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Does foraging mode mould morphology in lacertid lizards?

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Abstract

Evolutionary changes in foraging style are often believed to require concurrent changes in a complex suite of morphological, physiological, behavioural and life-history traits. In lizards, species from families with a predominantly sit-and-wait foraging style tend to be more stocky and robust, with larger heads and mouths than species belonging to actively foraging families. Here, we test whether morphology and foraging behaviour show similar patterns of association within the family Lacertidae. We also examine the association of bite force abilities with morphology and foraging behaviour. Lacertid lizards exhibit considerable interspecific variation in foraging indices, and we found some evidence for a covariation between foraging style and body shape. However, the observed relationships are not always in line with the predictions. Also, the significance of the relationships varies with the evolutionary model used. Our results challenge the idea that foraging style is evolutionarily conservative and invariably associated with particular morphologies. It appears that the flexibility of foraging mode and its morphological correlates varies among lizard taxa.

Introduction

Because of its alleged associations with many other functional traits, foraging strategy is often considered a key to an animal's general ecology (Eckhardt, 1979; Huey & Pianka, 1981; McLaughlin, 1989). According to the popular 'syndrome hypothesis' (McLaughlin, 1989), the behaviours that allow animals to find and capture food must be compatible with their morphology and physiology, and with other important ecological and behavioural functions. Pianka (1966) recognized two extreme types of foraging behaviour in predators: sit-and-wait foraging and active foraging. Sit-and-wait foragers watch out for prey from a fixed post and will launch quick attacks toward prey that venture too close. Active foragers move more frequently, search large areas, and may dig or probe actively for concealed prey.

Foraging modes of lizards have been studied relatively extensively and this group of animals was, until recently, considered representative of the bipolar view in foraging behaviour (Huey & Pianka, 1981; McLaughlin, 1989). Many aspects of lizard biology seem to be influenced by foraging mode, with corollaries found in vomeronasal morphology and chemosensory abilities (Cooper, 1994a, b), diet (Huey & Pianka, 1981; Gasnier *et al.*, 1994), food handling (McBrayer & Reilly, 2002), body form (Vitt & Congdon, 1978; Huey & Pianka, 1981), sprint speed and endurance (Regal, 1978; Huey *et al.*, 1984), thermoregulatory behaviour (Bowker, 1984; Belliure *et al.*, 1996), metabolism and water physiology (Anderson & Karasov, 1981; Nagy *et al.*, 1984), life history (Vitt & Congdon, 1978; Ballinger, 1982; Dunham *et al.*, 1988), relative clutch mass (Vitt & Congdon, 1978; Perry *et al.*, 1990), habitat choice (Vitt, 1990), learning abilities (Regal, 1978; Day *et al.*, 1999), reproductive mode (Vitt & Price, 1982; Vitt, 1990), predator avoidance (Vitt & Congdon, 1978; Vitt & Price, 1982) and even parasitic infection (Ribas *et al.*, 1998).

However, much evidence for the 'syndrome hypothesis' stems from studies correlating foraging mode and diverse aspects of lizard biology among members of a few ecologically and taxonomically distant taxa (e.g. highly active Teiidae vs. generally sit-and-waiting

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Phrynosomatidae). Such wide and disparate taxonomical sampling is dangerous, because it opens the door to unwarranted generalizations and the confounding of phylogenetic history and adaptation to local environmental conditions. Recent observations on lizard species belonging to the Lacertidae (Huey & Pianka, 1981; Perry *et al.*, 1990; Cooper & Whiting, 1999), Gekkonidae (Werner *et al.*, 1997; Cooper *et al.*, 1999) and Scincidae (Cooper & Whiting, 2000) reveal substantially more interspecific variation in foraging style than that reported from traditionally studied taxa (e.g. Teiidae, iguanids). The variation in foraging style also seems more gradual in these families, leading Perry (1999) to conclude that foraging modes in lizards are probably not as clearly dichotomous as has long been thought (see also Butler, 2005; Cooper, 2005). These findings offer the opportunity to test the prediction of an association between foraging behaviour and morphology within a relatively narrow phylogenetic context.

Foraging style is often predicted to affect morphological features relevant to locomotor capability, especially energetic efficiency and speed (Vitt & Congdon, 1978; White & Anderson, 1994). Locomotor costs constitute a significant part of the daily energy expenditure of lizards (White & Anderson, 1994), hence actively foraging lizards in particular should benefit from adaptations that reduce these costs. As gaits that combine low stride frequencies with large stride lengths are energetically more favourable (White & Anderson, 1994), and stride length in lizards is primarily determined by limb length and the flexibility of the trunk (e.g. Daan & Belterman, 1968; Sukhanov, 1968; Vanhooydonck *et al.*, 2002), one can expect actively foraging lizards to have relatively flexible bodies with long hind limbs. These features should also help lizards in attaining relatively high maximal sprinting speeds (e.g. Snell *et al.*, 1988; Sinervo & Losos, 1991; Vanhooydonck *et al.*, 2002), which would be an additional asset in active foragers, whose frequent movements may attract predators (Vitt, 1983; Arnold, 1988; Perry *et al.*, 1990). As the tail functions as a predator-deterrent device in many lizards, having a long tail should also benefit active foragers in particular.

Foraging style is also thought to affect the morphology of the feeding apparatus (Vitt & Congdon, 1978; Huey & Pianka, 1981; Pough *et al.*, 2001). Actively foraging lizards are more likely to find softer prey items because these tend to be more sedentary or cryptic (e.g. insect larvae). Given that sit-and-waiting predators follow a movement minimization strategy (Díaz & Carrascal, 1990) to avoid predation, they should concentrate on larger, more profitable prey items (Schoener, 1971; Andrews, 1979; Pough *et al.*, 2001; but see Magnusson *et al.*, 1985; Gasnier *et al.*, 1994). Such prey items tend to be relatively hard and tough (Herrel *et al.*, 1996) and can only be consumed by animals that can generate sufficient bite forces (Herrel *et al.*, 1999). Head size and shape, size and orientation of the jaw-closer muscles, differences in lever arms, and the physiological properties of the jaw muscles can all have an important effect on bite force in lizards (Herrel *et al.*, 1998a, b). Consequently, sit-and-waiting species are predicted to have higher and/or wider heads than actively foraging species. Having a wider head will increase both absolute and relative prey sizes that may be eaten (Emerson, 1985). If the other skeletal elements are equal in size and proportion, having a higher and/or wider head also allows for an increased mass of jaw adductor musculature and thereby increases the force production required to process large, hard and tough prey items. A higher head may also take advantage of complexly pennate jaw muscles, resulting in an increase in the physiological cross-section and thus bite force. On the other hand, active foragers should minimize gape cycle times during prey handling, given that their prey is patchily distributed (Emerson, 1985; McBrayer, 2004). Increased snout length is expected to correlate with an increased jaw closing out-lever, and should have a positive effect on jaw closing velocity at the tips of the jaws, thereby serving to minimize gape cycle times (Emerson, 1985); so, active foragers are predicted to have longer, narrower heads and smaller relative gapes than sit-and-waiting species (McBrayer, 2004). Optimization of speed in the jaw system goes with a diminishing of the force production (see Russell & Thomason, 1993; Weishampel, 1993).

In this paper, we test the predictions that more actively foraging species of lacertids will have: (1) more slender, elongated (flexible) bodies; (2) longer limbs; (3) longer tails; (4) narrower heads; and (5) smaller bite forces than species that take on a sit-and-wait strategy.

Material and methods

Study animals

The family Lacertidae is distributed throughout most of Eurasia and all of Africa. It comprises over 230 extant species of mostly small- to medium-sized lizards (adult snout–vent length between 33 and 210 mm, see Arnold, 1989). Throughout this range, species occupy a variety of habitats and microhabitats (Arnold, 1989). Most species primarily feed on arthropods, but the foraging style varies considerably, with some species adopting a sit-and-wait strategy, and others hunting actively for prey (Pianka *et al.*, 1979; Huey & Pianka, 1981; Perry *et al.*, 1990; Cooper & Whiting, 1999). Although lacertids have not evolved distinctive morphological adaptations such as adhesive pads, ballistic tongues or extreme armature (Arnold, 1989), there is substantial among-species variation in size and shape (Vanhooydonck & Van Damme, 1999; Verwaijen *et al.*, 2002; McBrayer, 2004). The choice of the study species was primarily based on practical considerations (accessibility of the populations). In total, 29 species were used in the analyses.

Morphometrics

Morphometric measurements were performed on live, unanaesthetized specimens of the species *Acanthodactylus aureus* Günther 1903, *Acanthodactylus boskianus* (Daudin 1802), *Acanthodactylus erythrurus* (Schinz 1833), *Lacerta monticola* Boulenger 1905, *Lacerta oxycephala* Duméril & Bibron 1839, *Lacerta schreiberi* Bedriaga 1878, *Lacerta vivipara* Jacquin 1787, *Podarcis melisellensis* (Braun 1877), *Podarcis muralis* (Laurenti 1768), *Podarcis peloponnesiaca* (Bibron & Bory 1833), *Psammodromus algirus* (Linneaus 1766), *Psammodromus hispanicus* Fitzinger 1826, and *Takydromus sexlineatus* Daudin 1802. In addition, body parts were measured of fixed specimens of *Acanthodactylus schreiberi* Boulenger 1878, *Acanthodactylus scutellatus* (Audouin 1809), *Heliobolus lugubris* (A. Smith 1838), *Ichnotropis squamulosa* Peters 1854, *Lacerta agilis* Linneaus 1758, *Lacerta laevis* Gray 1838, *Meroles knoxii* (Milne-Edwards 1829), *Meroles reticulates* (Bocage 1867), *Meroles suborbitalis* (Peters 1869), *Messalina guttulata* (Lichtenstein 1823), *Nucras intertexta* (A. Smith 1838), *Nucras tesselata* (A. Smith 1838), *Ophisops elegans* (Ménétriés 1832), *Pedioplanis lineoocellata* (Duméril & Bibron 1839), *Pedioplanis namaquensis* (Duméril & Bibron 1839), and *Pedioplanis undata* (A. Smith 1838), preserved in the Museum König in Bonn, Germany. The shape characteristics considered here are not affected by alcohol fixation (Vanhooydonck & Van Damme, 1999). Finally, head measures (from living animals) for *L. oxycephala* and *P. melisellensis* were taken from Verwaijen *et al.* (2002).

The following external measures were taken on each individual using digital callipers (model CD-15DC, Mitutoyo, Ltd, Telford, UK, to the nearest 0.01 mm): (1) snout–vent length (SVL; measured from the tip of the snout to the posterior edge of the anal scale); (2) humerus length (from armpit to elbow); (3) radius length (from elbow to wrist); (4) metacarpal length (from the wrist to the base of the fourth finger); (5) length of the fourth digit; (6) femur length (from the groin to the knee joint); (7) tibia length (from the knee joint to the heel); (8) metatarsal length (from the heel to the base of the fourth digit); (9) length of the fourth digit. Front leg length and hind leg length were calculated as the sum of their parts (2 + 3 + 4 + 5 and 6 + 7 + 8 + 9 respectively). We also noted (10) thigh diameter; (11) tail length (from the posterior edge of the anal scale to the tip of the tail; only taken on specimens with an intact, unregenerated tail); (12) distance from arm pit to groin (body length); (13) body width (where the body is at its broadest, and narrowing the callipers until its anterior movement is hindered by the animal's scales); (14) body height (where the body is at its highest, and further analogously to body width); (15) head length (tip of snout to the skull-vertebral column articulation); (16) head width (width where the head is at its widest point, including the bulging of the musculus pterygoideus); (17) head height (where the head reaches its maximal height, just posterior of the orbita). All morphometric measurements were performed by one of us (DV). Repeatability of measurements was tested in one species (*P. peloponnesiaca*) and proved to be sufficient, so we considered the procedure as reliable. In many lacertid lizards, relative head measures are sexually dimorphic, males having proportionally larger heads than females (e.g. Braña, 1996). To avoid possible confounding effects of sex and age, we used only data on adult males in the analyses.

Bite force

An isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland), mounted on a holder and connected to a Kistler charge amplifier (type 5058 A, Kistler Inc.) was used to measure bite forces. The animals were induced to bite on two plates fixed at a distance ranging from 3.14 (*P. hispanicus* and *T. sexlineatus*) to 3.88 mm. During biting, the upper plate rotates and exerts a pull on the piezo-electric force transducer. The bite forces were recorded using a computer equipped with an A/D converter. See Herrel *et al.* (2001a, b) for a more detailed description of the bite force measuring protocol.

Before being made to bite, the lizards were kept in cloth bags and placed in an incubator at 35 °C (32 °C for *L. vivipara*) for 1 h. A lizard was then removed from its bag and held in front of the bite plates, resulting in a characteristic threat response with the jaws wide open. The bite plates were then placed between the jaws, resulting in a forceful bite on these bite plates. This was repeated five times with each individual, leaving at least 1 h between successive tests. The maximal value obtained during these sessions was considered the maximal bite force for that individual animal. Only bite forces of males were used in the analyses. Bite forces of the following species were measured: *A. aureus*, *A. erythrurus*, *L. monticola*, *L. schreiberi*, *L. vivipara*, *P. muralis*, *P. peloponnesiaca*, *P. algirus*, *P. hispanicus*, *T. sexlineatus*. For *L. oxycephala* and *P. melisellensis*, bite forces from Verwaijen *et al.* (2002) were used (see Table 1).

Foraging mode

Indices of foraging behaviour were calculated from field observations on adult, nonreproductive animals active during peak activity hours and under optimal weather conditions (*A. aureus*, *A. erythrurus*, *L. vivipara*, *L. monticola*, *L. oxycephala*, *L. schreiberi*, *P. melisellensis*, *P. muralis*, *P. peloponnesiaca*, *P. algirus*, *P. hispanicus*) or from observations in a 5 × 5 m semi-natural terrarium (*T. sexlineatus*). In the terrarium, animals had the opportunity to bask under lamps for at least 1 h prior to observation. Field and laboratory measures of foraging behaviour are highly comparable (D. Verwaijen & R. Van Damme, unpublished work). Although observations of lizard

Table 1 Mean foraging indices, morphometrics and bite forces of male lizards of different species used in this study.

	Foraging behaviour							Morphometrics													Bite force
	#obs	⟨time⟩	PTM	MPM	PAM	#att	Source	*N*	SVL	FLL	HLL	FEMD	TAILL	BL	BW	BH	HL	HW	HH		
Acanthodactylus aureus	30	8′30″	6.68	2.41	0.19	16	Verwaijen pers. obs.	3	72.35	28.47	52.92	5.51	139.40	31.32	13.08	11.70	18.73	11.17	9.16		5.83
Acanthodactylus boskianus	7	7′05″	28.8	2.01			Perry *et al.* (1990)	3	70.31	24.34	47.21	5.59	136.30	34.41	12.72	10.99	18.02	10.52	8.59		
Acanthodactylus erythrurus	27	9′20″	16.26	3.16	0.45	22	Verwaijen pers. obs.	7	72.50	29.02	46.99	6.17	131.60	37.13	14.45	11.28	17.75	11.65	9.27		9.70
Acanthodactylus schreiberi	12	5′15″	30.5	1.54			Perry *et al.* (1990)	5	68.70	27.80	49.94	5.64	123.00	31.40	15.47	10.96	17.43	11.93	9.16		
Acanthodactylus scutellatus	26	5′54″	7.7	1.01			Perry *et al.* (1990)	8	76.70	28.89	51.64	6.33	132.60	35.37	16.13	13.05	19.64	13.01	10.31		
Heliobolis lugubris	15	4′49″	57.4	2.97	1		Huey & Pianka (1981)	7	57.04	23.65	43.80	4.84	129.00	25.48	11.91	9.77	14.48	9.58	7.95		
Ichnotropis squamulosa	5	4′11″	54.6	3.1			Huey & Pianka (1981)	2	74.34	27.33	42.24	5.24	110.00	32.94	16.59	12.61	17.62	10.70	8.75		
Lacerta agilis	25	7′23″	1.59	0.21	0		Nemes 2002	7	72.75	25.17	36.28	5.08	107.20	36.42	14.21	12.06	18.17	12.4	10.37		
Lacerta laevis	16	4′13″	28.7	1.17			Perry *et al.* (1990)	6	70.97	26.93	45.30	6.51	117.50	31.07	13.82	11.24	19.62	12.32	9.63		
Lacerta monticola	39	7′59″	19.1	3.04	0.4	15	Verwaijen pers. obs.	6	73.28	25.70	38.77	5.74	106.30	39.20	15.81	11.47	17.96	11.18	7.89		12.91
Lacerta oxycephala	56	7′19″	15.11	2.22	0.32	31	Verwaijen pers. obs.	5	58.4	22.32	34.00	4.56	103.00	27.85	12.48	7.77	15.1	8.2	5.8		5.9†
Lacerta schreiberi	5	8′51″	10.75	1.86			Verwaijen pers. obs.	7	95.57	36.91	55.64	7.78	153.20	47.27	19.86	16.98	24.58	17.01	13.22		34.23
Lacerta vivipara	21	5′53″	33.2	4.2	0.5	4	Verwaijen pers. obs.	8	52.63	16.53	23.50	3.07	71.58	29.63	8.24	6.92	11.54	7.19	5.71		2.29
Meroles knoxii	27	8′43″	7	0.61	0	6	Cooper & Whiting (1999)	2	52.82	23.09	38.38	3.72	108.90	22.83	10.59	8.12	13.37	8.10	6.21		
Meroles reticulates	4	8′44″	0	0.05			Cooper & Whiting (1999)	8	50.22	22.10	39.50	3.68	66.65	21.20	12.67	8.56	15.17	9.42	7.02		
Meroles suborbitalis	15	8′11″	13.5	1.83			Huey & Pianka (1981)	5	58.04	23.42	42.61	4.43	115.10	25.74	12.43	9.04	14.71	10.29	7.55		
Messalina guttulata	3	27′20″	30.5	0.15			Perry *et al.* (1990)	7	46.89	17.41	28.85	3.19	100.20	21.97	9.70	6.85	11.73	7.21	5.19		
Nucras intertexta	3	2′58″	64.5	3.69			Pianka *et al.* (1979)	2	70.91	23.01	34.78	4.96	127.50	35.76	10.6	10.07	16.06	10.15	8.35		
Nucras tesselata	11	5′26″	50.2	2.9	1	1	Huey & Pianka (1981)*	1	68.63	23.76	44.43	4.79	167.22	36.45	10.71	10.35	15.31	10.31	8.27		
Ophisops elegans			54.6	1.88			Barnea unpubl. in Perry (1999)	6	49.79	20.04	34.07	3.49	98.47	21.24	9.28	7.25	11.97	7.51	6.29		
Pedioplanis lineoocellata	15	10′10″	14.3	1.54	0	1	Huey & Pianka (1981)*	7	51.88	22.94	38.98	4.08	87.63	22.50	11.36	8.06	12.89	8.77	6.08		
Pedioplanis namaquensis	26	9′08″	54	1.87	0.95	58	Cooper & Whiting (1999)	3	50.47	18.82	35.71	3.08	66.53	24.91	8.22	5.77	12.25	7.23	4.83		
Pedioplanis undata	16	7′28″	50	1.39	1	4	Cooper & Whiting (1999)	8	55.03	23.46	41.54	3.93	115.70	24.02	10.84	7.72	13.80	8.29	5.94		
Podarcis melisellensis	58	7′54″	17.35	2.54	0.49	39	Verwaijen pers. obs.	7	60.9	20.63	34.42	4.19	114.30	29.32	11.63	9.45	14.9	8.0	6.3		6.7†
Podarcis muralis	47	7′50″	20.54	3.05	0.5	14	Verwaijen pers. obs.	9	59.34	20.26	32.40	3.92	89.50	28.18	10.64	8.55	15.63	8.94	6.52		6.42
Podarcis peloponnesiaca	73	9′14″	12.35	2.1	0.25	36	Verwaijen pers. obs.	9	75.50	28.84	49.36	4.82	114.80	38.38	12.6	9.84	19.66	11.83	9.67		13.45
Psammodromus algirus	43	7′54″	20.68	2.95	0.69	13	Verwaijen pers. obs.	12	67.10	24.43	37.50	5.15	142.10	37.90	12.19	9.62	16.44	10.19	8.15		8.61
Psammodromus hispanicus	6	7′34″	25.99	4.71			Verwaijen pers. obs.	6	41.10	15.92	25.47	3.09	73.75	21.12	8.02	6.19	10.72	6.56	5.24		2.26
Takydromus sexlineatus	37	9′53″	13.8	1.6	0.38	13	Verwaijen pers. obs.	9	54.45	20.47	29.41	2.51	222.60	28.13	6.60	6.52	13.73	6.24	5.43		0.56

#obs = number of observations used to calculate foraging indices; ⟨time⟩ = mean time of foraging observations; PTM = percentage of time spent moving; MPM = movements per minute; PAM = proportion of prey attacked while moving; #att = number of feeding attempts used in the calculation of PAM; *N* = sample size for morphometrics; SVL = snout–vent length; FLL = forelimb length; HLL = hind limb length; FEMD = diameter thigh; TAILL = tail length; BL = body length (intergirdle length); BW = body width; BH = body height; HL = head length; HW = head width; HH = head height. All morphometrical data are in mm; bite force in N.

*PAM taken from Cooper & Whiting (1999).

†Bite force data taken from Verwaijen *et al.* (2002).

foraging may include periods in which food may not have been the main motivation for the movement behaviour, it is difficult to separate such movements from foraging, as they are not mutually exclusive and may be combined. We excluded from analysis the (very infrequent) observational bouts during which the lizards were obviously disturbed by a predator or a conspecific. We saw no conflicts, displays, fights or copulations during our observations. Nor did we see any of the 'stress-indicating' behaviours typical for lacertid lizards (e.g. foot shakes, tail vibrations and sudden starts). One of us (DV) performed all observations.

The beginnings and endings of movement bouts and attacks to prey were recorded by means of a PSION Workabout MX (Psion Teklogix Inc., Mississauga, Canada). Changes in body orientation or postural changes, and movements of body parts not involving translational movement, were discarded. Pauses of one or more seconds were recorded as bouts of 'immobility'. Each individual was observed for at least 10 min where possible (see Perry, 2007). Occasionally, sessions had to be terminated because the lizard disappeared from sight. Only observations that took at least 3 min were included (see Table 1 for the number of observations and the mean time per observation per species). The number of movements per minute (MPM) and the percentage of the time moving (PTM), which generally are considered as indicators of foraging mode (Perry, 1999), were calculated. In addition, all feeding attempts were recorded, and it was noted whether these were initiated while the lizard was actively searching or while it was stationary. From these data, we calculated PAM values (proportion of prey attacked while moving), which are thought to reflect the importance of sit-and-waiting or active search for discovery of prey (Cooper *et al.*, 1999). PAM ranges from 0 (purely sit-and-waiting) to 1 (purely active foraging).

Foraging data for other lacertids were taken from the literature (see Table 1 for specific references).

Statistics

Species mean values and SEs for all variables were used as input in the analyses. As we were particularly interested in the relationship between body shape and foraging activity, we first removed the effect of size from all morphometric variables, using Mosimann's (1970) geometric mean method (Klingenberg, 1996; Butler & Losos, 2002) on $\log_{10}$-transformed data for size adjustment. To this end, we calculated a $\log_{10}$-transformed index for size ($\log_{10}$[SIZE]) that equals the geometric mean of $\log_{10}$-transformed variables (SVL, front leg length, hind leg length, thigh diameter, body length, body width, body height, tail length, head length, head height and head width). Each of the morphometric variables was adjusted for size by taking the difference of each $\log_{10}$-variable with $\log_{10}$(SIZE). For example, the size-adjusted value for front leg length is $\log_{10}$(front leg length) − $\log_{10}$(SIZE). Size-corrected bite force was calculated as $\log_{10}$(bite force) − $\log_{10}$(SIZE).

We then performed a principal component analysis (PCA, varimax rotation method) on the correlation matrix of these size-corrected variables. We performed a second PCA on Felsenstein (1985) contrasts of the size-corrected morphometric variables. The contrasts were calculated using the PDTREE program (Garland *et al.*, 1999). Similar analyses were carried out on the reduced set of species for which we had PAM data. Because these PCAs yielded similar results as for the original data set, we will report only the latter. Following Ord & Martins (2006), we used the results of the PCAs to identify representative morphometric variables and then correlated these to the foraging indices and bite force. This approach was chosen instead of using principal components, or other composite variables, to simplify the evolutionary interpretation of results (Ord & Martins, 2006). We used the phylogenetic generalized least squares (PGLS) module in the COMPARE 4.6 package (Martins, 2004) to examine pair-wise relationships among morphometric, performance and behavioural variables. A major advantage of this module is that it can be used to incorporate within-species variation. Also, it is flexible in the assumptions of the evolutionary mode applied, because it generates 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 of Felsenstein's independent contrasts method (FIC); when α is large ($\cong 15$), results are similar to that of a raw data analysis (TIPS). We present parameter estimates at low (FIC) and high (TIPS) values of α, and at the maximum-likelihood estimate of α (PGLS$\alpha_{\max}$). Because branch lengths in our candidate phylogenetic tree are unknown (see further), we repeated these analyses on a set of 100 trees with random branch lengths, generated with the COMPARE program. The confidence intervals for the parameter estimates obtained this way thus incorporate variance due to uncertain phylogeny (here: divergence times).

We also estimate the amount of phylogenetic signal (i.e. the tendency for evolutionary related organisms to resemble each other) present in the behavioural, morphological and performance variables, using PHYSIG Matlab code developed by Blomberg *et al.* (2003).

The phylogenetic methods described above require information on the topology and branch lengths of the phylogenetic tree. The phylogenetic hypothesis used in this study (see Fig. 1) is primarily based on Fu (2000), and further on Arnold (1991) (for *Pedioplanis*), Harris *et al.* (1998) (for the position of *Ichnotropis and L. laevis*), Harris & Arnold (2000) (for *Acanthodactylus*), Lamb & Bauer (2003) (for *Meroles*) and Poulakakis *et al.* (2005) (for *Podarcis*). Few data are available on the divergence times within Lacertidae; therefore, calculations were performed: (1) on a tree with all branch lengths set

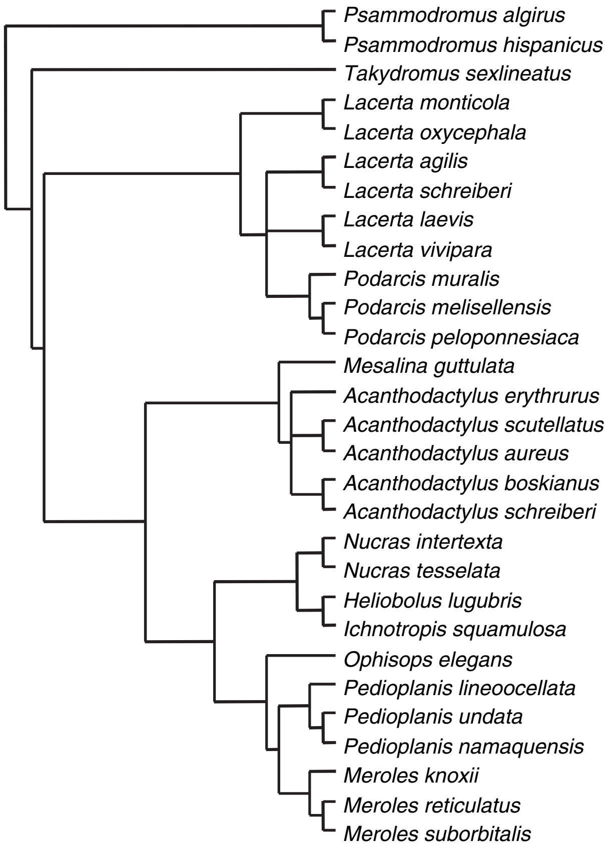

Fig. 1 Hypothesis on phylogenetic relationships among the species used in this study, see text for sources.

equal to one; and (2) on a set of 100 trees with random branch lengths.

Results

Table 1 presents an overview of the foraging behaviour indices, the morphometric data and the bite force data used in the analyses. Traditional (i.e. nonphylogenetic) PCA on the size-corrected morphometric measures extracted four new variables, which together explained 84% of the variation in the original data (36%, 23%, 14% and 10% respectively). In Table 2, the correlations between these principal components and the original data are presented. The first axis correlated positively with relative head width (0.94) and femur diameter (0.73). It correlated negatively with relative tail length (−0.81). The second axis is positively associated with the relative length of both the forelimb (0.87) and the hind limb (0.91). The third axis correlated positively with relative body width (0.81) and body height (0.84), and negatively with body length (−0.60). Size-corrected head length determines the fourth axis (0.92). PCA on the independent contrasts of the morphometric measures yielded three new axes (see Table 3). The first new axis explained 35% of the variation in contrasts, and was correlated with contrasts in forelimb (0.68) and hind limb length (0.74) and with body width (−0.83) and height (−0.92). The second axis (explaining another 25% of the total variation) was influenced by contrasts of head width (0.93), head height (0.79) and tail length (−0.80). The last axis correlated with body length contrasts (−0.93) only. We chose size-corrected hind limb length, body height, tail length and head width as indicators of body shape in subsequent analyses.

Table 2 Correlations between the principal component axes and the original (size-corrected) morphometric variables.

Size-corrected	PC1	PC2	PC3	PC4
Forelimb length	−0.06	0.87	−0.18	0.23
Hind limb length	−0.01	0.91	0.04	−0.11
Body length	−0.17	−0.60	−0.60	0.28
Tail length	−0.81	0.04	−0.45	−0.21
Femur diameter	0.73	−0.07	0.04	−0.52
Body width	0.42	0.07	0.81	0.04
Body height	0.01	−0.49	0.84	−0.19
Head length	0.07	0.04	−0.10	0.92
Head height	0.44	−0.46	0.31	−0.15
Head width	0.94	0.03	0.09	0.09

Table 3 Correlations between the principal components and the original contrasts of the morphometric variables.

Contrasts of	PC1	PC2	PC3
Forelimb length	0.68	0.00	0.20
Hind limb length	0.74	0.09	0.48
Body length	−0.05	−0.09	−0.93
Tail length	0.44	−0.80	−0.11
Femur diameter	−0.24	0.44	0.64
Body width	−0.83	0.32	0.33
Body height	−0.92	0.00	0.12
Head length	0.14	0.04	−0.09
Head height	−0.01	0.79	0.04
Head width	0.12	0.93	0.21

Variation in body size ($\log_{10}$SIZE) did not predict variation in PTM, MPM (Table 4) or PAM (Table 5). Although generally consistent with respect to the direction of the relationships, the different methods (PGLS, FIC and TIPS) disagreed on the significance of the association between the respective morphological measurements and MPM or PTM (Table 4). Models in which branch lengths were randomly assigned typically yielded more significant correlations than did models where branch lengths were fixed (punctual evolution). Overall, the analyses suggest that evolutionary changes towards a more active way of foraging (increased MPM and PTM) coincided with a decrease in relative body height and head width (Table 4). Evolutionary increa-

Table 4 Relationships between morphological variables, PTM and MPM for 29 species of lacertid lizards.

			PGLS					FIC				TIPS		
X	*Y*	Branch lengths	α	*r*	LnL	*b*	SE	*r*	LnL	*b*	SE	*r*	*b*	SE
SIZE	PTM	CONSTANT	1.18	−0.17	−91.96	−25.28	27.76	−0.16	−91.38	−22.55	26.11	−0.24	−46.80	36.50
SIZE	PTM	RANDOM	5.88	0.06	−95.07	9.51	29.10	0.24	−99.90	35.44	24.16			
SIZE	MPM	CONSTANT	6.58	0.01	−17.83	0.14	2.35	−0.02	−21.87	−0.22	2.38	0.03	0.32	2.33
SIZE	MPM	RANDOM	15.31	0.13	−19.41	1.42	2.27	0.14	−32.40	1.60	2.37			
HLL	PTM	CONSTANT	1.08	−0.03	−92.03	−5.84	33.07	−0.06	−91.72	−10.35	31.07	0.15	32.12	40.70
HLL	PTM	RANDOM	2.89	−0.36	−92.91	−41.20	22.86	−0.47	−95.42	**−49.87**	18.59			
HLL	MPM	CONSTANT	7.23	−0.08	−17.76	−1.04	2.60	0.09	−21.76	1.31	2.78	−0.13	−1.68	2.53
HLL	MPM	RANDOM	14.33	−0.14	−20.86	−2.20	2.48	−0.13	−35.22	−2.34	2.54			
BH	PTM	CONSTANT	1.09	−0.16	−91.66	−36.31	42.86	−0.16	−91.38	−35.04	40.46	−0.12	−37.80	59.70
BH	PTM	RANDOM	3.12	−0.44	−92.35	**−72.64**	30.05	−0.55	−95.07	**−81.53**	24.48			
BH	MPM	CONSTANT	9.30	−0.34	−16.16	−6.56	3.49	−0.22	−21.14	−4.26	3.59	−0.36	**−6.94**	3.48
BH	MPM	RANDOM	14.59	−0.45	−16.35	**−7.07**	2.84	−0.57	−27.00	**−7.99**	2.33			
TAILL	PTM	CONSTANT	1.14	0.14	−91.75	18.77	25.40	0.14	−91.50	16.93	23.60	0.19	35.75	36.10
TAILL	PTM	RANDOM	4.37	0.34	−93.93	**62.15**	30.18	0.52	−96.30	**107.37**	30.37			
TAILL	MPM	CONSTANT	6.50	−0.02	−17.83	−0.19	2.22	−0.10	−21.74	−1.07	2.13	0.01	0.14	2.28
TAILL	MPM	RANDOM	15.34	0.10	−19.75	1.25	2.30	0.20	−32.08	3.35	3.39			
HW	PTM	CONSTANT	1.09	−0.13	−91.78	−51.61	69.85	−0.14	−91.49	−51.61	69.85	−0.09	−45.10	100.00
HW	PTM	RANDOM	2.67	−0.49	−91.50	**−138.33**	49.49	−0.60	−93.57	**−150.45**	40.07			
HW	MPM	CONSTANT	5.70	−0.20	−17.28	−6.39	6.12	−0.26	−20.90	**−8.40**	6.13	−0.15	−4.99	6.13
HW	MPM	RANDOM	12.82	−0.37	−17.55	−9.65	5.03	−0.58	−27.01	**−13.85**	3.95			

α is the restraining force of the best PGLS model based on maximum likelihood, *r*s are the (phylogenetic) correlation coefficients, LnLs are the log-likelihood ratios, *b*s are the estimated slopes and SE the standard errors on the slopes. Shown are the results from PGLS analyses with α set at the estimated value, from Felsenstein's independent contrasts method (FIC) and from Pearson correlations of raw data (TIPS).
The PGLS and FIC analyses were performed on the candidate tree with all branch lengths set to one (CONSTANT) and on 200 trees with randomly generated branch lengths (RANDOM). For the latter analyses, mean correlations, LnLs, slopes and SEs are presented. In the PGLS analyses, the intraspecific variation in the traits was taken into consideration. Slopes for which the 95% confidence interval does not include zero, are in bold. PTM, percentage of time spent moving; MPM, movements per minute; SIZE, geometric mean of transformed variables, see text; HLL, size-corrected hind limb length; BH, size-corrected body height; TAILL, size-corrected tail length; HW, size-corrected head width.

Table 5 Relationships between the morphological variables and PAM for 17 species of lacertid lizards.

			PGLS					FIC				TIP		
X	*Y*	Branch lengths	α	*r*	LnL	*b*	SE	*r*	LnL	*b*	SE	*r*	*b*	SE
SIZE	PAM	CONSTANT	6.77	−0.22	10.66	−0.87	1.02	−0.13	8.24	−0.58	1.11	−0.24	−0.98	1.00
SIZE	PAM	RANDOM	12.91	−0.15	10.55	−0.66	1.02	−0.17	7.62	−0.98	1.22			
HLL	PAM	CONSTANT	8.45	0.25	10.74	0.91	0.91	0.01	8.09	0.02	1.09	0.29	1.05	0.90
HLL	PAM	RANDOM	13.15	0.25	10.82	0.71	0.78	0.23	4.18	0.50	0.65			
BH	PAM	CONSTANT	5.94	−0.07	10.31	−0.42	1.54	−0.13	8.24	−0.91	1.78	−0.04	−0.25	1.50
BH	PAM	RANDOM	11.91	−0.04	10.38	−0.36	1.52	−0.09	5.60	−1.27	2.32			
TAILL	PAM	CONSTANT	6.36	0.08	10.32	0.25	0.82	−0.01	8.09	−0.03	0.81	0.10	0.34	0.83
TAILL	PAM	RANDOM	12.16	0.11	9.99	0.34	0.88	0.22	3.53	1.07	1.45			
HW	PAM	CONSTANT	5.90	−0.12	10.38	−0.92	2.04	−0.17	8.34	−1.36	2.05	−0.09	−0.70	2.06
HW	PAM	RANDOM	11.62	−0.13	10.47	−0.84	1.91	−0.23	7.49	−1.68	2.06			

See Table 4 for abbreviations in the heading. As no measurement errors were available for PAM, PGLS analyses were run assuming no intraspecific variation. PAM, proportion of prey attacked while moving; SIZE, geometric mean of transformed variables, see text; HLL, size-corrected hind limb length; BH, size-corrected body height; TAILL, size-corrected length; HW, size-corrected head width.

ses in PTM also seem to concur with decreases in relative limb length and increases in relative tail length. No relationships were evident between PAM and body shape and size (Table 5).

Consistent with biomechanical predictions, bite force co-evolved with body size and relative head width (Table 6). However, we found no evidence for any co-evolution between bite performance and indices of foraging behaviour (Table 6).

All variables measured had phylogenetic signals (*K*) less than one, indicating that related species resembled each other less than expected under Brownian motion

Table 6 Relationships between bite force, morphology and foraging behaviour in lacertid lizards.

			PGLS					FIC				TIP		
X	*Y*	Branch lengths	α	*r*	LnL	*b*	SE	*r*	LnL	*b*	SE	*r*	*b*	SE
BF	PTM	CONSTANT	13.72	−0.23	−26.82	−4.41	6.20	−0.33	−29.27	−6.58	6.39	−0.23	−4.40	6.20
BF	PTM	RANDOM	15.03	−0.17	−26.91	−3.42	6.10	−0.30	−29.83	−7.72	6.75			
BF	MPM	CONSTANT	15.50	−0.09	−4.56	−0.22	0.82	−0.12	−7.75	−0.34	0.90	−0.09	−0.22	0.82
BF	MPM	RANDOM	15.31	−0.02	−4.76	−0.02	0.81	−0.10	−7.82	−0.29	0.91			
BF	PAM	CONSTANT	15.59	0.28	5.21	0.98	1.27	0.42	2.16	2.01	1.65	0.28	0.98	1.26
BF	PAM	RANDOM	13.60	0.07	13.02	0.02	0.15	0.02	10.83	0.00	0.16			
SIZE	BF	CONSTANT	3.25	0.73	9.16	**2.33**	0.73	0.77	8.17	**2.36**	0.65	**0.67**	2.27	0.83
SIZE	BF	RANDOM	3.05	0.77	9.72	**2.58**	0.67	0.82	9.18	**2.73**	0.61			
HW	BF	CONSTANT	15.50	0.52	7.06	**5.47**	3.01	0.26	3.61	2.83	3.45	**0.52**	5.51	3.01
HW	BF	RANDOM	14.99	0.38	6.64	4.09	2.93	−0.14	4.28	−0.80	2.54			

See Table 4 for abbreviations in the heading. BF, size-corrected bite force; PTM, percentage of time spent moving; MPM, movements per minute; PAM, proportion of prey attacked while moving; SIZE, geometric mean of transformed variables, see text; HW, size-corrected head width.

Table 7 Expected and observed MSE_0/MSE ratios for the trees used in the analyses, the phylogenetic signal (*K*) and the MSEs for the candidate trees and star phylogenies.

	MSE_0/MSE_{exp}	MSE_0/MSE_{obs}	*K*	MSE_{can}	MSE_{star}
PTM	2.448	1.904	0.778	198.137	348.285
MPM	2.448	1.162	0.475	1.605	1.340
PAM	2.331	0.980	0.420	0.134	0.122
SIZE	2.448	1.065	0.435	0.010	0.009
BL	2.448	0.950	0.388	0.004	0.003
BH	2.448	1.991	0.813	0.004	0.004
BW	2.448	1.951	0.797	0.003	0.002
TAIL	2.448	1.991	0.813	0.013	0.010
FLL	2.448	0.800	0.327	0.011	0.008
HLL	2.448	1.247	0.509	0.008	0.008
FEMD	2.448	1.503	0.614	0.002	0.002
HL	2.448	1.713	0.700	0.002	0.002
HH	2.448	0.775	0.317	0.002	0.001
HW	2.448	1.662	0.516	0.002	0.001
BITE	1.797	1.320	0.735	0.190	0.150

See legend in Table 1 for a description of variables.

evolution along the candidate trees. We found no obvious difference in *K* between morphological, performance and behavioural variables (Table 7).

Discussion

Our results provide mixed evidence for a co-evolutionary pattern between foraging style and morphology in lacertid lizards. Whereas some morphological features (head width and tail length) seem to change with foraging style in a way consistent with our predictions, others do not, or even seem to evolve in opposite directions (limb length and body height). Also, results from analyses with different assumptions of the evolutionary process are not always coherent. It could be argued that this equivocal outcome results from either our limited sample size (number of species examined) or inadequate selection of study species. However, both the traditional and phylogenetically informed analyses in this study grouped the original morphometrics into composite variables that seem biologically meaningful (e.g. separating species into long-limbed vs. short-limbed or stocky, short-tailed vs. slender, long-tailed groups). Also, well-established functional relationships between bite force capacities and head size measures (e.g. Herrel *et al.*, 2001a; McBrayer, 2004) were confirmed with our smaller data set, indicating that other trends of similar strength should have been detectable. Finally, the range of PTM and MPM values in our data set is considerable (in comparison with those reported from other lizards), and probably covers most of the variety in foraging strategies exhibited by this family. Therefore, we consider it useful to examine possible biological (rather than methodological) explanations for our findings.

Trunk, leg and tail morphology

Because active hunting lizards should benefit more from high sprint speed capacity and energetically efficient locomotion, we expected them to have more slender, flexible bodies and longer limbs than sit-and-wait strategists.

In both the traditional and phylogenetically informed PCA, relative limb length emerged as an important determinant of the composite variables explaining morphological variation among species (second and first axis respectively). However, we found no evidence for a positive association between long limbs and active foraging. The idea that limb length should affect maximal running speed is well established (Garland & Losos, 1994; Bauwens *et al.*, 1995; Bonine & Garland, 1999), and has been empirically tested in lacertid lizards (Vanhooydonck *et al.*, 2002). Lizards with longer limbs can take larger strides and thus can attain higher maximal sprint speeds than species with short limbs (Vanhooydonck *et al.*, 2002). It therefore seems safe to assume that limb length is a significant determinant of sprint speed. Less clear is whether an active foraging style selects for a high sprinting capacity. The idea that widely foraging lizards should be faster because their frequent movements expose them to increased predation pressure seems logical, but needs empirical verification. Moreover, Irschick *et al.* (2005) recently showed that some species of lacertids rarely use maximal sprint capacities when fleeing from simulated predator attacks in the field. It has also been argued that intensive foraging lizards may require speed for prey capture (White & Anderson, 1994). However, this idea needs to be substantiated by diet analyses and field observations on prey capture techniques in lizards of both foraging types. Active foraging lizards may be more likely to encounter sedentary prey that can be captured without pursuit, whereas sit-and-wait lizards will typically meet moving prey, and may therefore require high acceleration capacities. As maximal sprint speed and acceleration capacity tend to correlate positively in lizards (Huey & Hertz, 1982), selection pressures on sprint performance in actively foraging and sit-and-wait lacertids may not be as opposing as predicted. Finally, even if sit-and-wait species depend less on speed to evade predators and to seize prey, they might require agility for other reasons (e.g. during social interactions).

Biomechanical considerations suggest that lizards optimizing speed should have relatively high, but narrow trunks, because this would enhance their capacity for lateral undulation, and contribute to an increased step length. Increased body lengths (axilla–groin distances) should facilitate undulatory locomotion in a similar way. However, the role of trunk flexibility on sprint speed variation in lacertid has not been empirically verified. Further, all the considerations on the fitness gradient of sprint speed (see above) also apply here.

The relationships between morphology and locomotory energetic costs of lizards have been little explored beyond simple body mass effects under the assumption of geometric similarity (White & Anderson, 1994). Biomechanical theory predicts that costs of transport at a given speed should increase with increasing stride frequency (decreasing stride length), advantaging long-legged species. The validity of this argument has never been tested empirically in lacertids, however. As with sprint speed, the ecological relevance of energetic efficiency of locomotion in these lizards is also uncertain. Differences in energy expenditure between sit-and-wait and actively foraging lizards have been documented with doubly labelled water measurements of field metabolic rate (e.g. Anderson & Karasov, 1981; Nagy *et al.*, 1984), but the actual contribution of increased movement rate to the total energy budget has never been quantified.

Huey & Pianka (1981) have argued that selection should favour the evolution of longer tails in widely foraging lizards, because they are more likely to suffer from predation. Accordingly, in their set of six lacertids from the Kalahari Desert, the two sit-and-wait foraging species had the shorter tails (Huey & Pianka, 1981). Vitt (1983) also reasoned that a long, autotomous tail should be advantageous in actively foraging lizards, because these animals often rely on fast runs to escape predatory attacks (during which the tail is between the lizard's body and the predator in pursuit). For sit-and-wait lizards, which typically rely on crypsis, the value of a long tail is less clear. This prediction was supported by Vitt's comparison of 12 species of sympatric tropical lizards belonging to four families. Magnusson *et al.* (1985), however, did not find such a relation when comparing three teiid species and Perry *et al.* (1990) found a positive correlation with MPM, but not with PTM. Our current results suggest a positive relationship between relative tail length and foraging activity. The idea that tail size affects escape success in fleeing lizards stems mainly from studies showing reduced locomotor capacities or survival in individuals with autotomized tails (e.g. Daniels, 1983; Downes & Shine, 2001; but see, e.g. Webb, 2006). However, it is unclear whether the same reasoning applies to animals with intact tails differing in size. Also, as mentioned earlier, the underlying assumption that active foragers are under greater predation risk needs to be confirmed.

Head morphology

The idea that in lizards foraging style should be reflected in head morphology rests on two assumptions. First, the morphology of the feeding apparatus determines the types of prey that can be consumed. Higher and broader heads allow the attachment of more extensive jaw muscle mass, which in turn permits the generation of higher bite forces. Longer skulls, by contrast, allow shorter bite cycles, reduce the time required for processing the prey item, and thus minimize the time the feeding lizard is exposed to predators. There is good empirical evidence that these biomechanical predictions are correct (e.g. Herrel *et al.*, 2001a; Verwaijen *et al.*, 2002; McBrayer, 2004), and our results confirm this for the set of species under consideration. Second, actively foraging lizards on average encounter smaller, softer prey items than sit-and-wait foragers, and thus require less biting force and less massive heads (Huey & Pianka, 1981; Pianka, 1986). The validity of this second supposition is less certain – in general, and for our study system in particular. Our analyses seem to confirm the idea of wider heads in lizards with a sit-and-wait foraging strategy, but whether and how this affects their dietary opportunities is unclear. As we found no correlation between bite force and the foraging indices, there is no evidence that the advantages of being able to crush hard prey items drives the selection for wider heads in sit-and-wait foragers. Possibly, selection is on prey size, rather than prey hardness. Most lacertids are considered food generalists (Díaz, 1995), whose diets closely match the relative abundance of prey in the environment (e.g. Nouira, 1983; Mou, 1987; Pollo & Pérez-Mellado, 1988;

Pollo & Pérez-Mellado, 1991); however, most dietary studies on these lizards have centred on the taxonomical distribution of prey items, rather than on their physical properties. It would be interesting to correlate diet composition (in terms of prey size, hardness and mobility) with foraging style in lacertids to check the second assumption.

In the species group considered here, indices of foraging behaviour show an amount of phylogenetic signal (*K*) comparable with that found in morphological or performance measures. Moreover, *K*-values for all measurements are below one, indicating that related species resemble each other less than expected under Brownian motion evolution along the candidate tree (Blomberg *et al.*, 2003). This could be caused by different types of measurement errors (Blomberg *et al.*, 2003), but may also be indicative of considerable homeoplasy, adaptive evolution uncorrelated with the phylogeny. This possibility is interesting, because it would contradict the general notion that lacertids are morphologically and ecologically conservative (e.g. Arnold, 1989). Also, it would require reconsidering the general idea that foraging style is evolutionarily stable and a central feature in an adaptive complex (the syndrome hypothesis), the new question being why it is that whereas some taxa are locked in a stereotype foraging pattern, others are not.

We plead for more explicit tests of the many assumptions related to the putative link between foraging style and morphology. In particular, detailed observations on what determines foraging success in the field are urgently required. It would further be desirable to take into account other factors that might influence body shape, and that actually might be more decisive in this context than foraging mode. We would need to know not only the rate of movements, but also other ecological requirements of the species (microhabitat use, predation pressure and sexual selection) to compare the relative importance of these different selective forces in shaping morphology.

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