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Foraging mode and locomotor capacities in Lacertidae

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Abstract. Foraging strategy is often considered to play a central role in moulding diverse aspects of an animal's general biology. Active foragers should have greater locomotor endurance, allowing high movement activity rates, while sit-and-waiting foragers may be better adapted to sprinting, allowing catching prey by a quick attack from an ambush site, and going with specific predator escape tactics. In this study we investigate these predicted patterns in a set of lacertid lizard species. There is considerable variation in foraging activity within Lacertidae, which allows the close investigation of the co-evolution of the traits considered. We found a tendency of positive correlation of foraging measures (PTM, percentage of time moving; MPM, number of movements per minute) with laboratory measured endurance capacity. However, the relationship of foraging measures with maximal sprint speed remains less clear. MPM correlates negatively with maximal sprint speed, but PTM does not. When sprint speed was corrected for body size, no correlations were found at all.

Keywords: endurance, foraging, Lacertidae, lizards, locomotion, sprint speed.

Introduction

Foraging mode describes movement patterns during the acquisition of food (Pianka, 1966). Carnivores (and insectivores) generally can be assigned to one of two possible foraging methods (Pianka, 1966). Sit-and-wait predators are sedentary, search passively, wait in ambush for their prey and attack it when it comes within range; active or wide foragers move frequently through the habitat and actively search for prey. Lizards have become common study models of this apparent dichotomy (Huey and Pianka, 1981; McLaughlin, 1989) and many correlates of foraging mode have been postulated and found in this group (e.g. Regal, 1978; Vitt and Congdon, 1978; Anderson and Karasov, 1981; Huey and Pianka, 1981; Vitt and Price, 1982; Vitt, 1990; Cooper, 1994).

However, not all lizard species can be readily categorised as active or sit-and-waiting foragers, and other categories have been suggested (Regal, 1983; Butler, 2005). Perry (1999) argued that the dichotomy may be an artefact resulting from disparate sampling and comparing species without appropriate phylogenetic analyses. In reality, a continuum of foraging styles may exist, with species showing movement activity from very little, over intermediate to almost continuous movement (Perry, 1999; Cooper, 2005). Whether the many correlates of foraging style show parallel variation remains largely unexplored.

While foraging mode seems to be a conservative trait within most lizard families (Cooper, 1994), there appears to be more variation in moving rates and foraging behaviour in some families. This is the case for the Lacertidae. Despite substantial ecological radiation, primarily regarding microhabitat use, lacertids have remained similar in general body plan and biology (Arnold, 1987). Most species are diurnal heliotherms that primarily feed on arthropods, although some also eat substantial amounts of plant material (Van Damme, 1999). Active foraging is believed to be the ancestral condition in this family (Cooper, 1994). However, while some species move up to 70% of the time they are active, others are relatively sedentary and only move 10-15% (Huey and Pianka, 1981; Cooper and Whiting, 1999) or even less than 5% of their activity time (Nemes, 2002). Such a taxon is suitable to test the above-mentioned question in a close phylogenetic context, where

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drastic differences in general biology, as do exist among lizard species from different families, do not disturb comparative analyses.

Huey et al. (1984) studied endurance capacity and sprint performance of four closely related lacertid lizard species from the Kalahari desert, and found that locomotory abilities correlated with foraging behaviour in a predictable way: active foragers tended to have greater locomotor endurance while sit-and-waiting species were better adapted to sprinting. The general rationale behind the idea of correlated evolution of locomotor abilities and foraging style is that active foragers that are in motion for long periods should benefit from having high endurance (Garland, 1999), while sit-and-waiters may do without stamina, but must be able to move quickly to capture prey or escape predators. Predator escape tactic appears to be associated with foraging mode (Vitt and Congdon, 1978): sit-and-waiters tend to be cryptic in coloration, morphology, and behaviour and stay put until the predator is at close range. If at that moment crypsis fails, they rely on fast bursts for escape. Associated with considerable movement during foraging in actively foraging species is the ability to detect potential predators (wariness) and move rapidly over considerable distances to escape attacks. This presumably counterbalances the higher risk of mortality associated with the more conspicuous active foraging mode. The difference in locomotor performance between sit-and-waiters and active foragers may in turn be reflected in the types of prey they can catch: active foragers include relatively sluggish and inactive prey in their diet, while sit-and-waiters mainly may eat more mobile prey (Gerritsen and Strickler, 1977; Huey and Pianka, 1981).

In this study, we examine whether foraging behaviour of a larger set of lacertid species is correlated with endurance capacity and sprint speed.

Materials and methods

Most performance and behavioural data used in this study were obtained by one of us (DV). To this data set, we added data obtained from the literature (see table 1). Although there may be subtle differences in measuring locomotor performances between different observers, for example in the handling of the animals, previous studies have been able to find significant associations between traits using data obtained by different investigators (e.g. Garland, 1999).

Foraging behaviour

Foraging behaviour was observed by following active animals in the field during peak activity hours (*Acanthodactylus aureus*, *A. erythrurus*, *Lacerta bilineata*, *L. monticola*, *L. oxycephala*, *L. schreiberi*, *L. vivipara*, *Podarcis hispanica*, *P. melisellensis*, *P. muralis*, *P. peloponnesiaca*, *P. tiliguerta*, *Psammodromus algirus*, *Psammodromus hispanicus*) or in a 5 × 5 m semi-natural terrarium (*Takydromus sexlineatus*). In the terrarium, animals had the opportunity to bask under lamps for at least an hour prior to observation. Previous observations have shown that movement behaviours in the field and the terrarium are highly comparable (Verwaijen, personal observations). Location (coordinates) of the populations studied is as follows: *A. aureus*: 29°48′N, 9°50′W; *A. erythrurus*: 40°45′N, 0°50′E; *L. bilineata*: 41°55′N, 2°24′E; *L. monticola*: 40°20′N, 5°15′W; *L. oxycephala*: 43°05′N, 16°10′E; *L. schreiberi*: 40°20′N, 5°15′W; *L. vivipara*: 51°25′N, 4°25′E; *P. hispanica*: 41°15′N, 1°58′E; *P. melisellensis*: 43°05′N, 16°10′E; *P. muralis*: 42°30′N, 1°35′E; *P. peloponnesiaca*: 37°50′N, 22°30′E; *P. tiliguerta*: 42°24′N, 8°57′E; *P. algirus*: 41°08′N, 0°47′E; *P. hispanicus*: 42°15′N, 3°10′E. *Takydromus sexlineatus* was obtained from the pet trade.

A PSION Workabout MX handheld minicomputer (Psion Teklogix Inc.) was used for recording the beginnings and ends of movements. Changes in orientations or postural changes and movements of specific body parts not involving translational movement were not considered as movements. Pauses for one or more seconds were interpreted as immobility. Each individual was observed for at least 10 minutes if possible. Then the number of movements per minute (MPM) and the percentage of the time moving (PTM) were calculated. These two measures, proposed by Pianka et al. (1979) are most commonly used for the characterisation of foraging mode. Movements that were clearly the result of intraspecific interactions (animals chasing each other) or escape behaviour were removed from the total number of movements and time moved. Only the observations that were clearly not disturbed by the observer were included. In order not to record the same lizard twice, a different location for the next observation was chosen once the observation of an individual was finished. Only adults were observed. Only observations made on sunny days in peak-activity hours were used in the further calculations of PTM and MPM.

Locomotor performance tests

Outside experimentation, lizards were housed in glass terrariums (1.0 × 0.3 m, length × width) with a sandy substrate, different types of hiding places (flat rocks, branches,

Table 1. Foraging and locomotion data (<x>: mean and SD: standard deviation) and SVL of the species under study. MPM = number of movements per minute; PTM = percentage of the time moving; SVL = snout-vent length (in mm); rel. sprint = sprint speed/SVL; n gives the number of animals of which foraging behaviour was observed, and used in the sprint and endurance measurements respectively. Sources: *: own measurements; °: Vanhooydonck et al., 2001; +: Bauwens et al., 1995; ″: Huey and Pianka, 1981; ^: Huey et al., 1984; [2]: Perry et al., 1990; [3]: Nemes, 2002.

Species	MPM		PTM		n	Sprint (m/s)		n	Endurance (s)		n	SVL (mm)
	<x>	SD	<x>	SD		<x>	SD		<x>	SD		<x>
Acanthodactylus aureus	2.41*	1.85	6.68*	6.00	30	2.81*	0.44	13	276.38*	82.41	13	62.20*
Acanthodactylus boskianus	2.01[2]	1.46	28.80[2]	25.70	7	2.98*	0.55	9	261.78*	79.01	9	60.46*
Acanthodactylus erythrurus	3.16*	1.75	16.26*	11.21	27	2.47*	0.41	14	406.93*	169.68	14	65.78*
Acanthodactylus scutellatus	1.01[2]	0.75	7.70[2]	7.12	26	2.80°	0.26	4	74.22°	27.79	4	67.70°
Heliobolus lugubris	2.97″	1.08	57.4″	14.70	15	1.58	0.49	23				
Lacerta agilis	0.21[3]	0.25	1.59[3]	2.41	25	1.68+	0.49	9				
Lacerta bilineata	0.98*	0.91	6.27*	6.82	11	2.68°	0.56	6	276.60°	144.22	6	92.69°
Lacerta monticola	3.04*	1.33	19.10*	11.41	39	2.76*	0.86	15	363.17*	169.38	15	72.46*
Lacerta oxycephala	2.22*	1.37	15.11*	12.40	56	2.02°	0.34	16	109.60°	39.34	16	56.77°
Lacerta schreiberi	1.86*	1.35	10.75*	7.65	5	1.79+	0.36	6	263.00*	74.95	2	92.60+
Lacerta vivipara	4.20*	1.84	33.20*	15.85	21	0.87°	0.15	20	370.33°	241.27	20	50.99*
Nucras tesselata	2.90″	1.23	50.2″	17.3	11	2.05	0.19	4				
Pedioplanis lineoocellata	1.54″	1.63	14.3″	11.6	15	2.63	0.33	13				
Pedioplanis namaquensis	1.87″	1.55	54.0″	26.0	26	2.68	0.23	9				
Podarcis hispanica	3.12*	1.40	21.39*	10.87	22	1.85+	0.48	9				54.84+
Podarcis melisellensis	2.54*	1.51	17.35*	12.82	58	1.91*	0.34	14				
Podarcis muralis	3.05*	1.71	20.54*	11.52	47	2.14°	0.47	21	184.90°	57.04	21	57.38*
Podarcis peloponnesiaca	2.10*	1.46	12.35*	10.27	73	2.67*	0.41	12	299.64*	77.59	12	74.10*
Podarcis tiliguerta	1.74*	1.40	9.26*	10.79	21	1.55°	0.47	14	194.79°	67.03	14	56.87°
Psammodromus algirus	2.95*	2.18	20.68*	16.67	43	2.33*	0.65	18	307.44*	135.92	18	66.51*
Psammodromus hispanicus	4.71*	3.29	25.99*	17.99	6	1.40*	0.40	10	139.80*	52.59	10	41.21*
Takydromus sexlineatus	1.60*	1.27	13.80*	11.88	37	1.42*	0.26	10	85.70*	24.13	10	54.97*

dry leaves) and a drinking bowl. Species were kept separate, with no more than 4 animals per terrarium. Light bulbs (100 W) were suspended 25 cm above the sandy surface and provided light and heat for 10 h per day, thus allowing lizards to obtain their preferred body temperatures. Food (live crickets, *Acheta domesticus* and invertebrate prey obtained by sweeping a nearby field with a net) was provided twice a week. All experiments took place within a month after housing the lizards in the laboratory.

Prior to experimentation and between trials, animals were placed for at least 1 hour in an incubator set at a temperature near the species selected body temperature (32°C for *L. vivipara*; 35°C for *A. aureus*, *A. erythrurus*, *L. monticola*, *L. oxycephala*, *L. schreiberi*, *P. melisellensis*, *P. muralis*, *P. peloponnesiaca*, *P. algirus*, *P. hispanicus*, and *T. sexlineatus*). These temperatures are within the range of field active temperatures (Castilla et al., 1999; Vanhooydonck et al., 2001). We had no constant-temperature room at our disposal, but the racetrack and treadmill used to measure locomotor performance were positioned near a heat source so that the animals could perform at a temperature near their selected body temperature. Sprint speed and endurance were measured on different days. An assumption of performance measurements is that it is *maximal* performance that is actually measured. Taking this into account, measurements of individuals that clearly performed submaximally or that not cooperated were excluded (see Losos et al., 2002). Only adult animals (both males and non-gravid females) were used in this study.

Sprint speed was measured using eight pairs of photocells, placed at 0.25 m intervals along a 2.5 m long racetrack with a cork substrate, providing sufficient traction. Maximal sprint speed was elicited by chasing lizards along the track. The elapsed time between passing two subsequent cells was stored in a computer and sprint speed over each interval was calculated. Maximal sprint performance was estimated as the highest speed over any 0.25 m interval. Every animal was tested five times. Between each trial, lizards were allowed to recover for at least 1 hour.

Endurance was estimated as the running time until exhaustion on a treadmill moving at constant speed (0.22 m/s; a speed typically displayed by undisturbed lacertid lizards, see Vanhooydonck et al., 2001). After a short burst at the beginning of the experiment, the animals calmed down and moved at speeds near the speed of the treadmill. When necessary, the animal was encouraged to move by touching the tail or hind legs. Animals were considered exhausted when they did not show a righting response after being placed on their backs (see Huey et al., 1990). Each animal was tested three times, with each trial being held on a different day. As an estimate of maximal endurance, the longest running time over the three trials was used.

Statistical analyses

Means per species (with data of both sexes pooled) of PTM, MPM, sprint speed and endurance were calculated. In the further statistical analyses these means were used. Numerous empirical studies suggest that in the majority of animals, locomotor speed is positively correlated to body size (Heglund et al., 1974; Garland and Losos, 1994; Van Damme and Vanhooydonck, 2001). Although locomotor capacities are generally measured as absolute, instead of size-relative measures because interactions among organisms in natural conditions are considered to depend on absolute and not relative performance (Garland, 1994), the dependence of locomotor speed on size poses a problem when animals of different size are compared (Van Damme and Van Dooren, 1999). Therefore, size-corrected "relative" sprint speed was calculated by dividing mean sprint speed by mean SVL.

Unless the characteristics considered are evolutionary labile, the study of coevolution of traits among related species requires a phylogenetically informed statistical analysis (e.g. Harvey and Pagel, 1991; Garland et al., 1993). We here report correlations between locomotion and foraging variables obtained with the program COMPARE v4.6 (Martins, 2004), following three approaches: (1) correlation of the raw tip data (TIP), which corresponds to conventional, non-phylogenetic analyses; (2) correlation (through the origin) of Felsenstein's (1985) independent contrasts (FIC); (3) the phylogenetic generalized least squares approach (PGLS). The latter approach is 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 toward a central state. When α is small, the method yields results similar to that obtained through FIC analyses; when α is large (~ 15), results are similar to 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. The relationships between the Afrotropical, advanced Saharan and Eurasian clades follow Harris et al. (1998) (morphological and mtDNA sequence characters). Relationships within the Eurasian clade follow Arnold et al. (2007) (mtDNA tree). The *Acanthodactylus* species were arranged as proposed in Harris and Arnold (2000) (mtDNA tree). Information (where available) on branch lengths was taken from Arnold et al. (2007). Because divergence estimates are incomplete and still debated in Lacertidae, we also ran analyses with all branch lengths set to unity (CONSTANT, i.e. assuming a punctual evolution model) and on 200 trees with branch lengths randomised (RANDOM, using the "generate trees" module in COMPARE).

Results

Foraging, endurance and sprint speed data are presented in table 1. The outcome of our analyses of the relationships between foraging indices and locomotion characteristics was mostly independent of the method used. The correlation coefficients and regression parameters obtained were generally consistent in size and direction, although different methods yielded slightly different significance levels (table 2).

The more active lacertid lizard species show the highest endurance capacity in the laboratory (table 2; fig. 1), although this relationship was only in one case significant for PTM. For MPM, a negative correlation was found with sprint speed, but we found no evidence for such relationship between PTM and sprint speed (table 2; fig. 2). SVL correlates negatively with both PTM (Pearson correlation: $r = -0.60$; $N = 16$; $P < 0.05$) and MPM ($r = -0.57$; $N = 16$; $P < 0.05$), indicating that larger species tend to move less frequently. No significant relationship was found between foraging variables and size-corrected relative sprint speed.

Discussion

As pointed out in the introduction, active foragers are predicted to have high endurance capacity, allowing high movement rates (Huey and Pianka, 1981; Huey et al., 1984; Garland, 1994, 1999), while sit-and-waiters may attain higher maximal sprint speeds, allowing catching prey by a quick attack from a standstill (Huey et al., 1984). We found support for the expected relationship between foraging activity measures and endurance capacity, but less clearly so for the relationship between foraging and sprint speed capacity.

Comparing a set of 15 lizard species belonging to 9 different families, Garland (1999) indeed found that the more active species in the field (at least as far as PTM is concerned) show highest endurance capacities in laboratory trials. Miles et al. (2007) found similar results. This is to some extent confirmed by our analyses in the family Lacertidae. Garland (1999) also hypothesized, but did not find a significant relationship of MPM with endurance. To our surprise, in our set of species, it was MPM rather than PTM that showed the expected relationship with en-

Table 2. Relationships among the foraging and locomotion indices of lacertid lizards. Shown are the parameter estimates obtained through Pearson correlation of the raw data (TIPS), through phylogenetic generalized least squares estimation (at $\alpha_{\max}$) and using Felsenstein's independent contrasts method (FIC). "Alfa" are the restraining force of the best PGLS model based on maximum likelihood, "r" are the (phylogenetic) correlation coefficients, "b" are the estimated slopes and "se" the standard errors on the slopes. Slopes for which the 95% confidence interval does not include zero, are in bold. Results shown are for alternative topologies with branch lengths based on estimated divergence times ("real"), all branch lengths set equal to one ("constant"; punctuated model) and with branch lengths randomised ("random"; average estimates for 100 runs). The 95% confidence interval of the PGLS slope reflects variance due to unknown phylogeny (branch lengths).

	branch lengths	PGLS					FIC			TIPS		
		alfa	r	b	se	95% CI	r	b	se	r	b	se
sprint speed − MPM	real	2.5	−0.34	−0.63	0.4	−1.41-0.15	−0.3	−0.6	0.41	−0.36	**−0.64**	0.37
	constant	5.99	−0.34	−0.6	0.38	−1.34-0.14	−0.3	−0.5	0.38			
	random	9.02	−0.42	**−0.6**	0.31	−1.20-0.00	−0.4	**−0.4**	0.27			
sprint speed − PTM	real	2.17	−0.18	−4.86	5.82	−16.25-6.54	−0.2	−6.2	6.35	−0.15	−4.07	5.86
	constant	2.38	−0.2	−4.64	5.2	−14.84-5.56	−0.2	−4.3	4.85			
	random	2.75	−0.28	−4.39	3.91	−12.24-3.46	−0.3	−3.9	3.28			
rel. sprint speed − MPM	real	4.25	−0.15	−0.02	0.03	−0.08-0.04	−0.2	−0	0.03	−0.07	−0.01	0.03
	constant	5.1	−0.08	−0.01	0.03	−0.06-0.04	−0.1	−0	0.03			
	random	7.42	−0.27	−0.03	0.03	−0.09-0.02	−0.3	−0	0.03			
rel. sprint speed − PTM	real	2.51	0.13	0.24	0.4	−0.54-1.02	0.1	0.2	0.46	0.15	0.25	0.38
	constant	2.61	0.07	0.13	0.4	−0.65-0.91	0.05	0.08	0.41			
	random	2.83	−0.09	−0.11	0.37	−0.96-0.74	−0.1	−0.1	0.34			
endurance − MPM	real	1.41	0.43	**0**	0	0.00-0.01	0.55	**0**	0	0.34	**0**	0
	constant	7.32	0.34	0	0	0.00-0.01	0.38	**0**	0			
	random	14.8	0.29	0	0	−0.01-0.02	0.25	0	0			
endurance − PTM	real	10.9	0.32	0.02	0.02	−0.01-0.05	0.51	**0.02**	0.01	0.26	0.02	0.02
	constant	15.5	0.25	0.02	0.02	−0.02-0.06	0.2	0.01	0.02			
	random	14.7	0.22	0.01	0.02	−0.07-0.10	0.23	0.01	0.02			

durance decisively. Possibly, the qualitative differences in movement characteristics among our species do not differ to the extent as in Garland's (1999) study, which may impede the expected straightforward relationship between PTM and endurance to show up. And as for quantitative differences, the range of PTM of the species for which also endurance data were available in our study is relatively limited (6.27 for *Lacerta bilineata* to 33.20 for *L. vivipara*), and there was only a 5-fold difference in endurance capacity for these species. Inclusion of more species, and especially more extreme species (e.g. *Nucras intertexta*, see Pianka et al., 1979) might thus show the same significant relationship of PTM with endurance (compare with the differences in PTM ranging from 1.5 to 81.3, and endurance differences as big as 60-fold in Garland's (1999) study). On the other hand, our data may suggest that the current paradigm on the links between foraging modes and endurance performance needs to be refined. Whether laboratory measures of endurance are good measures of endurance over an ecologically relevant time scale remains to be tested (analogously for sprint speed, see Irschick and Losos, 1998).

At the same time, the relevance of sprint speed capacities to the foraging process remains unclear. In their study, Huey et al. (1984) compared four lacertid species from the Kalahari Desert, and three of them did, but one of them did not fit the scheme that SW should have higher burst sprint capacity. However, their analyses were based on an outdated phylogenetic hypothesis and may be inconclusive (Perry and Pianka, 1997). We know of only two other studies that explicitly compared sprint speeds of sit-and-waiting and actively foraging lizards

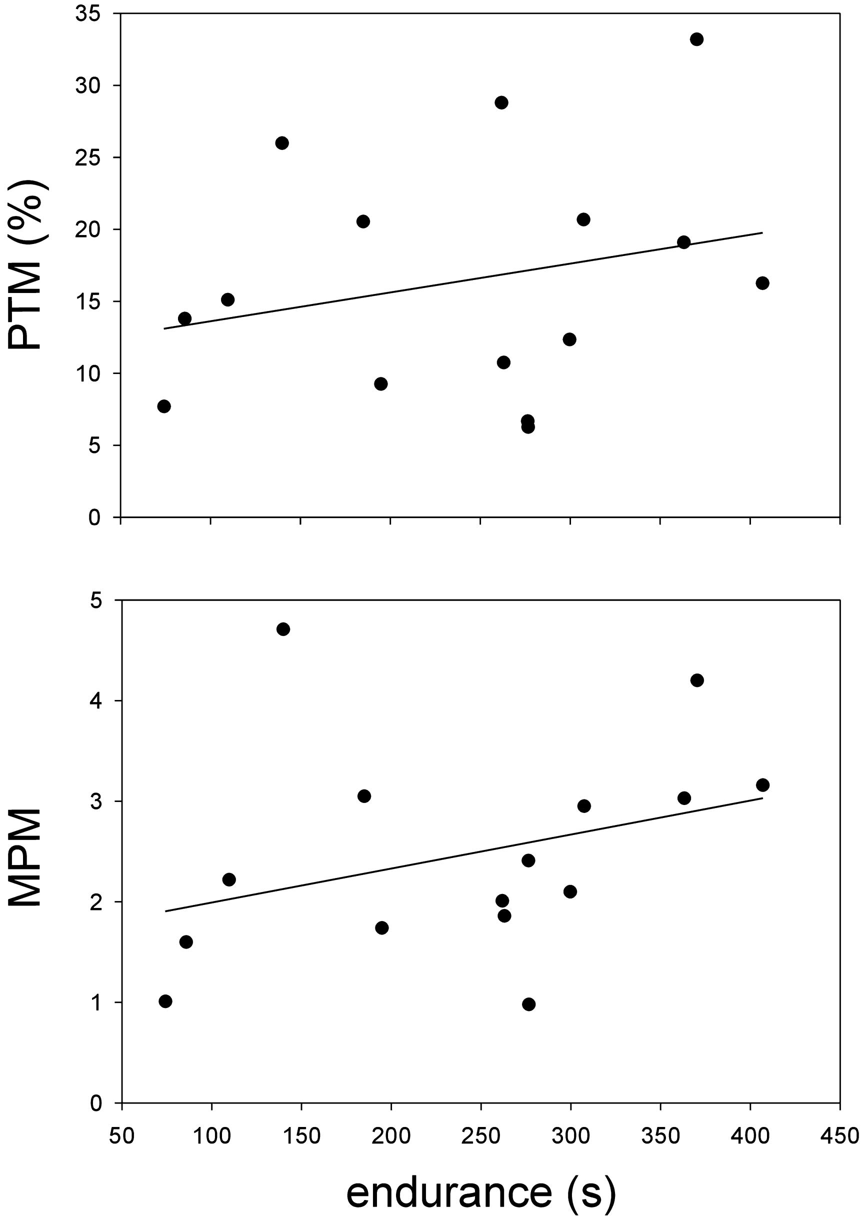

Figure 1. Endurance versus foraging measures in 15 species of lacertid lizards.

(Van Damme and Vanhooydonck, 2001; Miles et al., 2007). The first authors did not find an association between foraging mode and sprint speed, comparing 94 lizard species of diverse families. However, lizards were only roughly classified as sit-and-waiters or active foragers. For example, these authors classified all lacertid species in their analysis as active foragers, and on the base of PTM-values some of them should be rather categorised as sit-and-waiters. Using quantified field activity levels should offer a more nuanced approach. With a dataset that was highly overlapping with the one of Van Damme and Vanhooydonck (2001), but after including some additional taxa and after correcting some classifications of species as sit-and-waiters or

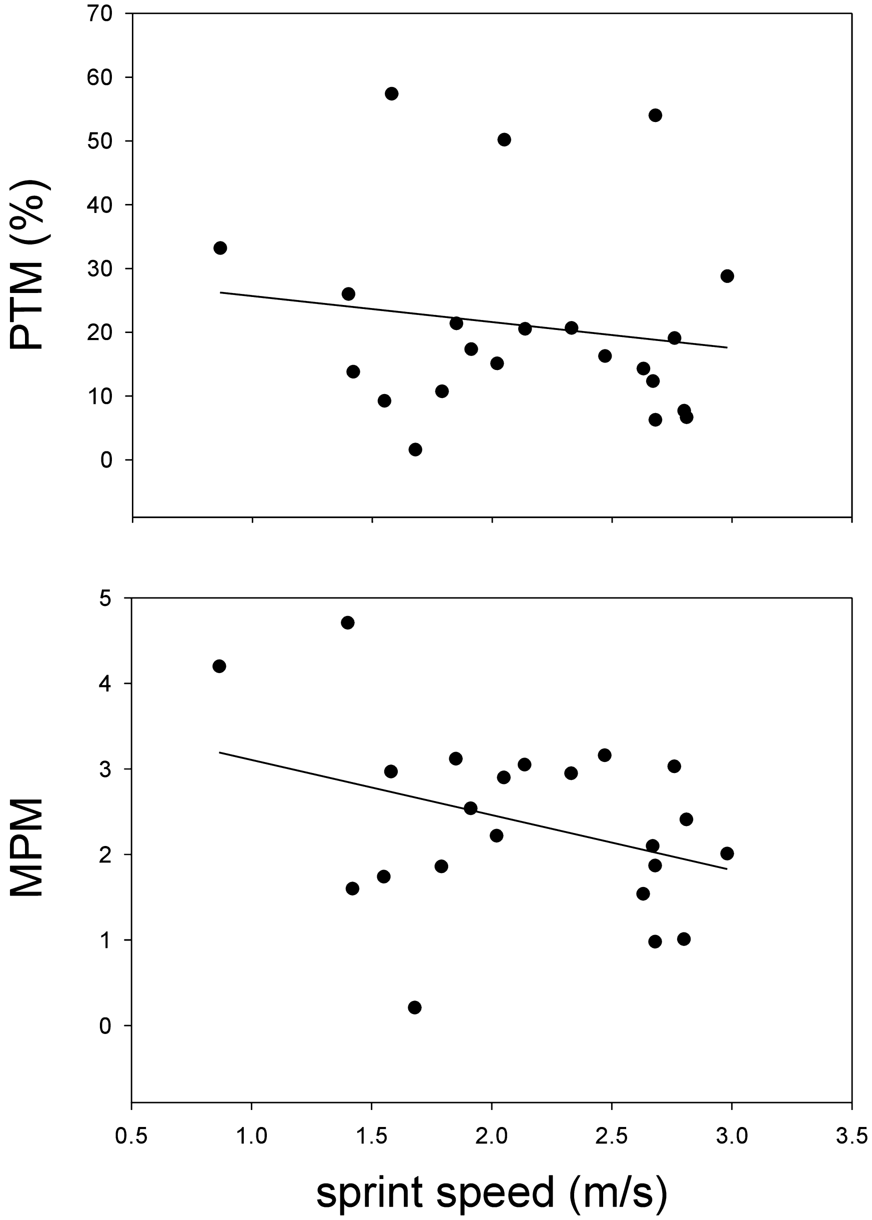

Figure 2. Maximal sprint speed versus foraging measures in 22 species of lacertid lizards.

active foragers, Miles et al. (2007) found that sit-and-waiters have higher sprint speeds than active foragers. However, when comparing locomotor performance with continuous foraging measures, they did not find an association of sprint speed with MPM or PTM.

In our present study, the expected negative relationship of PTM and sprint speed was not found, which again invalidates the view that sit-and-waiters should have the higher sprint capacities. At the same time, MPM appears to correlate negatively with sprint speed. Species with high MPM-values must accelerate and decelerate frequently. Because of, at least theoretically, conflicting requirements for high maximal sprint speeds and high acceleration capacity with regard to the locomotor muscle mass and the force versus velocity characteristics of these muscles, it has been suggested that a trade-off between sprint speed and acceleration capacity may exist on the whole-animal level (Vanhooydonck et al., 2006; Vanhooydonck et al., 2007). If acceleration capacity that demand considerable power output is negatively correlated to maximal sprint speed capacity, this might explain the negative relation with MPM, with species that frequently pause thus having good acceleration but low maximal sprint capacities. However, two previous studies on sprint speed and acceleration capacity in iguanian lizards (Huey and Hertz, 1984; Vanhooydonck et al., 2006) showed a positive relationship between both locomotor performance aspects. How they relate in lacertids remains to be tested.

The view that sit-and-waiting predators should have higher sprint speeds, compared to active foragers arose from considering their putative prey preferences and anti-predatory strategies (see introduction). However, it is not clear whether in the present set of species, differences in preferred prey types are as pronounced as previously reported for other sit-and-waiting and actively foraging lizards (Huey and Pianka, 1981). Most lacertids are considered food generalists (Díaz, 1995), whose diets closely match the relative abundance of prey in the environment (e.g. Pollo and Pérez-Mellado, 1988, 1991). Vanhooydonck et al. (2007) reports that in a set of 14 lacertid species, the expected relationship between sprint speed and estimated prey evasiveness, faster lizards capturing more evasive prey, was not found. Possibly, predator acceleration capacity may be more determining for success in catching evasive prey, than the final sprint speed (Huey and Hertz, 1984). At the same time, it remains untested whether the anti-predator behaviour of lacertids is distinct in the way and to the extent as observed when comparing diverse lizard families (Vitt and Congdon, 1978). The general defensive strategies may well differ between active foragers and sit-and-waiters, but an active forager surprised by a predator (possibly in ambush, see Huey and Pianka, 1981), will also benefit from a high sprint capacity. Clearly, as long as quantification of functionally relevant prey and predator characteristics for both sit-and-waiting and actively foraging lizards are missing, these considerations will remain speculative. Apart from prey capture and predator escape techniques, high sprint speed capacity may also enhance the ability to dominate social interactions (Garland et al., 1990; Husak et al., 2006). Sit-and-waiters and active foragers may differ in social system and reproductive strategies (Stamps, 1977). Whether or to what extent this is true for sit-and-waiting or actively foraging lacertids and how the social system of these species relates to locomotor capacity remains to be tested.

Similarly, high endurance capacities may play a role in diverse ecological and behavioural contexts (patrolling of a home range, territorial defence, searching and acquiring mates).

Many important physiological features of animals seem to have evolved excessive capacities with respect to their routine functional demands (Gans, 1979). It is hypothesised that the upper limit of performance should be fixed according to the level of maximum requirements for some critical activities with important fitness consequences, even if they are infrequent (Hertz et al., 1988). Which of the above, or other, functions cause these high sprint and endurance capacities to have evolved and the exact role of the foraging strategy therein remains unclear.

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