fast launches towards prey and the occasional change of lookout site. In contrast, AF foragers move frequently and explore the environment, actively searching for prey. The apparent dichotomy in

foraging modes seems to be associated with a parallel disparity in various morphological, physiological, ecological and behavioural characteristics (see Huey and Pianka, 1981; Anderson and Karasov, 1981; Magnusson et al., 1985; Perry et al., 1990; Huey et al., 1984; Cooper, 1994a, b).

Although still under debate (e.g. Cooper, 2005; Huey and Pianka, 2007), publication of foraging behavioural data from a wider range of lizard taxa, and the application of phylogenetically informed statistics, has led many students to abandon the dichotomous view of foraging styles for a more continuous picture, with examples of “real” SW and AF foragers at the extremes, but also with intermediate styles (Perry, 1999; Cooper, 2005). This urges a re-evaluation of the associations between foraging style and other aspects of the animals' biology. In this paper, we concentrate on the possible interactions between foraging style and thermal ecology.

Body temperature affects the rate of all biochemical and physiological processes and thus has a profound effect on a lizard's whole-animal performance and, ultimately, its fitness (Huey and Stevenson, 1979; Huey, 1982). In environments with sub-optimal or fluctuating thermal conditions, selection will therefore favour a certain degree

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of thermoregulation. For instance, lizards that maintain body temperatures near the physiological optimum will maximize the efficiency of muscular contraction and neuromuscular coordination (Putnam and Bennett, 1982; Marsh and Bennett, 1985), resulting in higher sprint speeds (e.g. Bennett, 1980) and an improved capacity to capture prey or to escape predation (Christian and Tracy, 1981; Avery et al., 1982; Van Damme et al., 1991; Díaz, 1994). Most often, lizards regulate their body temperatures behaviourally. However, like foraging, behavioural thermoregulation can also be costly in terms of time, energy and increased risk, and the balance between costs and benefits is reflected in thermoregulatory precision (Huey and Slatkin, 1976). The central role of temperature regulation in lizard biology has prompted a large body of research (reviews in Huey, 1982; Angilletta et al., 2002).

Although nobody will doubt that foraging and thermoregulation play central roles in lizard biology, surprisingly few studies have explored possible interactions between both functions quantitatively. There are two ways in which such interactions may arise: (1) body temperature can affect foraging style directly and (2) thermoregulatory behaviour, needed to maintain a certain body temperature, may interfere with foraging activity. However, it is not a priori clear in which direction these interactions will work. In the scant literature on the issue, assertions in both directions can be found.

Some authors claim that AF foragers require high body temperatures to maintain their high level of movement (e.g. Magnusson et al., 1985; Bergallo and Rocha, 1993). This seems plausible, given the thermal dependence of locomotor capacity (e.g. Bennett, 1980; Van Berkum, 1986; Van Damme et al., 1989) and tongue flick rates (e.g. Van Damme et al., 1991). The maximal performance of organisms with high optimal temperatures may be greater than that of organisms with low optimal temperatures (the “hotter is better” hypothesis, see Huey and Kingsolver, 1989). Among lizard species, high endurance capacity, characteristic for AF (Garland, 1999), correlated with high body temperatures (Garland, 1994). SW predators may not need elevated body temperatures for prolonged foraging bouts or chemoreception, but they do require the ability to strike explosively and precisely, often at more agile prey. Acceleration is an understudied function in lizards, but is likely to be highly temperature dependent (see e.g. Greenwald, 1974). In the other direction, maintaining high body temperatures will increase metabolic expenditure and hence food intake requirements. Body temperature therefore plays a role in foraging economics and, depending on other factors (such as food availability), may promote a more active or passive foraging style (Karasov and Anderson, 1984).

Several authors have hinted at possible interactions between thermoregulatory behaviour and foraging behaviour. With a limited time budget, time spent in one type of activity (e.g. thermoregulating) may be at the expense of the other activity (foraging), unless both activities can be

combined. In this respect, one might expect SW predators to be better off, because they can more easily combine thermoregulatory behaviour with prey seeking, e.g. basking at their foraging post. Following similar reasoning, Regal (1983) suggested that because thermoregulation requires complex behaviours (e.g. postural adjustments, selection of thermally favourable sites), precise thermoregulation is incompatible with frequent movements and hence AF. In contrast, Magnusson et al. (1985) argued that an AF style would allow predators to exploit the thermal patchiness of their environment better and hence increase their thermoregulatory precision. Secor and Nagy (1994) noted that the prolonged immobility needed for ambushing prey precludes shuttling thermoregulation, forcing SW predators to accept sub-optimal and variable body temperatures.

In this paper, we explore relationships between foraging style and thermal ecology within lacertid lizards. With a distribution covering large parts of Eurasia and all of Africa, members of the Lacertidae can be found in a wide variety of climates, habitats and microhabitats. Although most species are typical heliothermic diurnal lizards, attained field body temperatures vary considerably among species (Castilla et al., 1999). Most species primarily feed on arthropods, but some also eat substantial amounts of plant material (Van Damme, 1999). Foraging strategies vary from SW to active hunting (Pianka et al., 1979; Huey and Pianka, 1981; Perry et al., 1990; Cooper and Whiting, 1999; Verwajen and Van Damme, submitted for publication).

2. Material and methods

2.1. Data sources

Foraging data on the following species were taken from the literature (see Table 1 for sources): *Acanthodactylus boskianus*, *A. schreiberi*, *A. scutellatus*, *Heliobolus lugubris*, *Ichnotropis squamulosa*, *Lacerta agilis*, *Meroles suborbitalis*, *Nucras intertexta*, *N. tessellata*, *Ophisops elegans*, *Pedioplanis lineocellata*, and *P. namaquensis*. For an additional set of species (*Acanthodactylus erythrurus*, *Lacerta monticola*, *L. oxycephala*, *L. schreiberi*, *L. vivipara*, *Podarcis hispanica*, *P. melisellensis*, *P. muralis*, *P. peloponnesiaca*, *P. tiliguerta*, *Psammodromus algirus*, and *Psammodromus hispanicus*), foraging indices were calculated from behavioural observations performed on adult, non-reproductive animals, during peak activity hours and under optimal weather conditions (see Table 1, pers. obs.). Details on the methodology and the location of the populations are described elsewhere (Verwajen and Van Damme, submitted for publication), but, in short, lizards were observed from a safe distance, using binoculars, and the beginning and end of their movement bouts were recorded using a PSION Workabout MX minicomputer. We also noted the occurrence of attacks towards prey. Only observations on individuals not disturbed by the observer, a predator or a conspecific were retained for further analysis. Changes in body orientation or postural

Table 1

Measures of foraging strategies (PTM: percentage of time spent moving, MPM: number of movements per minute, PAM: proportion of prey caught while moving) and thermal characteristics (T_b : field body temperatures; T_a : field air temperatures; Δ : $T_b - T_a$) for the lacertid lizard species used in this study

Species	PTM		MPM		PAM	Reference	T_b		T_a		Reference
	x	SE	x	SE			x	SE	x	SE	
<i>Acanthodactylus boskianus</i>	28.80	9.71	2.01	0.55		Perry et al. (1990)	34.3	1.0	31.5	1.3	Pérez-Mellado (1992)
<i>Acanthodactylus erythrurus</i>	16.26	2.16	3.16	0.34	0.45	Pers. obs.	33.1	0.4	24.1	0.4	Carretero and Llorente (1995)
<i>Acanthodactylus schreiberi</i>	30.50	5.95	1.54	0.25		Perry et al. (1990)	40.6	0.2			Duvdevani and Borut (1974)
<i>Acanthodactylus scutellatus</i>	7.70	1.40	1.01	0.15		Perry et al. (1990)	39.3	0.2	33.9		Duvdevani and Borut (1974)
<i>Heliobolus lugubris</i>	57.40	3.80	2.97	0.28	1.00	Huey and Pianka (1981)	37.7	0.2	29.1	0.2	Huey and Pianka (1977)
<i>Ichnotropis squamulosa</i>	54.60	7.90	3.10	0.14		Huey and Pianka (1981)	36.3	0.2	31.3	0.2	Huey and Pianka (1977)
<i>Lacerta agilis</i>	1.59	0.48	0.21	0.05	0.00	Nemes (2002)	29.8		27.4		Tertyshnikov (1976)
<i>Lacerta monticola</i>	19.10	1.83	3.04	0.21	0.40	Pers. obs.	29.4	0.2	18.3	0.3	Martín and Salvador (1993)
<i>Lacerta oxycephala</i>	15.11	1.66	2.22	0.18	0.32	Pers. obs.	31.6	0.2	25.2	0.3	Scheers and Van Damme (2002)
<i>Lacerta schreiberi</i>	10.75	3.42	1.86	0.60		Pers. obs.	31.1	0.2	26.0		Salvador and Argüello (1987)
<i>Lacerta vivipara</i>	33.20	3.46	4.20	0.40	0.50	Pers. obs.	29.9	0.1	20.3	0.2	Van Damme et al. (1986, 1987)
<i>Meroles suborbitalis</i>	13.50	1.60	1.83	0.19		Huey and Pianka (1981)	35.5	0.1	26.5	0.2	Huey and Pianka (1977)
<i>Nucras intertexta</i>	64.50	3.90	3.69	0.27		Pianka et al. (1979)	38.9	0.9	34.0	0.3	Huey and Pianka (1977)
<i>Nucras tessellata</i>	50.20	5.20	2.90	0.37	1.00	Huey and Pianka (1981)	39.3	0.4	31.6	0.4	Huey and Pianka (1977)
<i>Ophisops elegans</i>	54.60		1.88			Barnea, unpubl. in Perry (1999)	33.1	0.1			Pérez-Mellado et al. (1993)
<i>Pedioplanis lineoocellata</i>	14.30	3.00	1.54	0.42	0.00	Huey and Pianka (1981)	36.9	0.1	28.9	0.2	Huey and Pianka (1977)
<i>Pedioplanis namaquensis</i>	54.00	4.00	1.87	0.15	0.95	Cooper and Whiting (1999)	37.8	0.2	30.1		Huey and Pianka (1977)
<i>Podarcis hispanica</i>	21.39	2.32	3.12	0.30		Pers. obs.	35.1	0.5	19.9		Pérez-Mellado (1983)
<i>Podarcis melisellensis</i>	17.35	1.68	2.54	0.20	0.49	Pers. obs.	34.1	0.2	23.9	0.3	Scheers and Van Damme (2002)
<i>Podarcis muralis</i>	20.54	1.68	3.05	0.25	0.50	Pers. obs.	33.8	0.2	23.0	0.2	Braña (1991)
<i>Podarcis peloponnesiaca</i>	12.35	1.20	2.10	0.17	0.25	Pers. obs.	30.7	0.4	25.5	0.5	Maragou et al. (1997)
<i>Podarcis tiliguerta</i>	9.26	2.35	1.74		0.77	Pers. obs.	30.8	0.3	15.0	0.2	Van Damme et al. (1989)
<i>Psammotromus algirus</i>	20.68	2.54	2.95	0.33	0.69	Pers. obs.	32.6	0.5	26.1	0.6	Carrascal and Díaz (1989)
<i>Psammotromus hispanicus</i>	25.99	7.34	4.71	1.34		Pers. obs.	32.6	0.3	22.4		Pérez-Quintero (2001)
<i>Takydromus sexlineatus</i>	13.80	1.95	1.60	0.21	0.38	Pers. obs.	31.5				Zhang and Ji (2004)

Pers. obs.: personal observations.

changes, and movements of body parts not involving translational movement were not counted. Pauses of one or more seconds were recorded as bouts of “immobility”. Each individual was observed for at least 10 min where possible. Occasionally, sessions had to be stopped because the lizard disappeared from sight; only observations that lasted at least 3 min were retained. From these observations, we later

calculated the number of movements per minute (MPM), the percentage of time spent moving (PTM) and the proportion of attacks while moving (PAM, i.e. the number of attacks while moving divided by the total number of attacks). To this dataset, we added observations on *Takydromus sexlineatus* performed in semi-natural conditions (a 5 × 5 m terrarium with vegetation mimicking the species’ natural habitat and

with optimal thermal conditions ensured by six 150 W spots). Field and laboratory measures of foraging behaviour are highly comparable in lacertids (Verwajen and Van Damme, submitted for publication).

Data on field body temperatures (T_b) and air temperatures (T_a) were taken from the literature (Table 1). We are aware that T_a is a poor descriptor of the thermal environment of an ectotherm (e.g. Hertz et al., 1993), but operative temperatures are seldom available. We calculated Δ , the difference between T_b and T_a , as a crude measure of thermoregulatory effort, assuming that lizards that have high body temperatures compared to the prevailing air temperatures are more active thermoregulators. Again, we are aware of the pitfalls of this measure and the existence of much more elegant ways of measuring thermoregulatory precision and accuracy (Hertz et al., 1993). However, with data on optimal, selected and operative temperatures missing for most of the species in the dataset, Δ is the only estimate of thermoregulatory effort that is available. For some species, several sources of thermal characteristics were available. In these cases, we gave priority (1) to the source reporting both T_b and T_a and (2) to the source with the larger sample size.

2.2. Statistical analyses

Examining relationships between characteristics of (closely) related species is best performed in an explicitly phylogenetic context (e.g. Felsenstein, 1985; Garland et al., 1992). We here report correlations between thermal and foraging variables obtained with the program COMPARE v4.6 (Martins, 2004), contrasting three approaches: (1) correlation of the raw tip data (TIP), (2) correlation (through the origin) of Felsenstein's independent contrasts (FIC) and (3) the phylogenetic generalized least-squares approach (PGLS). The latter approach has the major advantage in that it can account for the intraspecific variation in the variables under consideration. It is also flexible in the assumptions of the evolutionary model applied, generating parameter estimates at a range of different values of a parameter α , which can be interpreted as the magnitude of the restraining force or pull towards a central state. When α is small, the method yields results similar to that obtained through FIC analyses; when α is large (~ 15), results resemble those of TIP analyses. We here present parameters at the maximum likelihood estimate of α . The PGLS and FIC methods require information on the phylogenetic relationships among the species studied. For the topology, we used the two final hypotheses presented by Fu (2000), based on DNA sequences of six mitochondrial genes. The study is inconclusive on the exact position of *Takydromus*, so we performed all analyses (1) with *Takydromus* basal to lacertids of the African and Eurasian clades (Fu's Fig. 2A) and (2) with *Takydromus* well nested within the Eurasian clade (Fu's Fig. 2B). Alas, information on divergence times is almost completely lacking for Lacertidae. We therefore ran all

analyses twice: once on trees with all branch lengths set to unity (CONSTANT, i.e. assuming a punctual evolution model) and once on 100 trees with branch lengths randomised (RANDOM, using the "generate trees" module in COMPARE).

3. Results

The outcome of our analyses of the relationships among foraging indices and between foraging indices and thermal characteristics was largely independent of the method used. The correlation coefficients and regression parameters obtained were consistent in size and direction, although different methods yielded slightly disparate significance levels (Tables 2 and 3).

Although all three indices of foraging behaviour (PTM, MPM and PAM) correlated positively, the association between PTM and PAM was clearly stronger than that between MPM and PAM or PTM and MPM (Table 2). Variation in (the contrasts of) PTM accounted for less than half of the variation in (the contrasts of) MPM, suggesting that these two variables index different aspects of the foraging strategy.

Lacertid lizards that are active at high body temperatures (T_b) tend to spend larger proportions of their time moving (PTM, Fig. 1) and catch a larger percentage of their prey while moving (PAM, Fig. 3). However, we found no evidence for a relationship between body temperature and the number of MPM (Fig. 2). Environmental temperatures (T_a) correlated positively with PTM, but not with the two other foraging indices. Finally, the difference between body and air temperatures (Δ) did not correlate with PTM and MPM, but did show a positive trend with PAM (Table 3; Fig. 3).

4. Discussion

Our results strongly indicate that lacertid lizards that maintain high body temperatures in the field tend to have a more AF style than lizards active at lower body temperatures, which seems to contest Regal's (1983) idea of a conflict between thermoregulatory and feeding behaviours. Bauwens et al. (1995) demonstrated that the morphology (body size, relative hind limb length), thermal physiology (optimal body temperatures, thermal performance breadth) and thermoregulatory behaviour (preferred body temperature) of lacertid lizards have evolved in concert, presumably in response to co-adaptational selection pressures. Our data suggest that this pattern extends to variables associated with foraging behaviour.

What causes the relationship between high activity temperatures and AF (PTM) in lacertids? These lizards tend to live in habitats that are relatively open and in which direct solar radiation is readily available. On the other hand, most lacertids seem seldom at risk of overheating, because they typically tend to stay near structural features of the habitat (plants, rocks) that provide opportunities to

Table 2
Relationships among the foraging indices of lacertid lizards

	Branch			PGLS				FIC			TIPS		
	Tree	Lengths	α	r	Slope	SE	95% CI	r	Slope	SE	r	Slope	SE
PTM–MPM	A	Constant	5.25	0.44	0.03	0.01	0.00–0.05	0.48	0.03	0.01	0.42	0.02	0.01
	A	Random	3.16	0.51	0.03	0.01	0.01–0.06	0.61	0.04	0.01			
	B	Constant	4.99	0.43	0.03	0.01	0.00–0.05	0.47	0.03	0.01			
	B	Random	6.39	0.48	0.03	0.01	0.01–0.06	0.66	0.05	0.01			
PTM–PAM	A'	Constant	15.5	0.81	0.02	0.003	0.01–0.02	0.81	0.02	0	0.81	0.02	0
	A'	Random	13.4	0.8	0.02	0	0.00–0.03	0.73	0.02	0			
	B'	Constant	15.5	0.81	0.02	0	0.01–0.02	0.81	0.02	0			
	B'	Random	12.96	0.8	0.02	0	0.00–0.03	0.72	0.02	0			
MPM–PAM	A'	Constant	15.5	0.43	1.29	0.74	–0.16–2.74	0.4	1.3	0.82	0.44	1.29	0.74
	A'	Random	9.34	0.49	1.44	0.71	0.02–2.85	0.54	1.71	0.75			
	B'	Constant	15.5	0.43	1.29	0.74	–0.16–2.74	0.39	1.26	0.82			
	B'	Random	14	0.48	1.41	0.73	–0.03–2.86	0.52	2.04	0.94			

Shown are the parameter estimates obtained through Pearson's correlation of the raw data (TIPS), through phylogenetic generalized least-squares estimation (at α_{\max}) and using Felsenstein's independent contrasts method (FIC). Calculations were repeated using different phylogenetic hypotheses: trees A and B follow the topologies proposed by Fu (2000, his Figs. 2A and B respectively). Trees A' and B' have the same topology as trees A and B, but contain only those species for which PAM data were available. Results shown are for alternative topologies, with all branch lengths held constant ("constant"; punctuated model) and with branch lengths randomised ("random"; average estimates for 100 runs). COMPARE reports regression slopes and their standard errors. The 95% confidence interval of the PGLS slope includes sampling variance (if available) and variance due to unknown phylogeny (branch lengths).

cool down. Therefore, interference of foraging bouts and thermoregulatory shuttling is likely to be low in most lacertids. So it seems unlikely that the relationship would result from the fact that a sedentary foraging strategy handicaps thermoregulatory faculty (Magnusson et al., 1985; Secor and Nagy, 1994). A more attractive idea is that AF actually requires high body temperatures, because these allow greater locomotory performance (e.g. Bennett, 1980; Van Berkum, 1986; Garland, 1994). Perhaps the high body temperatures are necessitated for other bodily functions associated with AF, for example, chemoreception (e.g. Cooper and van Wyk, 1994; Cooper, 1994a, b). Tongue flick rates tend to vary with body temperature (Van Damme et al., 1991). If chemoreceptive prey location or recognition is more thermally dependent than eyesight, this might explain why lizards with low activity temperatures adopt an SW strategy. The causality may also be reversed: maintaining higher body temperatures will increase metabolic expenditure (Cragg, 1978) and this may call for a more AF style (in circumstances where such a strategy produces a higher net energy income; Karasov and Anderson, 1984). Finally, it is also possible that higher body temperatures and a more AF style are consequences of a third, un-quantified factor and have no direct causal relationship. For instance, they might reflect differences in habitat structure or social system (Avery, 1976). Presently, we have no reliable data on these factors; hence we cannot explore this possibility yet.

Field activity temperatures tended to correlate with PTM and PAM, but not with the number of MPM. This suggests that PTM/PAM on the one hand and MPM on the other represent different aspects of foraging strategy, an idea that is corroborated by the high correlation of PTM with PAM, and the lower associations between PTM and MPM, and MPM and PAM. This would imply considerable interspecific variation in the duration of foraging bouts, with "hotter" lizards performing longer bouts. Longer foraging bouts could be connected to improved aerobic capacity (Magnusson et al., 1985; Bergallo and Rocha, 1993).

Ectothermic animals can maintain high body temperatures by being active at high environmental temperatures, and/or by keeping their body temperatures above environmental temperatures through behavioural thermoregulation. Lacertid lizards are active baskers and often have body temperatures well above air temperature (review in Castilla et al., 1999). We found little evidence that differences in foraging strategy relate to differences in thermoregulatory effort (as estimated by Δ , but see Section 2 for a cautionary note). Of the three foraging indices, only PAM showed a positive trend with Δ . This suggests that the differences in foraging style are related to differences in body temperature as such, and are not a consequence of differential thermoregulatory behaviour.

In conclusion, we found a relationship between foraging style and thermal characteristics in lacertid lizards, but

Table 3
Relationships between field thermal characteristics and foraging indices in lacertid lizards

	Branch			PGLS				FIC			TIPS		
	Tree	Lengths	α	r	Slope	SE	95% CI	r	Slope	SE	r	Slope	SE
T_b -PTM	A	Constant	4.71	0.38	2.14	1.1	0.00–4.29	0.11	0.66	1.27	0.52	2.85	0.97
		Random	4.38	0.35	1.66	1	–0.39–3.71	0.22	0.91	1.05			
	B	Constant	3.81	0.35	1.98	1.11	–0.19–4.16	0.09	0.55	1.27			
		Random	4.14	0.33	1.56	1.02	–0.54–3.66	0.16	0.63	1.08			
T_b -MPM	A	Constant	6.43	–0.06	–0.02	0.07	–0.15–0.11	–0.1	–0.04	0.08	–0.04	–0.01	0.06
		Random	5.26	–0.03	–0.02	0.06	–0.16–0.11	0.08	0.01	0.07			
	B	Constant	5.44	–0.07	–0.02	0.07	–0.16–0.11	–0.15	–0.06	0.09			
		Random											
T_b -PAM	A'	Constant	15.5	0.54	0.05	0.02	0.01–0.10	0.36	0.06	0.04	0.55	0.05	0.02
		Random	5.67	0.59	0.05	0.02	0.01–0.10	0.61	0.06	0.02			
	B'	Constant	15.5	0.54	0.05	0.02	0.01–0.10	0.36	0.06	0.04	0.55	0.05	0.02
		Random	3.99	0.59	0.06	0.02	0.01–0.10	0.62	0.06	0.02			
T_a -PTM	C	Constant	6.88	0.53	3.07	1.09	0.93–5.21	0.13	0.89	1.51	0.59	3.36	1.02
		Random	4.42	0.39	1.98	1.09	–0.29–4.25	0.2	0.9	1.21			
T_a -MPM	C	Constant	4.91	–0.28	–0.06	0.05	–0.16–0.03	–0.36	–0.1	0.06	–0.25	–0.05	0.04
		Random	4.66	–0.34	–0.07	0.04	–0.16–0.02	–0.33	–0.06	0.04			
T_a -PAM	C'	Constant	15.5	0.12	0.01	0.02	–0.03–0.05	–0.2	–0.02	0.03	0.13	0.01	0.02
		Random	4.51	–0.23	–0.02	0.02	–0.07–0.03	–0.51	–0.04	0.02			
Δ -PTM	C	Constant	2.13	–0.06	–0.28	1.04	–2.31–1.76	–0.06	–0.25	0.98	–0.12	–0.62	1.18
		Random	2.91	0.03	–0.02	0.7	–1.43–1.38	0.06	0.05	0.58			
Δ -MPM	C	Constant	4.77	0.33	0.1	0.06	–0.01–0.22	0.3	0.09	0.06	0.35	0.11	0.06
		Random	4.86	0.32	0.07	0.05	–0.03–0.17	0.31	0.05	0.04			
Δ -PAM	C'	Constant	9.18	0.39	0.04	0.03	–0.01–0.09	0.45	0.05	0.03	0.38	0.04	0.03
		Random	1.21	0.71	0.05	0.01	0.02–0.07	0.77	0.05	0.01			

Tree C contains the subset of species in trees A and B for which T_a data were available. Tree C' has the same topology as tree C, but contains only the species for which PAM data were available. We refer to Table 2 and the text for details on the procedure and for the meaning of the abbreviations.

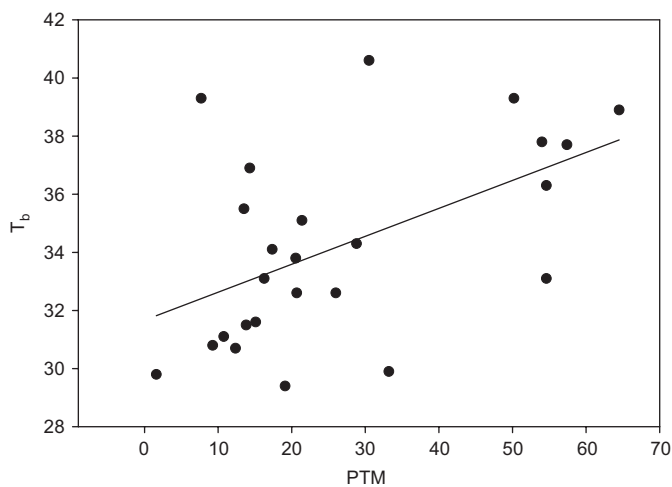


Fig. 1. Field body temperature (T_b , °C) versus percentage of time moving (PTM) of 25 species of lacertid lizards.

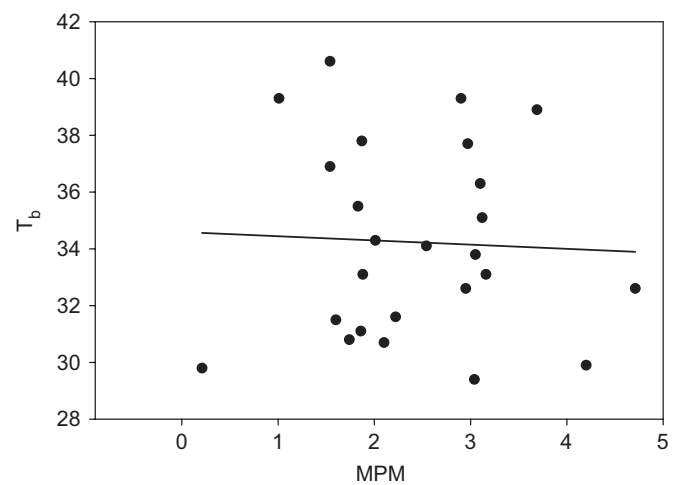


Fig. 2. Field body temperature (T_b , °C) versus number of movements per minute (MPM) of 25 species of lacertid lizards.

understanding the causality of this relationship will require further investigation. Also, because the species in this study stem mostly from open habitats, our results may not apply

to many species of other lizard families, who live in “expensive” habitats, such as forests with closed canopies, or desert habitats with little shelter (Huey and Slatkin,

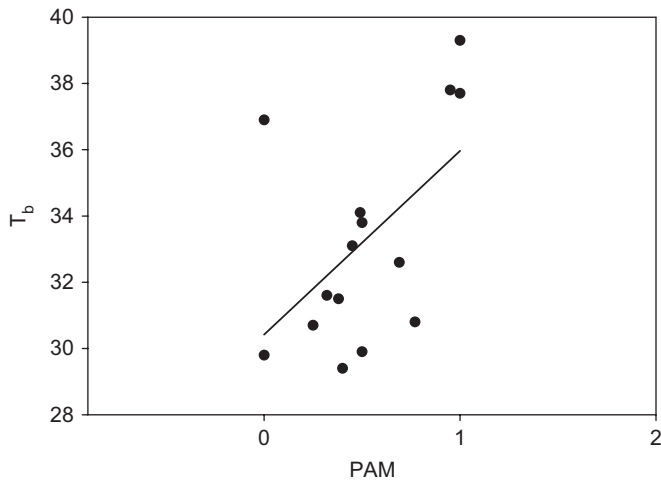


Fig. 3. Field body temperature (T_b , °C) versus proportion of attacks while moving (PAM) of 15 species of lacertid lizards.

1976). In such families, there may be a different relationship between foraging strategy and activity temperatures. A deeper and broader examination of the relationship between foraging and thermoregulatory strategies seems worthwhile.

References

- Anderson, R.A., Karasov, W.H., 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* 49, 67–72.
- Angiletta Jr., M.J., Niewiarowski, P.H., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* 27, 249–268.
- Avery, R.A., 1976. Thermoregulation, metabolism and social behaviour in Lacertidae. In: Bellairs, A.d'A., Cox, C.B. (Eds.), *Morphology and Biology of Reptiles*. Linnean Society Symposium Series, no. 3, pp. 245–257.
- Avery, R.A., Bedford, J.D., Newcombe, C.P., 1982. The role of thermoregulation in lizard biology: predatory efficiency in a temperate diurnal basker. *Behav. Ecol. Sociobiol.* 11, 261–267.
- Bauwens, D., Garland Jr., T., Castilla, A.M., Van Damme, R., 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49, 848–863.
- Bennett, A.F., 1980. The thermal dependence of lizard behaviour. *Anim. Behav.* 28, 752–762.
- Bergallo, H.G., Rocha, C.F.D., 1993. Activity patterns and body temperatures of two sympatric lizards (*Tropidurus torquatus* and *Cnemidophorus ocellifer*) with different foraging tactics in southeastern Brazil. *Amphibia–Reptilia* 14, 312–315.
- Braña, F., 1991. Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. *Herpetol. J.* 1, 544–549.
- Carrascal, L.M., Díaz, J.A., 1989. Thermal ecology and spatio-temporal distribution of the Mediterranean lizard *Psammotromus algirus*. *Holarctic Ecol.* 12, 137–143.
- Carretero, M.A., Llorente, G.A., 1995. Thermal and temporal patterns of two Mediterranean Lacertidae. *Sci. Herpetol.*, 213–223.
- Castilla, A.M., Van Damme, R., Bauwens, D., 1999. Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. *Nat. Croat.* 8, 253–274.
- Christian, K.A., Tracy, C.R., 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* 49, 218–223.
- Cooper Jr., W.E., 1994a. Prey chemical discrimination, foraging mode, and phylogeny. In: Vitt, L.J., Pianka, E.R. (Eds.), *Lizard Ecology: Historical and Experimental Perspectives*. Princeton University Press, Princeton, NJ, pp. 95–116.
- Cooper Jr., W.E., 1994b. Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. *J. Chem. Ecol.* 20, 439–487.
- Cooper Jr., W.E., 2005. The foraging mode controversy: both continuous variation and clustering of foraging movements occur. *J. Zool. (Lond.)* 267, 179–190.
- Cooper Jr., W.E., van Wyk, J.H., 1994. Absence of prey chemical discrimination by tongue-flicking in an ambush-foraging lizard having actively foraging ancestors. *Ethology* 97, 317–328.
- Cooper Jr., W.E., Whiting, M.J., 1999. Foraging modes in lacertid lizards from southern Africa. *Amphibia–Reptilia* 20, 299–311.
- Cragg, P.A., 1978. Oxygen consumption in the lizard genus *Lacerta* in relation to diurnal variation, maximum activity and body weight. *J. Exp. Biol.* 77, 33–56.
- Díaz, J.A., 1994. Effects of body temperature on the predatory behaviour of the lizard *Psammotromus algirus* hunting winged and wingless prey. *Herpetol. J.* 4, 145–150.
- Duvdevani, I., Borut, A., 1974. Mean body temperature and heat absorption in four species of *Acanthodactylus* lizards (Lacertidae). *Herpetologica* 30, 176–181.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125, 1–15.
- Fu, J., 2000. Toward the phylogeny of the family Lacertidae—why 4708 base pairs of mtDNA sequences cannot draw the picture. *Biol. J. Linn. Soc.* 71, 203–217.
- Garland Jr., T., 1994. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: Vitt, L.J., Pianka, E.R. (Eds.), *Lizard Ecology: Historical and Experimental Perspectives*. Princeton University Press, Princeton, NJ, pp. 237–259.
- Garland Jr., T., 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Anim. Behav.* 58, 77–83.
- Garland Jr., T., Harvey, P.H., Ives, A.R., 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41, 18–32.
- Greenwald, O.E., 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974, 141–148.
- Hertz, P.E., Huey, R.B., Stevenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142, 796–818.
- Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia*, vol. 12. London, Academic Press, pp. 25–91.
- Huey, R.B., Kingsolver, J.G., 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* 4, 131–135.
- Huey, R.B., Pianka, E.R., 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology* 58, 1066–1075.
- Huey, R.B., Pianka, E.R., 1981. Ecological consequences of foraging mode. *Ecology* 62, 991–999.
- Huey, R.B., Pianka, E.R., 2007. Preface: on widely foraging for Kalahari lizards. Feeding ecology in the natural world. In: Reilly, S.M., McBrayer, L.D., Miles, D.B. (Eds.), *Foraging Behavior in Lizards*. Cambridge University Press, Cambridge, UK.
- Huey, R.B., Slatkin, M., 1976. Cost and benefits of lizard thermoregulation. *Quart. Rev. Biol.* 51, 363–384.
- Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19, 357–366.
- Huey, R.B., Bennett, A.F., John-Alder, H., Nagy, K.A., 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Anim. Behav.* 32, 41–50.
- Karasov, W.H., Anderson, R.A., 1984. Interhabitat differences in energy acquisition and expenditure in a lizard. *Ecology* 65, 235–247.

- Magnusson, W.E., Junqueira de Paiva, L., Moreira da 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.
- Maragou, P., Valakos, E.D., Chondropoulos, B.P., 1997. Comparative ecology of two sympatric lizard species, *Lacerta graeca* and *Podarcis peloponnesiaca* endemic to Peloponnisos (Greece). *Herpetol. Bonn.* 1997, 265–271.
- Marsh, R.L., Bennett, A.F., 1985. Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the lizard *Dipsosaurus dorsalis*. *J. Comp. Physiol. B* 155, 541–551.
- Martín, J., Salvador, A., 1993. Thermoregulatory behaviour of rock lizards in response to tail loss. *Behaviour* 124, 123–136.
- Martins, E.P., 2004. COMPARE, version 4.6b. Computer programs for the statistical analysis of comparative data. Distributed by the author at <http://compare.bio.indiana.edu/>. Department of Biology, Indiana University, Bloomington, IN.
- McLaughlin, R.L., 1989. Search modes of birds and lizards: evidence for alternative movement patterns. *Am. Nat.* 133, 654–670.
- Nemes, S., 2002. Foraging mode of the sand lizard, *Lacerta agilis*, at the beginning of its yearly activity period. *Russ. J. Herpetol.* 9, 57–62.
- Pérez-Mellado, V., 1983. Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884). *Cienc. Biol. Ecol. Syst. (Portugal)* 5, 5–12.
- Pérez-Mellado, V., 1992. Ecology of lacertid lizards in a desert area of eastern Morocco. *J. Zool. (Lond.)* 226, 369–386.
- Pérez-Mellado, V., Valakos, E.D., Guerrero, F., Gil-Costa, M.J., 1993. Ecological similarity of lacertid lizards in the Mediterranean region—the case of *Ophisops elegans* and *Psammadromus hispanicus*. In: Valakos, E.D., Böhme, W., Pérez-Mellado, V., Maragou, P. (Eds.), *Lacertids of the Mediterranean Region—A Biological Approach*. Hellenic Zoological Society, Athens, Greece, pp. 231–242.
- Pérez-Quintero, J.C., 2001. Thermal biology and activity cycles of two sympatric *Psammadromus* species in a sandy coastal area. In: Vicente, L., Crespo, E.G. (Eds.), *Mediterranean Basin Lacertid lizards: A Biological Approach*. Instituto da Conservação da Natureza, Lisboa, Portugal.
- Perry, G., 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *Am. Nat.* 153, 98–109.
- Perry, G., Lampl, I., Lerner, A., Rothenstein, D., Shani, E., Sivan, N., Werner, Y.L., 1990. Foraging mode in lacertid lizards: variations and correlates. *Amphibia-Reptilia* 11, 373–384.
- Pianka, E.R., 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47, 1055–1059.
- Pianka, E.R., Huey, R.B., Lawler, L.R., 1979. Niche segregation in desert lizards. In: Horn, J.D., Mitchell, R.D., Stains, G.R. (Eds.), *Analysis of Ecological Systems*. Ohio State University Press, Columbus, pp. 67–115.
- Putnam, R.W., Bennett, A.F., 1982. Thermal dependence of isometric contractile properties of lizard muscle. *J. Comp. Physiol. B* 147, 11–20.
- Regal, P.J., 1983. The adaptive zone and behavior of lizards. In: Huey, R.B., Pianka, E.R., Schoener, T.W. (Eds.), *Lizard Ecology: Studies of a Model Organism*. Harvard University Press, Cambridge, MA, USA, pp. 105–118.
- Reilly, S.M., McBrayer, L.D., Miles, D.B., 2006. *The Evolutionary Consequences of Foraging Mode in Lizards*. Cambridge University Press, Cambridge.
- Salvador, A., Argüello, J.A., 1987. Temperaturas corporales del lagarto verdinegro (*Lacerta schreiberi*) (Sauria: Lacertidae). *Rev. Española Herpetol.* 2, 71–82.
- Scheers, H., Van Damme, R., 2002. Micro-scale differences in thermal habitat quality and a possible case of evolutionary flexibility in the thermal physiology of lacertid lizards. *Oecologia* 132, 323–331.
- Secor, S.M., Nagy, K.A., 1994. Bioenergetic correlates of foraging mode of the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* 75, 1600–1614.
- Tertyshnikov, M.F., 1976. Influence of weather and climate on activity of sand and varicoloured lizards. *Ekologiya* 3, 57–61.
- Van Berkum, F.H., 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* 40, 594–604.
- Van Damme, R., 1999. Evolution of herbivory in lacertid lizards: effects of insularity and body size. *J. Herpetol.* 33, 663–674.
- Van Damme, R., Bauwens, D., Verheyen, R.F., 1986. Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations. *J. Therm. Biol.* 11, 219–222.
- Van Damme, R., Bauwens, D., Verheyen, R.F., 1987. Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. *Herpetologica* 43, 405–415.
- Van Damme, R., Bauwens, D., Castilla, A.M., Verheyen, R.F., 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. *Oecologia* 80, 516–524.
- Van Damme, R., Bauwens, D., Verheyen, R.F., 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. *Funct. Ecol.* 5, 507–517.
- Verwajen, D., Van Damme, R., submitted for publication. Foraging mode and its flexibility in lacertid lizards from Europe.
- Zhang, Y.-P., Ji, X., 2004. The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae). *J. Therm. Biol.* 29, 45–53.