

Interactions between habitat use, behavior, and the trophic niche of lacertid lizards

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Introduction

The existence of evolutionary trade-offs prevents simultaneous optimization of different functions that require opposing biomechanical or physiological adaptations (Stearns, 1992). Consequently, trade-offs likely play an important role in niche partitioning, in that species specialized in exploiting one type of niche (e.g. microhabitat) are expected to be less proficient at exploiting others. For instance, in *Anolis* lizards, a trade-off exists between sprint speed and sure-footedness because long limbs are required to move fast, whereas short limbs aid sure-footedness (Losos and Sinervo, 1989; Losos and Irschick, 1996). Accordingly, species that predominantly move on broad surfaces (i.e. trunk-ground ecomorph) specialize for speed and have long limbs, whereas species living on narrow substrates (i.e. twig ecomorph) are specialized in slower but secure movements.

In a similar fashion, species specializing in different dietary niches may have diverged morphologically because the biomechanical demands on the feeding and/or locomotor apparatus are often not reconcilable within one phenotype. Clearly, the ability of a predator to exploit a certain prey type will depend on the functional characteristics of the prey (e.g. prey distribution, hardness, and escape response) and the performance of the feeding and locomotor system of the predator. For instance, in labrid fishes the amount of force potentially generated by the jaws trades off with the speed of jaw movement because of differences in the four-bar linkage system of the jaws and hyoid (long links aid high force outputs, but rapid movements are realized by short links) (Westneat, 1994, 1995). Consequently, species feeding mainly on hard prey will typically possess long links, whereas species feeding on evasive prey have short links, and thus have faster jaw movements (Westneat, 1994, 1995). Similarly, lizard species eating a lot of small evasive prey benefit from high jaw opening and closing

velocities, but at the same time appear to be constrained in bite force potential (Meyers and Herrel, 2005).

In addition, trade-offs between locomotor performance traits (e.g. endurance, sprint speed) may also affect an organism's feeding ecology. For instance, species feeding mainly on clumped prey need to spend a lot of their time moving around looking for food, and thus benefit from having a high endurance capacity (Huey and Pianka, 1981; Huey *et al.*, 1984; Garland, 1999). Since endurance and sprint speed may trade off (see, for example, Reidy *et al.*, 2000; Vanhooydonck *et al.*, 2001; Van Damme *et al.*, 2002), species specialized in feeding on clumped prey may not be able to catch fast, evasive prey, thus potentially resulting in a dichotomy in foraging strategy. In general it is thought that active foraging species eat clumped prey and have a high endurance, and that sit-and-wait predators eat evasive prey and excel in sprinting capacities (Huey and Pianka, 1981; Huey *et al.*, 1984). In addition, it has been suggested that sit-and-wait predators have high bite strengths, because evasive prey are often hard (McBrayer, 2004), suggesting that dietary niche is affected by locomotor and feeding performance simultaneously. Similarly, specialists on clumped prey benefit from high stamina, but at the same time need fast jaw movements to capture and process these small prey (Meyers and Herrel, 2005).

Lacertid lizards are an excellent study system to explore the correlates of feeding ecology and behavior because, of all lizard families, they display the greatest interspecific variation in movement patterns and rates (Cooper and Whiting, 1999; Perry, 1999). Moreover, in Kalahari lacertids, the differences in activity level appear to be correlated with differences in energy expenditure (Nagy *et al.*, 1984), locomotor performance (speed and endurance) (Huey *et al.*, 1984), and diet (Huey and Pianka, 1981). Additionally, lacertids exhibit precisely defined patterns of prey selection (Diaz, 1995) and vary greatly in diet (see, for example, Pollo and Pérez-Mellado, 1988; Pérez-Mellado and Corti, 1993; Herrel *et al.*, 2001c; Verwaijen *et al.*, 2002).

Here, we combine data on locomotor performance (i.e. sprint speed, endurance, and climbing speed) (Vanhooydonck *et al.*, 2001; Vanhooydonck and Van Damme, 2001), bite strength (Herrel *et al.*, 2004), and head morphology (Herrel *et al.*, 2004) in different species of lacertid lizard to test the idea that functional trade-offs play an important role in the interspecific partitioning of the dietary niche. Moreover, we explore how functional trade-offs arising through habitat specialization and locomotion may affect diet in lacertid lizards.

We specifically address two questions. First, we investigate how the trade-off between sprint speed and endurance (Vanhooydonck *et al.*, 2001) affects dietary niche in lacertid lizards. Since endurance capacity appears to be

positively correlated with the amount of time lizards spend moving (Garland, 1999), and since species that move around frequently (i.e. widely foraging) are expected to eat more clumped and sedentary prey (see, for example, Huey and Pianka 1981), we can expect species that typically feed on sedentary prey to have great endurance capacity. However, because of the speed–endurance trade-off, specializing in stamina may hamper the same predators' ability to catch fast, evasive prey.

Second, we investigate whether a saxicolous lifestyle (i.e. occurring on vertical, rocky surfaces), typical of many lacertid lizard species, constrains their feeding performance and hence restricts their dietary niche. Lacertids occurring on vertical walls and cliffs tend to have a dorsoventrally flattened head and body (Vanhooydonck and Van Damme, 1999). In addition, a flattened head seems advantageous in climbing lacertids as they frequently hide and/or forage in crevices and cracks in between the rocks (Miles, 1994; Vanhooydonck and Van Damme, 1999). Head size (e.g. head height), however, is a determinant of bite force in lizards (Herrel *et al.*, 2001a; McBrayer, 2004), and in lacertids in particular (see, for example, Herrel *et al.*, 1999, 2001c, 2004; Verwajen *et al.*, 2002). Because bite force and a vertical lifestyle thus seem to pose conflicting demands on the morphology of the head, we can expect a trade-off between both bite force and climbing ability (saxicolous species excel in climbing speed) (Vanhooydonck and Van Damme, 2003). Moreover, the limitations on bite force, due to a flattened head, in saxicolous species might restrict their diet to softer prey.

Methods

In the analyses, we use performance (sprint speed, endurance, climbing speed, and bite force), morphological (snout–vent length and head height), and ecological (diet) data. Sprint speed was measured on an electronic racetrack 2 m long by 0.15 m wide, lined with a cork substrate. Eight pairs of photocells, placed at 0.25 m intervals, recorded the time taken for lizards to cross each successive infrared beam. To measure climbing speed, an electronic racetrack 1 m long by 0.15 m wide was tilted to an angle of 70° and the eight pairs of photocells were positioned at 0.15 m intervals. The racetrack was lined with smooth slate to mimic a rocky surface. We measured endurance as the running time till exhaustion on a treadmill moving at a low and constant speed (0.22 m/s). Lastly, bite force was measured by using an isometric Kistler force transducer. Morphological measurements were made to the nearest 0.01 mm by using digital calipers. All performance and morphological data were published previously; we refer to these studies for a detailed description of the

experimental protocol (sprint speed: Bauwens *et al.*, 1995, Vanhooydonck *et al.*, 2001; endurance: Vanhooydonck *et al.*, 2001; climbing speed: Vanhooydonck and Van Damme, 2001; bite force: Herrel *et al.*, 2004; snout-vent length: Vanhooydonck and Van Damme, 2001; Herrel *et al.*, 2004; head height: Herrel *et al.*, 2004). As for dietary information, we used published accounts that contained information on the proportion of each prey type (by number) present in the diet of the species for which morphological and performance data were available (Angelici *et al.*, 1997; Mou and Barbault, 1986; Molina-Borja, 1991; Nourira, 1983; Pérez-Mellado and Corti, 1993; Pollo and Pérez-Mellado, 1988; Roig-Fernandez, 1998; Valido and Nogales, 1994, 2003). If results from different seasons or different years were reported, we used those for which the sample size was the largest. Data for males and females were pooled, as were data obtained from both stomach and fecal pellet samples. In addition, we supplemented the literature data with new data on diet for two species, *L. oxycephala* and *P. melisellensis* (unpubl. data).

We classified each prey item into three categories according to hardness (hard, soft, intermediate) and evasiveness (evasive, sedentary, intermediate). We chose these two characteristics because they are relevant with respect to the measured performance traits, and presumably foraging strategy, of the predator. Our classification is based on the actual forces needed to crush various prey items (Herrel *et al.*, 2001c; Aguirre *et al.*, 2003, pers. obs.) and on the observed escape tactics of invertebrates (see Table 14.1). We subsequently calculated the proportion each category represented in the lizards' diet. If we obtained data from different populations of the same species, we used the average over the different populations in the analyses.

Raw data on the morphology, performance and diet for all species used in this study are given in Table 14.2 and 14.3. Prior to statistical analyses, we logarithmically ($\log_{10}$) transformed all performance traits (sprint speed, endurance, climbing speed, and bite force) and morphological measurements (SVL and head height). Proportions were arcsin transformed (see Sokal and Rohlf, 1995). We used the independent contrast approach (Felsenstein, 1985, 1988) to take into account the evolutionary relatedness of the different species. To calculate independent contrasts between two nodes, the values of the variables in question must be subtracted. The direction of subtraction is entirely arbitrary, and consequently there is ambiguity in assigning signs to contrasts. The ambiguity in assigning signs makes it necessary to force the regression of one contrast against the other through the origin (see Appendix 1 in Garland [1992] for full explanation). Independent contrasts were calculated by using PDTREE (Garland *et al.*, 1999). Information on the topology of the phylogenetic tree was drawn from various sources (Arnold, 1989, 1998; Fu, 2000;

Table 14.1 *Classification of each prey type according to hardness and evasiveness level*

The taxonomic grouping is the same as the one used in the original papers from which the diet data were taken (see text for references). Taxonomic groups are ordered alphabetically.

taxon	hardness	evasiveness
Acari	soft	sedentary
Araneae	soft	sedentary
Blattaria	soft	evasive
Chilopoda	soft	intermediate
Coleoptera	hard	intermediate
Collembola	soft	sedentary
Dermaptera	soft	intermediate
Diplopoda	soft	sedentary
Diptera	soft	evasive
Dytiscoptera	soft	evasive/sedentary
Formicidae	hard	intermediate
Gastropoda	hard	sedentary
Heteroptera	soft	intermediate
Homoptera	hard	sedentary
Hymenoptera (except Formicidae)	hard	evasive
Isopoda	intermediate	sedentary
Isoptera	soft	sedentary
Larvae	soft	sedentary
Lepidoptera	soft	evasive
Lithobiomorpha	soft	intermediate
Mantodea	soft	sedentary
Mecoptera	soft	intermediate
Myriapoda	soft	sedentary/intermediate
Neuroptera	soft	intermediate
Odonata	intermediate	evasive
Oligochaeta	soft	sedentary
Opilionida	soft	intermediate
Orthoptera	intermediate	evasive
Phasmida	soft	sedentary
Pseudoscorpionida	soft	sedentary
Scorpionida	soft	sedentary
Solifugae	hard	sedentary
Stylommatophora	hard	sedentary
Thysanura	soft	sedentary
Trichoptera	soft	evasive
Vegetable matter	hard	sedentary
Vertebrate	hard	evasive

Table 14.2 Means and standard errors of morphological and performance traits

Means of sprint speed (sprinting, m/s), endurance (s) and climbing speed (climbing, m/s) are given per species; means of snout-vent length (SVL, mm), head height (mm) and bite force (N) are given for each sex separately. Habitat use (hab), i.e. saxicolous (sax) versus terrestrial (ter) lifestyle, is indicated per species (see Vanhooydonck and Van Damme, 2003).

species	morphology			performance					bite force	
	SVL			head height		sprinting	endurance	climbing	male	female
	hab	male	female	male	female					
<i>G. galloti</i>	ter	112.6 ± 2.6	92.1 ± 1.6	16.3 ± 0.7	11.6 ± 0.2	1.93 ± 0.13	311.38 ± 28.23	0.34 ± 0.06	107.6 ± 8.3	34.6 ± 3.2
<i>P. algeris</i>	ter	74.8 ± 1.1	63.2 ± 3.8	8.8 ± 0.2	6.8 ± 0.5	2.53 ± 0.15	—	—	11.5 ± 0.6	5.2 ± 1.2
<i>P. hispanicus</i>	ter	43.0 ± 1.0	44.2 ± 0.6	4.8 ± 0.1	4.10 ± 0.2	1.50 ± 0.35	—	—	2.3 ± 0.3	1.0 ± 0.2
<i>L. oxycephala</i>	sax	59.3 ± 1.1	49.7 ± 2.3	5.9 ± 0.1	4.8 ± 0.2	2.02 ± 0.09	109.6 ± 13.40	1.25 ± 0.08	3.9 ± 0.2	1.6 ± 0.2
<i>L. bedriagae</i>	sax	67.9 ± 2.5	63.1 ± 3.7	6.9 ± 0.3	6.2 ± 0.4	1.79 ± 0.15	437.6 ± 38.68	0.99 ± 0.08	7.2 ± 1.0	3.8 ± 0.8
<i>L. vivipara</i>	ter	49.7 ± 0.7	50.4 ± 1.3	5.4 ± 0.1	4.6 ± 0.1	0.87 ± 0.05	370.33 ± 105.34	—	2.1 ± 0.1	1.4 ± 0.1
<i>P. melisellensis</i>	ter	56.7 ± 1.5	53.7 ± 1.3	6.3 ± 0.2	5.1 ± 0.1	1.30 ± 0.12	—	—	4.0 ± 0.3	1.8 ± 0.1
<i>P. hispanica</i>	ter	55.4 ± 1.3	53.8 ± 0.7	5.9 ± 0.2	4.9 ± 0.1	2.03 ± 0.40	—	0.62 ± 0.06	4.3 ± 0.3	2.1 ± 0.1
<i>P. atrata</i>	ter	63.7 ± 0.6	58.4 ± 0.6	7.2 ± 0.2	5.4 ± 0.1	1.09 ± 0.42	—	0.19 ± 0.22	7.8 ± 0.6	2.6 ± 0.1
<i>P. muralis</i>	ter	56.3 ± 1.4	55.6 ± 1.4	6.3 ± 0.2	5.4 ± 0.1	2.14 ± 0.21	184.9 ± 12.39	0.29 ± 0.03	6.5 ± 0.8	3.1 ± 0.3
<i>P. tiliguerta</i>	ter	55.1 ± 1.2	50.1 ± 1.2	6.0 ± 0.2	4.6 ± 0.2	1.55 ± 0.13	194.79 ± 18.91	0.45 ± 0.06	3.6 ± 0.3	1.1 ± 0.1
<i>P. sicula</i>	ter	67.7 ± 1.4	65.3 ± 1.1	7.7 ± 0.2	6.5 ± 0.2	1.67 ± 0.10	266.07 ± 30.65	0.47 ± 0.04	6.6 ± 0.5	3.5 ± 0.3
<i>P. lilfordi</i>	ter	62.1 ± 0.9	60.7 ± 0.8	7.7 ± 0.3	6.5 ± 0.2	2.34 ± 0.11	—	—	10.7 ± 0.3	6.0 ± 0.4
<i>L. bilineata</i>	ter	90.4 ± 1.8	98.2 ± 1.2	11.8 ± 0.2	11.2 ± 0.8	2.68 ± 0.23	276.6 ± 30.18	0.28 ± 0.05	23.3 ± 0.1	14.5 ± 1.1
<i>A. scutellatus</i>	ter	—	—	—	—	2.80 ± 0.13	74.22 ± 7.77	0.14 ± 0.15	—	—
<i>A. pardalis</i> ^a	ter	59.0 ± 0.8	60.69	8.1 ± 0.2	6.69	2.62 ± 0.19	87.83 ± 4.36	0.32 ± 0.08	4.9 ± 0.3	1.88
<i>A. erythrurus</i>	ter	73.0 ± 1.4	—	8.2 ± 0.2	—	3.13 ± 0.14	—	—	8.4 ± 0.4	—
<i>L. longicaudata</i>	ter	90.4 ± 3.1	76.6 ± 3.25	9.5 ± 0.3	7.9 ± 0.2	3.34 ± 0.17	51.71 ± 4.47	1.05 ± 0.19	7.0 ± 1.2	4.6 ± 0.4

^a Data for one female included in the analyses.

Table 14.3 *Proportion of different prey types present in the diet of the lacertid species included in this study*

Proportions per category according to evasiveness (evasive [evas], intermediate [int e], sedentary [sed]) and hardness (hard, intermediate [int h], soft).

species	evasiveness			hardness		
	evas	int e	sed	hard	int h	soft
<i>G. galloti</i>	0.069	0.262	0.651	0.438	0.487	0.088
<i>P. algirus</i>	0.145	0.345	0.502	0.548	0.040	0.403
<i>P. hispanicus</i>	0.147	0.294	0.534	0.429	0.032	0.519
<i>L. oxycephala</i>	0.009	0.801	0.176	0.835	0.035	0.127
<i>L. vivipara</i>	0.434	0.150	0.415	0.196	0.023	0.781
<i>P. melisellensis</i>	0.111	0.532	0.271	0.569	0.078	0.203
<i>P. hispanica</i>	0.325	0.363	0.309	0.655	0.015	0.328
<i>P. muralis</i>	0.256	0.347	0.387	0.524	0.050	0.415
<i>P. tiliguerta</i>	0.368	0.276	0.333	0.460	0.058	0.460
<i>P. sicula</i>	0.227	0.355	0.365	0.418	0.114	0.415
<i>P. lilfordi</i>	0.025	0.589	0.378	0.949	0.015	0.028
<i>L. bilineata</i>	0.148	0.365	0.371	0.488	0.330	0.066
<i>A. pardalis</i>	0.051	0.532	0.405	0.886	0.038	0.064
<i>A. erythrurus</i>	0.080	0.774	0.144	0.723	0.015	0.260

Harris and Arnold 1999) (Fig. 14.1). Since no information is available on divergence times, we set all branch lengths to unity.

In subsequent statistical analyses, we tested how the speed–endurance trade-off and the (potential) bite force – climbing speed trade-off affect the dietary niche of lacertid lizards. In the former case, we hypothesized that (1) sprint speed is positively correlated with the proportion of evasive prey and/or prey of intermediate evasiveness and (2) endurance is positively correlated with the proportion of sedentary prey taken; in the latter case we hypothesized that (3) bite force and climbing speed are negatively correlated, mediated by differences in head height; (4) bite force is negatively correlated with the proportion of soft prey items present, whereas climbing speed is positively correlated with the proportion of soft prey. Because head shape and bite force are known to be sexually dimorphic in lacertid lizards (see, for example, Olsson and Madsen, 1998; Herrel *et al.*, 1999, 2001c, 2004), all analyses including these traits are done for males and females separately. To test hypotheses (1), (2), and (4), we performed regressions through the origin with one of the performance traits as dependent variable and one of the diet traits as independent variable. To test the trade-off hypothesis (3) we first calculated the residuals of the contrasts in bite force, climbing speed, and head height against the contrasts in SVL. We took

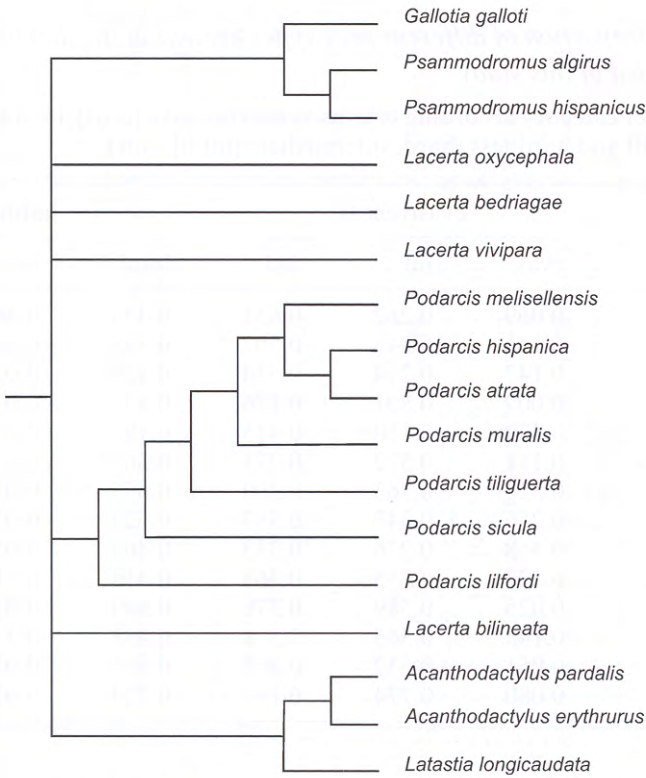


Figure 14.1. Phylogenetic relationships among the lacertid lizard species used in this study. Topology is based on both morphological and molecular data (see text for references); branch lengths are not to scale.

SVL into account in the latter analysis, because we were particularly interested in how shape (i.e. head shape) differences affect performance and whether both performance traits are related irrespective of known interspecific differences in SVL. We subsequently performed regressions through the origin of the residual contrast in bite force against the residual contrast in climbing speed, and of each of those against the residual contrast in head height.

Results and discussion

All bivariate correlations (Spearman rank) between the raw performance and diet data (log₁₀ transformed) and between residual head height, climbing speed, and bite force are given in Appendixes 14.1 and 14.2, respectively. The results from regression analyses on the same variables but taking into account phylogenetic relatedness among the different species, are shown in Appendixes 14.3 and 14.4, respectively. In this chapter, however, we limit

ourselves to discussing the results related to the four specific hypotheses put forward in the sections above.

Speed–endurance trade-offs and dietary niche

Contrary to our expectations, the contrasts in sprint speed are negatively correlated with the contrasts in the proportion of evasive prey present in the diet ($r = -0.54$, $F_{1, 12} = 5.02$, $p = 0.045$). However, there is a tendency for the contrasts in the proportion of intermediate evasive prey present to be positively correlated with the contrasts in sprint speed ($r = 0.46$, $F_{1, 12} = 3.19$, $p = 0.099$). The contrasts in endurance, on the other hand, tend to be positively correlated with the contrasts in the proportion of sedentary prey present in the diet ($r = 0.69$, $F_{1, 6} = 5.37$, $p = 0.060$) (Fig. 14.2).

Thus, among lacertid lizards, endurance capacity and eating sedentary prey tend to co-evolve. This is not unexpected as lizards need to move around frequently to encounter this type of prey, and to do so great stamina is required (Garland, 1999). Moreover, it further corroborates the idea that sedentary and clumped prey items are mostly eaten by widely foraging species, which in turn

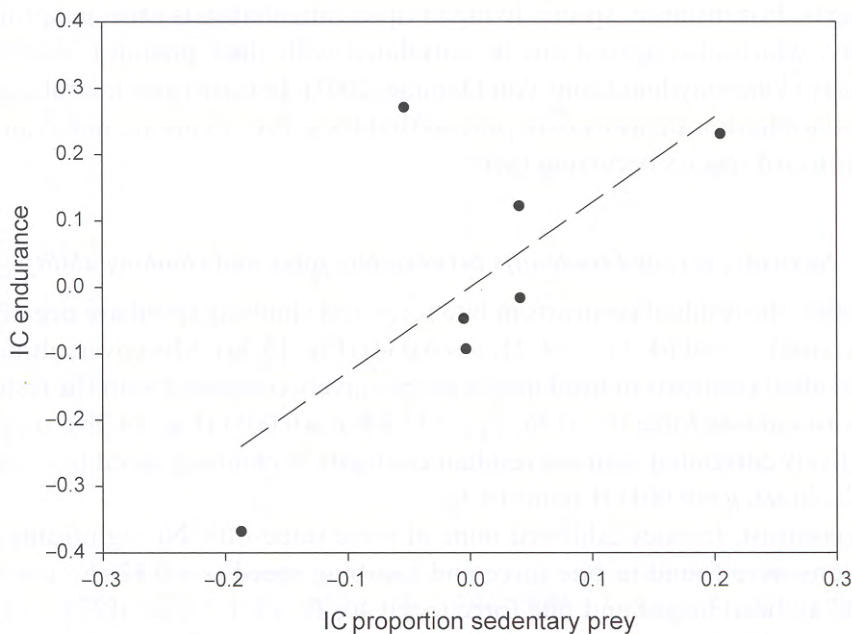


Figure 14.2. Plot of independent contrasts (IC) of endurance against the independent contrasts of the proportion of sedentary prey present in the samples. Among lacertids, eating sedentary prey tends to co-evolve with endurance capacity ($r = 0.69$, $p = 0.060$).

appear to have great stamina (Huey and Pianka, 1981; McBrayer, 2004). Sprint speed, on the other hand, seems to have co-evolved with eating evasive prey but in a way opposite to that predicted: a small increase in sprint speeds results in eating more evasive prey. Clearly, among lacertids, maximal sprint speed does not seem to determine the capacity to capture evasive prey items. Sprint speed, however, does seem relevant for catching prey classified as of “intermediate evasiveness.” Possibly, to catch evasive prey, predator acceleration capacity is more important than sprint speed *per se*. The prey items we categorized as “evasive” are prey that typically jump or fly (e.g. flies, dragonflies, grasshoppers) (see Table 14.1). Because no pursuit is possible, at least not by lizards, these prey types can only be captured by very short, quick dashes of movement from a standstill. Prey items classified as of “intermediate evasiveness”, on the other hand, typically escape by running away (e.g. bugs, beetles, ants, centipedes) (see Table 14.1) and thus they may be captured after a prolonged, fast chase. The negative correlation between the proportion of evasive prey and sprint speed in these lizards is in itself suggestive of a trade-off between sprint speed and acceleration capacity. Unfortunately no data on acceleration capacity in lacertids are available to test this hypothesis.

In addition, sprint speed in lacertids might be selected for in other ecological contexts. For instance, species living in open microhabitats excel in sprinting ability, which also appears to be correlated with their predator avoidance strategy (Vanhooydonck and Van Damme, 2003). In turn, open microhabitats might not harbor many evasive prey so that these prey items are not available to the lizard species occurring there.

Saxicoly, sex, and trade-offs between bite force and climbing ability

In males, the residual contrasts in bite force and climbing speed are negatively correlated ($r = -0.64$, $F_{1,9} = 6.21$, $p = 0.034$) (Fig. 14.3a). Moreover, although the residual contrasts in head height are positively correlated with the residual contrasts in bite force ($r = 0.78$, $F_{1,9} = 13.81$, $p = 0.005$) (Fig. 14.3b), they are negatively correlated with the residual contrasts in climbing speed ($r = -0.84$, $F_{1,9} = 20.80$, $p = 0.001$) (Figure 14.3c).

In contrast, females exhibited none of these trade-offs. No significant correlations were found in bite force and climbing speed ($r = 0.12$, $F_{1,9} = 0.12$, $p = 0.74$), head height and bite force ($r = 0.40$, $F_{1,9} = 1.73$, $p = 0.22$), or head height and climbing speed ($r = -0.50$, $F_{1,9} = 3.02$, $p = 0.12$).

In male lacertid lizards, bite force and climbing ability trade-offs appear to be because of the differential effect of head height on either performance trait. Whereas males with higher heads are able to generate more bite force, males

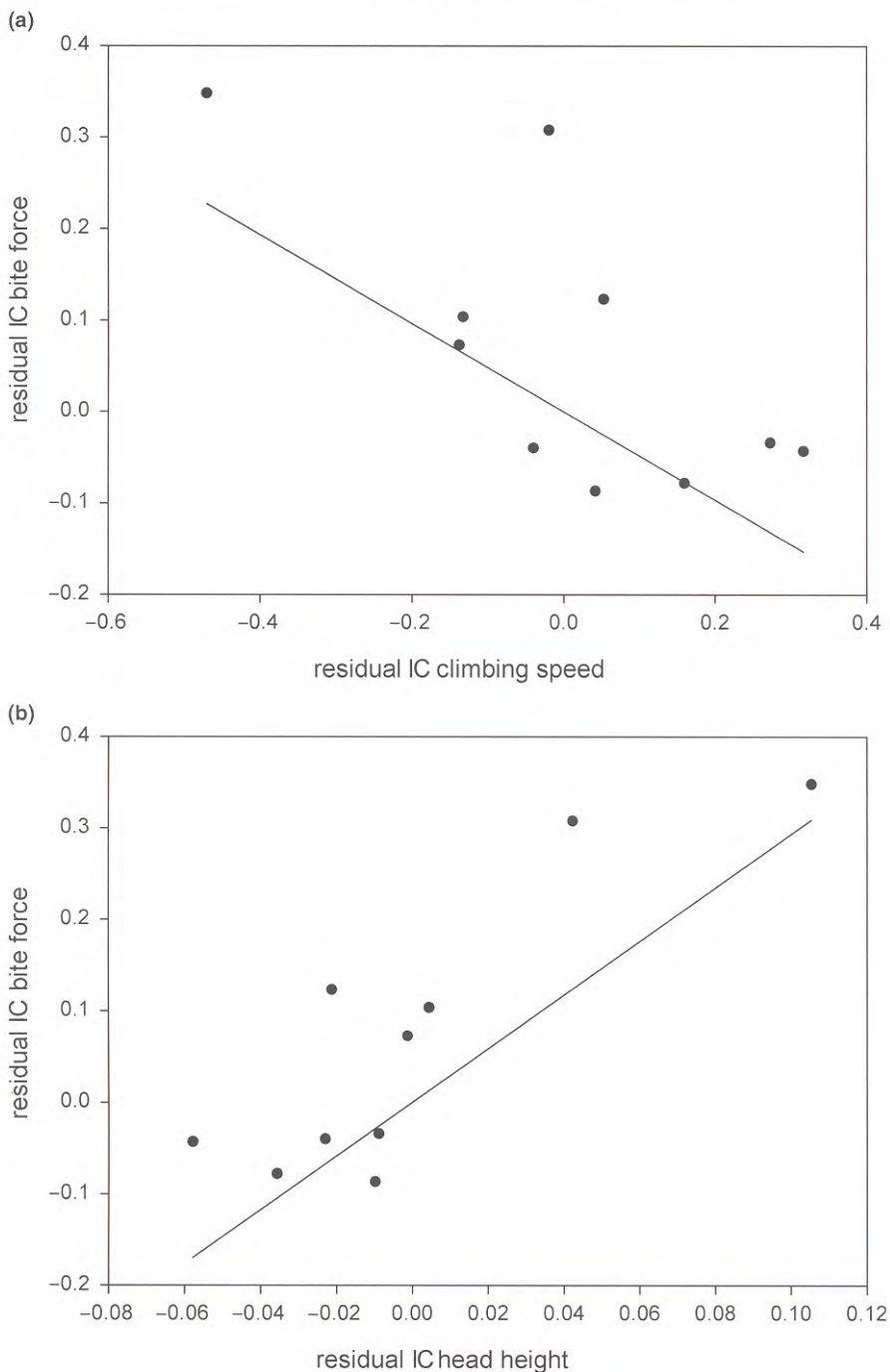


Figure 14.3. Relations between bite force, climbing speed and head height in male lacertid lizards. (a) Plot of residual contrasts in bite force against residual contrasts in climbing speed. Bite force and climbing speed trade-off

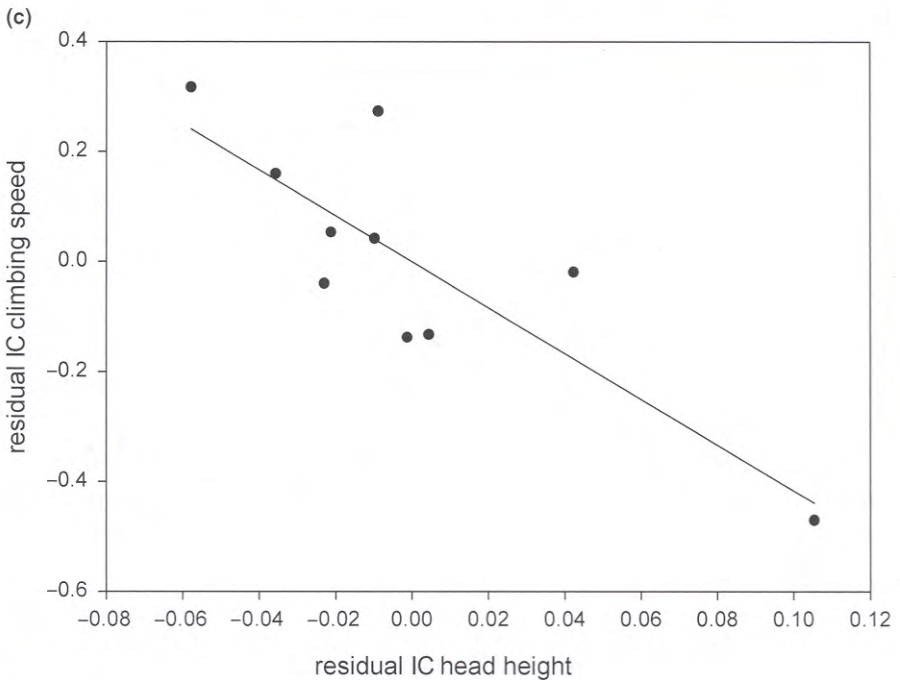


Figure 14.3. (cont.)

($r = -0.64$, $p = 0.030$). (b) Plot of residual bite force against residual head height. An increase in head height results in an increase in bite force ($r = 0.78$, $p = 0.005$). (c) Plot of residual climbing speed against residual head height. An increase in head height results in a decrease in climbing ability ($r = -0.84$, $p = 0.001$).

with lower heads seem to be faster climbers. The fact that head height is positively correlated with bite force is not surprising. Even more so, head dimensions have been previously shown to be determinant of bite force not only in lacertids, or lizards in general (Herrel *et al.*, 1999, 2001a, c), but in a wide range of taxonomic groups, such as bats (Aguirre *et al.*, 2002), birds (Herrel *et al.*, 2005), and turtles (Herrel *et al.*, 2002b). When climbing up steep inclines, on the contrary, having a shallow head could be advantageous. Having a tall head may shift the centre of mass (COM) of the head segment relative to the position of the COM of the body segment. This in turn would generate a moment arm (i.e. head COM and body COM are no longer aligned) resulting in a torque around the (overall) centre of mass away from the substrate (Fig. 14.4c). Because of this torque the upper part of the body will be pulled away from the substrate, causing the animals to topple backwards. The COM of a shallow head, on the contrary, is shifted relative to the COM of the body so that a counterclockwise torque may be generated (Fig. 14.4a).

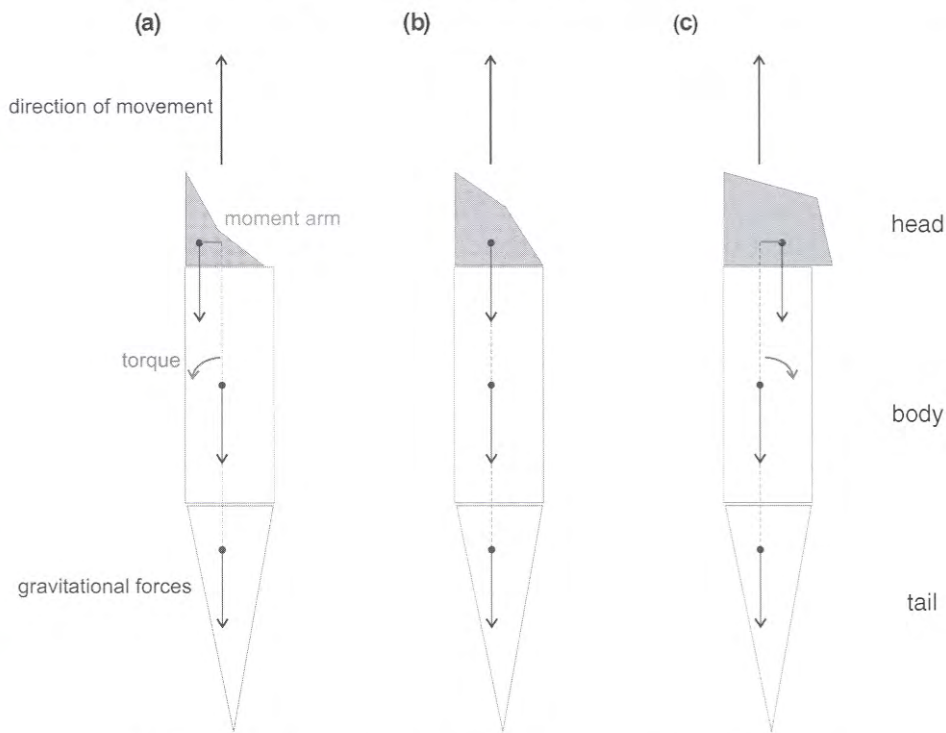


Figure 14.4. Free-body representation of a lizard moving up a vertical incline. Gravitational forces (arrows pointing down) act opposite to the direction of movement (arrows pointing up). The hypothetical COMs of the head, body and tail segment are represented by black circles. Torques are represented by arrows; moment arms by short lines. (a) Shallow heads could potentially result in a counterclockwise torque, pulling the upper part of the body towards the substrate. (b) If the COMs of the segments are in line, no torque is generated (moment arm = 0). (c) Tall heads, on the other hand, may result in a clockwise torque, pulling the upper part of the body away from the substrate.

A counterclockwise torque will pull the upper part of the body towards the substrate, thus preventing climbing animals from falling backwards (Cartmill, 1985; Pounds, 1988; Miles, 1994). Although in some lizard families saxicolous and arboreal species tend to have lower heads and/or bodies, and use a more sprawling gait to lower their stance than their terrestrial sister species (Vanhooydonck and Van Damme, 1999; Herrel *et al.*, 2001b, 2002a; Zaaf *et al.*, 2001; Bickel and Losos, 2002; Spezzano and Jayne, 2004), to our knowledge this is the first study that shows a significant correlation between head shape and climbing performance.

If we consider climbing ability and bite force in female lacertid lizards, we do not find evidence for a trade-off. The lack of a trade-off in females might be

due to the fact that head height does not detrimentally affect climbing performance in females. We hypothesize that differential selection on head dimensions exists between males and females. Head shape in lacertids is sexually dimorphic, with males typically having larger heads than females (Molina-Borja *et al.*, 1997; Olsson and Madsen, 1998; Herrel *et al.*, 1999, 2001c, 2004; Verwaijen *et al.*, 2002; Gvozdik and Van Damme, 2003). The larger head, through its effect on bite force, in males is advantageous both during male-male contests (winners have larger heads) (Molina-Borja *et al.*, 1997; Gvozdik and Van Damme, 2003) and during matings, as males with larger heads are able to grasp females faster (Gvozdik and Van Damme, 2003). Male head size thus appears to be under strong sexual (directional) selection. In saxicolous species, however, the selection for high heads is countered by (natural) selection for lower heads. This does not seem to hold true for females. Possibly, the lower heads in females do not impede climbing ability as they are too low to cause a substantial torque around the centre of mass for the animal. Thus, it seems plausible that a threshold for head height may need to be reached before its negative effects on locomotion are observed. Although some interspecific variation in relative head height exists among females, none of their head heights might actually reach this threshold, thus explaining the absence of a correlation between head height and climbing speed. A plot of residual climbing speed against residual head height for both males and females (Fig. 14.5) suggests that the variation in residual head height is lower in females as compared with males and that head height detrimentally affects climbing ability only after a certain threshold has been reached (dotted line on Fig. 14.5).

That the above trade-off is indeed an ecologically relevant one is suggested by the analysis of diet: in males, the contrasts in bite force are negatively correlated with the proportion of soft prey eaten ($r = -0.62$, $F_{1, 12} = 7.51$, $p = 0.018$) (Fig. 14.6). This suggests that an increase in bite force has co-evolved with eating fewer soft prey items. Similarly, the contrasts in female bite force tend to be negatively correlated with the proportion of soft prey present in the sample ($r = -0.53$, $F_{1, 11} = 4.35$, $p = 0.061$). The contrasts in climbing speed, however, are not correlated with the contrasts in the proportion of soft prey ($r = -0.003$, $F_{1, 6} = 0.0001$, $p = 0.99$).

Our *a priori* prediction that fast climbers should eat proportionally more soft-bodied prey, and have lower bite force, is based on optimal foraging theory (McArthur and Pianka, 1966; Schoener, 1971; Arnold, 1993; Emerson *et al.*, 1994; Roughgarden, 1995). Optimal foraging theory posits that animals should balance the costs and benefits of feeding bouts by selecting those prey items that can be efficiently processed and have a high caloric content. Because an increase in bite force reduces the time it takes to subdue prey (Herrel *et al.*, 1999;

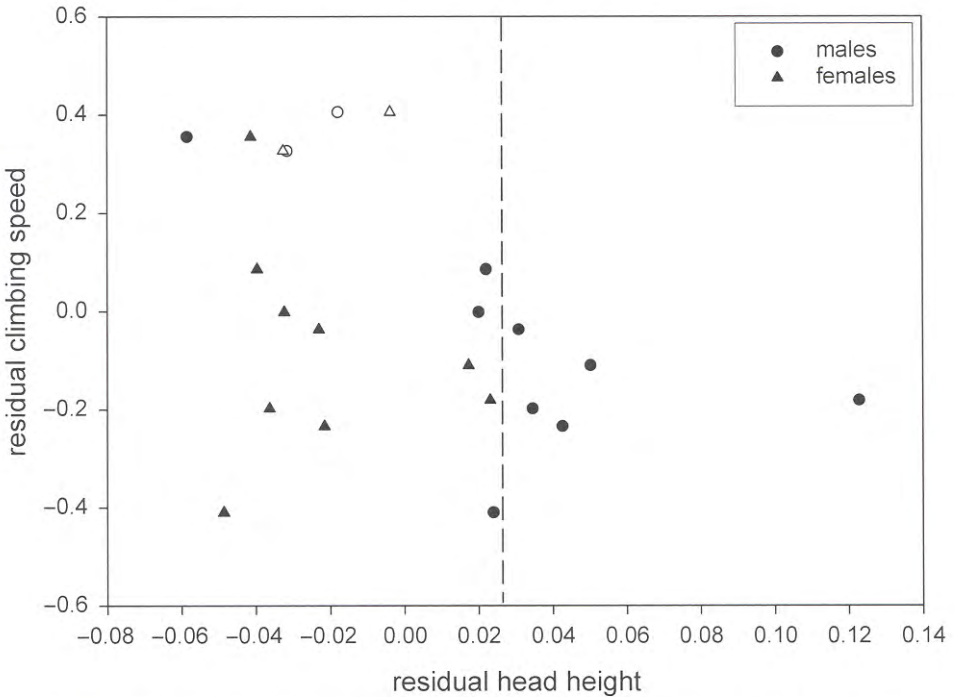


Figure 14.5. Plot of residual climbing speed against residual head height in males (circles) and females (triangles). At a residual head height of about 0.03, climbing speed drops off dramatically (dotted line), corroborating our hypothesis that head height detrimentally affects climbing speed after a certain threshold has been reached. In females, residual head height falls below this threshold. Open symbols refer to saxicolous species.

Verwajen *et al.*, 2002), tougher prey become energetically more interesting for animals with great bite strength. This idea is corroborated by the fact that bite force and proportion of soft-bodied prey are negatively correlated among lacertids. The increased handling times of tough prey items (at least for species with decreased bite strength), however, do not seem to prevent fast climbers from eating them. Indeed, prey selection experiments in two lacertid species showed that, despite a large difference in bite capacity, both species preferred the largest of the available prey items (Herrel *et al.*, 2001c). Possibly, the cost of an increased handling time does not outweigh the energetic benefit of eating a large and/or tough prey item. In addition, prey availability may differ among microhabitats (see also above). For instance, when comparing food availability for two sympatric species with a distinct microhabitat use, *L. oxycephala* and *P. melisellensis*, it was found that soft-bodied prey were much more common among the vegetation, and thus available to the latter species, than they were on the stone walls, home to the former species (Verwajen *et al.*, 2002). Although it

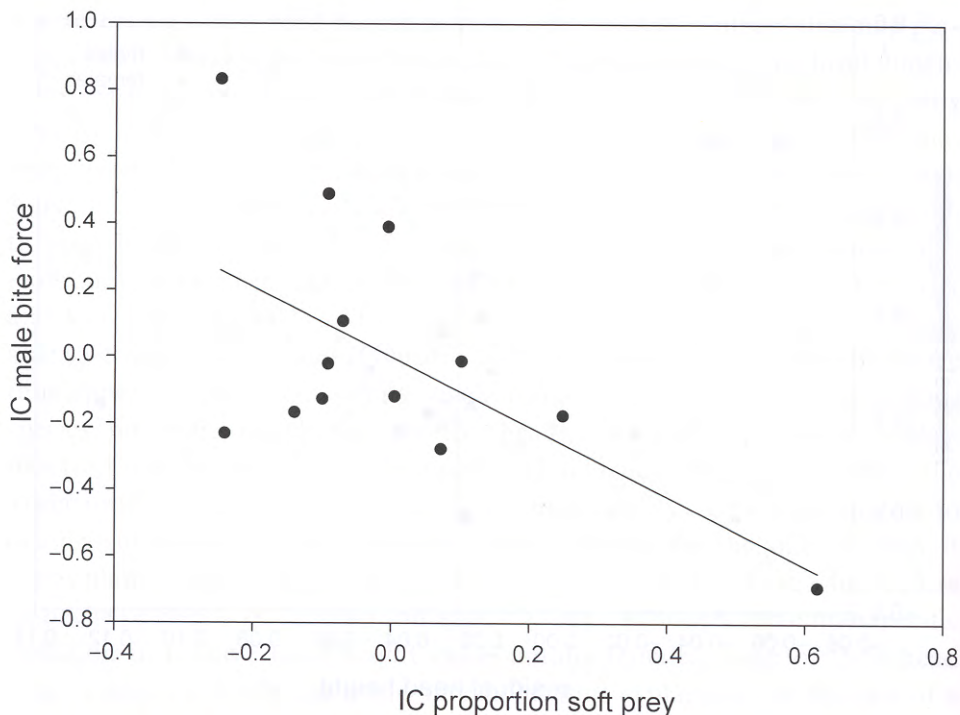


Figure 14.6. Plot of independent contrasts (IC) in bite force against the independent contrasts in proportion of soft prey present in the male samples. A decrease in proportion of soft prey eaten is paralleled by an increase in bite force ($r = -0.62$, $p = 0.018$). Similar results were found when considering females only.

is unclear at the moment how general this pattern of differential prey availability is, it may explain why typical rock climbing species eat less soft-bodied prey.

Conclusions

We found at least some indications that functional trade-offs among performance traits (speed vs. endurance and bite force vs. climbing speed) might be important in the evolution of foraging strategies and the feeding ecology of lacertid lizards. However, detailed data on rates and patterns of movement in a whole suite of species (specifically for the European clade within Lacertidae) are required to further test this hypothesis. In addition, our results clearly show the need for quantification of functionally relevant traits of different prey types (e.g. hardness, escape speed) to directly link these prey-specific performance traits to the predator's performance capacity. Lastly, data on prey availability are largely lacking. However, to be able to interpret dietary

differences, for instance among species with distinct microhabitat usage, it is of prime importance to know which prey items are actually available to each predator.

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Appendix 14.1 *Non-parametric bivariate correlations (Spearman Rank) between the performance and diet variables*

Correlations between bite force and diet are given for the sexes separately. Significant correlations (at the $p = 0.05$ level) are shown in bold.

		diet					
		evasiveness			hardness		
		evas	int e	sed	hard	int h	soft
sprinting	<i>r</i>	−0.39	0.56	−0.15	0.60	−0.17	0.29
	<i>p</i>	0.16	0.04	0.62	0.02	0.56	0.49
	<i>n</i>	14	14	14	14	14	14
endurance	<i>r</i>	0.52	− 0.76	0.48	− 0.88	0.31	0.36
	<i>p</i>	0.18	0.03	0.23	0.004	0.46	0.39
	<i>n</i>	8	8	8	8	8	8
climbing	<i>r</i>	−0.02	0.19	− 0.74	0.07	−0.52	0.29
	<i>p</i>	0.96	0.65	0.04	0.87	0.18	0.49
	<i>n</i>	8	8	8	8	8	8
bite force, males	<i>r</i>	−0.30	0.17	0.16	0.20	0.35	− 0.60
	<i>p</i>	0.19	0.55	0.58	0.48	0.22	0.02
	<i>n</i>	14	14	14	14	14	14
bite force, females	<i>r</i>	−0.28	0.14	0.18	0.15	0.43	− 0.60
	<i>p</i>	0.36	0.64	0.57	0.62	0.14	0.03
	<i>n</i>	13	14	13	13	13	13

Appendix 14.2 *Non-parametric bivariate correlations (Spearman Rank) between residual head height, residual climbing speed, and residual bite force for males and females separately*

Significant correlations (at the 0.05 level) are shown in bold.

Males		residual climbing	residual bite force
residual head height	<i>r</i>	-0.75	0.67
	<i>p</i>	0.008	0.02
	<i>n</i>	11	11
residual climbing	<i>r</i>		-0.71
	<i>p</i>		0.02
	<i>n</i>		11
Females		residual climbing	residual bite force
residual head height	<i>r</i>	0.17	0.37
	<i>p</i>	0.61	0.26
	<i>n</i>	11	11
residual climbing	<i>r</i>		0.06
	<i>p</i>		0.87
	<i>n</i>		11

Appendix 14.3 *Regressions through the origin on the independent contrasts of the performance variables against the independent contrasts of the diet variables*

Regressions of the independent contrasts of bite force against the independent contrasts in the diet variables are given for each sex separately. Significant relationships at the $p = 0.05$ level are shown in bold; significant relations at the $p = 0.10$ level are shown in italic.

		diet					
		evasiveness			hardness		
performance		evas	int e	sed	hard	int h	soft
sprinting	<i>r</i>	-0.54	<i>0.46</i>	-0.26	0.58	0.20	-0.72
	<i>p</i>	0.05	<i>0.10</i>	0.38	0.03	0.50	0.004
	<i>n</i>	13	<i>13</i>	13	13	13	13
endurance	<i>r</i>	<i>0.67</i>	-0.85	<i>0.69</i>	-0.98	0.53	0.54
	<i>p</i>	<i>0.07</i>	0.008	<i>0.06</i>	<0.0001	0.18	0.16
	<i>n</i>	7	7	7	7	7	7
climbing	<i>r</i>	-0.33	0.79	<i>-0.69</i>	0.53	-0.50	-0.003
	<i>p</i>	0.43	0.02	<i>0.06</i>	0.18	0.21	0.99
	<i>n</i>	7	7	7	7	7	7
bite force, males	<i>r</i>	-0.36	-0.001	0.30	0.08	0.83	-0.62
	<i>p</i>	0.21	0.99	0.30	0.79	<0.0001	0.02
	<i>n</i>	14	14	14	14	14	14
bite force, females	<i>r</i>	-0.27	-0.12	0.46	-0.02	0.83	<i>-0.53</i>
	<i>p</i>	0.37	0.69	0.11	0.96	<0.0001	<i>0.06</i>
	<i>n</i>	13	13	13	13	13	<i>13</i>

Appendix 14.4 Regressions through the origin on the residual independent contrasts of head height, climbing speed and bite force for males and females separately

Significant relations (at the $p = 0.05$ level) are shown in bold.

Males		residual climbing	residual bite force
residual head height	<i>r</i>	-0.84	0.78
	<i>p</i>	0.001	0.005
	<i>n</i>	10	10
residual climbing	<i>r</i>		-0.64
	<i>p</i>		0.03
	<i>n</i>		10
Females		residual climbing	residual bite force
residual head height	<i>r</i>	-0.50	0.40
	<i>p</i>	0.12	0.22
	<i>n</i>	10	10
residual climbing	<i>r</i>		0.12
	<i>p</i>		0.74
	<i>n</i>		10