

Origins of interspecific variation in lizard sprint capacity

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Summary

1. Data were compiled on maximal sprint speed, body mass and temperature in squamate lizards from the literature and from our own data on lacertid lizards.
2. Both traditional (i.e. non-phylogenetic) and phylogenetic statistical analyses showed that sprint speed is positively correlated with body mass ('bigger is better') and temperature ('hotter is better').
3. Additionally, we tested whether sprint speed correlates with behavioural and ecological characteristics, i.e. foraging mode (sit-and-wait or active), activity (diurnal or nocturnal), microhabitat use (saxicolous, arboreal or terrestrial) and climate (Mediterranean, xeric, cool or temperate). Lizards from Mediterranean and xeric climates, diurnal lizards, sit- and wait predators and terrestrial species are expected to run the fastest. Traditional tests suggest that lizards from Mediterranean and desert areas are faster than lizards from cool and tropical regions; that diurnal species are faster than nocturnal species; and that saxicolous animals have higher sprint capacities than do arboreal and terrestrial species. No difference was found between sit-and-wait predators and actively foraging animals.
4. However, the effects of climate, activity period and microhabitat use were no longer significant when the data were analysed in a proper phylogenetic context. This seems to suggest that differences in sprint speed reflect phylogeny, rather than ecology. The discrepancy between the results of phylogenetic and traditional analyses forms a strong case for the use of phylogenetic information in comparative studies.

Key-words: Ecomorphology, evolution, locomotion, sprint performance

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Introduction

Lizard species differ substantially in locomotor capacities, and several studies have addressed the mechanistic or evolutionary bases of this variation (Huey & Bennett 1987; Losos 1990; Garland 1994; Miles 1994; Bauwens *et al.* 1995; Zani 1996; Van Damme, Aerts & Vanhoooydonck 1998; Bonine & Garland 1999). In an extensive comparative study of treadmill endurance, Garland (1994) identified body mass and temperature as important proximate causes of the variation among 57 species and subspecies of lizards. Garland (1994) suggested habitat heterogeneity, availability of cover and prey or predator abundance as potential evolutionary determinants of stamina, but was unable to find strong statistical evidence for this assertion. Possibly, this was due to the lack of detailed quantitative ecological and behavioural data on the species under study.

While several studies have compared sprint speeds of species within restricted clades of lizards (e.g. Lacertidae: Bauwens *et al.* 1995; Phrynosomatidae: Miles 1994; Bonine & Garland 1999), no study has yet considered the interspecific variation in sprinting capacity on a

taxonomical level comparable to that of Garland's study of endurance capacity. Sprint speed is considered ecologically relevant in lizards, because it may affect fitness via its effects on predator escape success (Christian & Tracy 1981; Jayne & Bennett 1990), foraging success (Greenwald 1974; Webb 1984) and social dominance (Garland *et al.* 1990). In this paper, we combine data on sprint speed of lizards available in the literature with our own data for lacertid lizards. We investigate the importance of body mass and temperature as proximate causes of interspecific variation in sprint speed. We also test whether sprint speed correlates with ecological or behavioural characteristics, namely climate, activity (diurnal/nocturnal), microhabitat use and foraging mode.

While most intraspecific studies on lizards find some positive relationship between body size and speed (e.g. Garland 1985, 1994), the scaling of sprint speed remains equivocal in interspecific comparisons (Garland 1994). For instance, snout–vent length and sprint speed have evolved together in Caribbean *Anolis* (Losos 1990b), but not in Costa Rican *Anolis* (van Berkum 1986). Evolutionary changes in body length were not correlated with changes in sprint speed among 13 lacertid lizards (Bauwens *et al.* 1995) or among 27 species of phrynosomatid lizards (Bonine & Garland 1999). However, Zani (1996) reported a strong correlation between

sprint speed and snout–vent length in a data set consisting of 39 lizard species from 11 families.

The ‘hotter is better’ hypothesis (Huey & Kingsolver 1989) predicts a positive relationship between maximal performance of organisms and optimal temperatures. The hypothesis is based on the thermodynamic principle that biochemical and physiological systems operating at high temperatures have potentially high catalytic capacity. Bauwens *et al.* (1995) corroborated this idea: the optimal temperature of 13 species of lacertid lizards was positively correlated with maximum running speed.

Climate could affect sprinting capacity in many ways. Lizards living in different climates are subject to different environmental temperatures and have different opportunities for thermoregulating. They are faced with different numbers of prey and predators, and probably have different opportunities to hide from them. We will use a very coarse classification of climates here (cool, Mediterranean, tropical and xeric). Considerations about thermal conditions and habitat structure incline us to predict that lizards from xeric and Mediterranean climates will run faster than lizards from cool or tropical climates.

Nocturnal lizards are confronted with different kinds and, possibly, numbers of prey and predators than diurnal lizards. This may affect the intensity of selection on sprint capacities. Although never tested explicitly, it has been suggested that relatively low predation pressure and high overall capture rate of nocturnal prey has resulted in low speeds of night-active lizards (Huey & Pianka 1983; Huey & Bennett 1987). Thermal considerations also predict lower sprint capacities in nocturnal lizards. At night, the absence of short-wave solar radiation hinders behavioural thermoregulation, and therefore nocturnal lizards are often forced to be active at relatively low and variable body temperatures (Huey *et al.* 1989; Autumn, Weinstein & Full 1994). In response, their thermal physiology may evolve in two (not mutually exclusive) ways. The first option is a reduction of the optimal temperature (but see Autumn *et al.* 1999). According to the ‘hotter is better’ hypothesis, such a shift should come with a reduction in maximal performance (see above). The second option is a broadening of the thermal performance breadth, so that near-maximal sprinting is allowed at a wider range of temperatures. In this case, the putative trade-off between maximal performance and thermal breadth of performance (the ‘jack-of-all-temperatures’ hypothesis, Huey & Hertz 1984) will reduce locomotor performance. In view of these considerations, we expect nocturnal lizards to have lower sprint capacities than diurnal lizards (but see Autumn *et al.* 1994, 1997).

Many lizard species tend to specialize in using particular (micro) habitats. It is often assumed that specialism in one microhabitat will go at the expense of reduced fitness in other microhabitats (Losos 1990; Garland 1994). This will eventually lead to ‘ecomorphs’: species that are morphologically adapted to, and therefore perform best in, the specific microhabitat they

occupy (e.g. Losos & Sinervo 1989; Sinervo & Losos 1991). Owing to the way it is usually measured (on level racing tracks or moving belts), maximal sprint speed primarily constitutes a predictor of speed capacity on smooth, level terrain without obstacles. This may not be relevant for species that are primarily arboreal or saxicolous, or live in densely vegetated areas. Moreover, it has been argued that trade-offs between locomotor abilities (e.g. climbing capacity, manoeuvrability, sure-footedness) and horizontal running speed may reduce maximal running capacity of non-cursorial lizards (Hildebrand 1982; Cartmill 1985; Losos & Sinervo 1989; Sinervo & Losos 1991; Losos, Walton & Bennett 1993; but see Van Damme *et al.* 1998). We therefore predict that microhabitat use will influence maximal running speed.

Foraging strategy is also thought to influence sprint capacities in lizards. Lizard species are traditionally classified either as ‘sit-and-wait’ or as ‘active foragers’ (Pianka 1966; Schoener 1971; Regal 1983). The former group is expected to have greater sprinting capacities, while the latter should have greater endurance (Garland 1994). Here also, the notion of trade-off (between speed and endurance) is implicit. One study (Huey *et al.* 1984) corroborates this hypothesis.

Methods

SPRINT SPEED MEASUREMENTS

Several methods have been used to measure maximal sprint speed in lizards. Most studies use a racetrack equipped with photocells positioned at set intervals (see Huey *et al.* 1981; Miles & Smith 1987 for descriptions). Racetracks differ among studies in length, substrate, inclination and distance between the photocells. The length of the tracks varies between 1 and 6 m, but most studies use tracks between 2 and 3 m long. It is unclear exactly how long a track should be to obtain reliable maximal speeds. Sprinting in lizards is usually explosive, and animals will reach their top velocity within milliseconds of their departure (Huey & Hertz 1982; Irschick & Jayne 1998). The substrate used also varies, but most studies employ materials that are thought to provide good traction (e.g. rubber, cork, foam board, sandpaper, window screening, linen cloth, rough-cut hardwood). Other studies, especially of desert lizards, prefer sand because it would better resemble the natural substrate of the animals. The effects of substrate on running speed have seldom been tested explicitly. Running speeds of *Uma scoparia* on sandy and rubberized substrates proved highly similar (Carothers 1986). Some lizards, for unknown reasons, seem to run more readily on substrates that are (slightly) inclined. Therefore, a number of authors tilt their racetrack to some degree (van Berkum 1986; Losos *et al.* 1989, 1991; Losos 1990; Irschick & Losos 1998). The distance between the photocells is usually 0.25 or 0.5 m.

A second category of studies uses tracks similar to the racetracks mentioned above, but uses different

ways to measure the speed of the lizards. Some have used stopwatches (e.g. Snell *et al.* 1988; Losos *et al.* 1993; Zani 1996; Klukowski, Jenkinson & Nelson 1998), others have filmed or videotaped the lizards (e.g. Daniels 1983; Avery *et al.* 1987; Farley 1997; Márquez & Cejudo 1999). In the latter case, it is often unclear over what distance the speed was calculated.

Finally, several studies use high-speed treadmills (John-Alder, Garland & Bennett 1986; Beck *et al.* 1995; Dohm *et al.* 1998; Bonine & Garland 1999; Irschick & Jayne 1999). The speed of the belt is varied until it matches the apparent maximal running speed of the lizard. Alas, studies with high-speed treadmills often yield higher estimates of maximal sprint speed than do studies with photocell-timed racetracks (see Table 6 in Bonine & Garland 1999). Therefore, we choose not to use treadmill estimates of speed in our analysis.

Body temperature has a profound effect on sprint speed (e.g. Bennett 1980; Crowley 1985; Marsh & Bennett 1986; van Berkum 1986, 1988; Van Damme *et al.* 1989, 1990; Bauwens *et al.* 1995), and maximal running speed will be attained only at near-optimal body temperatures. Most authors acknowledge this fact and state that lizards were tested at optimal temperatures, or at temperatures close to that of animals in the field. In the latter case, it is assumed that animals in the field are active at near-optimal body temperatures. This may not always be true, but (at least in diurnal lizards, see Huey *et al.* 1989), field body temperatures are probably a good proxy for optimal body temperatures. We disregard data from one older study (Urban 1965) because the author admits that the temperatures of the animals in his photographic cage were not controlled.

Sprint speed may also vary with age (e.g. Garland 1985; van Berkum *et al.* 1989; Carrier 1996; Elphick & Shine 1998), sex (e.g. Huey *et al.* 1990; Dohm *et al.* 1998), reproductive condition (e.g. Van Damme *et al.* 1989; Cooper *et al.* 1990), hormone levels (Klukowski *et al.* 1998), feeding status (Huey *et al.* 1984) and tail loss (e.g. Ballinger, Nietfeldt & Krupa 1979; Pond 1981; Punzo 1982; Arnold 1984; Formanowicz, Brodie & Bradley 1990; but see Daniels 1983, 1985; Huey *et al.* 1990). Many studies do not provide information on some of these factors. We will assume that their effects are small in comparison to the interspecific variation studied here. When sprint speeds of males and females of a species are given separately, we calculate the weighted average. Data from juveniles, gravid females, males with experimentally elevated testosterone concentrations and lizards without tails are not used in the analysis.

BODY MASS ESTIMATES

Some studies report the snout–vent length (SVL), rather than the mass of the animals used. In these cases, the mass is calculated from the following equation:

$$\log_{10}(m) = -1.767 + 3.201 \times \log_{10}(\text{SVL}).$$

This empirical allometric equation is based on 123 species or populations in our database, for which we had both SVL and mass. The coefficient of determination of this regression is 0.92.

TEMPERATURE DATA

The mean body temperature of animals active in the field was used to characterize the thermal biology of the species. In a few cases (see Table 1), where these data were not available, selected body temperatures were used.

ECOLOGICAL DATA

The ecological data (climate, activity, microhabitat use, foraging mode) were obtained from various sources. Apart from the papers on sprint speed themselves, these include Arnold, Burton & Ovenden (1978); Cogger (1992); Cooper (1994); Vitt *et al.* (1995, 1998); Vitt, Zani & Caldwell (1996); Leal *et al.* (1998); Vitt & Zani (1998). One species in the data set, *Amblyrhynchus cristatus*, is a herbivorous lizard. Therefore, it was not included when testing for differences in sprint speed according to foraging mode.

PHYLOGENETIC ANALYSES

In recent years it has repeatedly been stressed that comparative data need to be analysed in an explicit phylogenetic context (Felsenstein 1985, 1988; Harvey & Pagel 1991; Garland *et al.* 1993). Because species share parts of their evolutionary history, they cannot be considered independent data points in statistical analyses and thus traditional (i.e. non-phylogenetic) tests are invalid. In this study, two different approaches were used to circumvent the problem of non-independence.

To evaluate the importance of body mass and temperature in explaining interspecific variation in sprint speed, the phylogenetic independent contrasts of these three variables were calculated (PDTREE computer program, Garland *et al.* 1999). A multiple regression was then performed with sprint speed contrasts entered as the dependent variable and body mass and temperature contrasts as independent variables (SPSSwin 10.0; SPSS Inc., Chicago, IL, USA). The regression was forced through the origin (see Garland, Harvey & Ives 1992).

Phylogenetic simulations (Garland *et al.* 1993) were used to test whether sprint speed differs among sets of species with different climate (tropical, Mediterranean, xeric or cool), microhabitat use (terrestrial, arboreal or saxicolous), activity patterns (diurnal or nocturnal) and foraging mode (sit-and-wait or active foraging). In phylogenetic simulations, *F* statistics are compared with empirical *F* distributions, rather than to standard tabular values. The empirical null distributions are obtained by performing analyses of variance on the results of computer simulation models of continuous traits evolving along a known phylogenetic tree. The PDSIMUL computer programs by Garland *et al.* (1999)

Table 1. Data on maximal sprinting speeds (v , in m s^{-1}) and body mass (m , in g) of lizards, compiled from the literature. Where new names have been assigned to genera, the old names (as mentioned in the paper from which the speed data were taken) are given between parentheses. The body mass given is the mean for the animals tested. Body masses marked by an asterisk (*) were calculated from SVL (see text). Also indicated are the distance over which speed was calculated (Δs , in m), the substrate of the racetrack (sub, a, astroturf; c, cork; f, foam board; h, hardwood; r, rubber; s, sand; sp., sandpaper; w, window screening), whether the track was inclined (i: +), and the temperature at which the animals were tested (t , in °C). The temperature data used in the analyses are also listed (fbt, in °C). These are mainly mean field body temperatures (FBT) of active animals in the field, except for the cases marked by an asterisk (*), which refer to body temperatures selected in the laboratory. Finally, the climate (t, tropical; x, xeric; m, Mediterranean; c, cool), activity patterns (d, diurnal; n, nocturnal), microhabitat use (arb, arboreal; sax, saxicolous; ter, terrestrial) and foraging mode (A, actively foraging; H, herbivorous; SW, sit-and-wait predator) of the species is indicated (see references in text)

Species	v	m	t	Δs	sub	i	Reference	FBT	Reference	for	Climate	Activity	Habitat
Leiolepidinae													
<i>Leiolepis belliani</i>	2.200	40.0	35.0	0.25		+	Losos <i>et al.</i> 1989			SW	t	d	ter
Agaminae													
<i>Laudakia (Stellio) stellio</i> (Giv'at Em, Israel)	2.700	40.1	38.8	0.5	r		Hertz <i>et al.</i> 1983	36.0	Hertz <i>et al.</i> 1983	SW	m	d	sax
<i>Laudakia (Stellio) stellio</i> (Avedat, Israel)	2.400	55.1	40.6	0.5	r		Hertz <i>et al.</i> 1983	34.4	Hertz <i>et al.</i> 1983	SW	m	d	sax
<i>Laudakia (Stellio) stellio</i> (Berekhat Ram, Israel)	2.500	41.1	39.9	0.5	r		Hertz <i>et al.</i> 1983	34.1	Hertz <i>et al.</i> 1983	SW	m	d	sax
<i>Laudakia (Stellio) stellio</i> (Mt Hermon, Israel)	2.300	41.9	37.0	0.5	r		Hertz <i>et al.</i> 1983	32.9	Hertz <i>et al.</i> 1983	SW	m	d	sax
<i>Trapelus (Agama) savignyi</i>	2.700	22.0	38.4	0.5	r		Hertz <i>et al.</i> 1983	37.9	Hertz <i>et al.</i> 1983	SW	x	d	sax
<i>Ctenophorus (Amphibolurus) nuchalis</i>	2.563	13.8	40.0	0.5	r		Garland 1985	36.1	Pianka 1986	SW	x	d	ter
Chamaeleonidae													
<i>Chamaeleo dilepis</i>	0.210	20.1	30.0	0.5	a		Losos <i>et al.</i> 1993	31.2	Stebbins 1961; Pianka 1986	SW	x	d	arb
<i>Chamaeleo jacksonii</i>	0.160	22.4	30.0	0.5	a		Losos <i>et al.</i> 1993	30.0	Losos <i>et al.</i> 1993	SW	t	d	arb
Phrynosomatidae													
<i>Uma scoparia</i>	2.381	18.5		0.5	s		Carothers 1986	37.3	Pianka 1986	SW	x	d	ter
<i>Uta stansburiana</i>	1.850	3.0*	37.0	0.25	s		Miles 1994	35.3	Pianka 1986	SW	x	d	ter
<i>Petrosaurus mearnsi</i>	2.350	11.3*	37.0	0.25	s		Miles 1994	36.0	Brattstrom 1965	SW	x	d	sax
<i>Urosaurus graciosus</i>	1.770	3.6*	37.0	0.25	s		Miles 1994	36.2	Pianka 1986	SW	x	d	arb
<i>Urosaurus ornatus</i>	2.110	3.5*	37.0	0.25	s		Miles 1994	35.6	Pianka 1986	SW	x	d	arb
<i>Urosaurus microscutatus</i>	1.790	2.3*	37.0	0.25	s		Miles 1994	32.9	Pianka 1986	SW	x	d	ter
<i>Sceloporus clarkii</i>	1.890	12.0*	37.0	0.25	s		Miles 1994			SW	x	d	arb
<i>Sceloporus undulatus</i> (Colorado pop)	1.620	5.9*	41.0	0.25	r		Crowley 1985	35.1	Crowley 1985; Gillis 1991	SW	m	d	arb
<i>Sceloporus undulatus</i> (New Mexico pop)	1.730	5.6*	41.0	0.25	r		Crowley 1985	35.1	Crowley 1985; Gillis 1991	SW	m	d	arb
<i>Sceloporus undulatus hyacinthus</i>	2.140	10.0	35.0	0.25			Klukowski <i>et al.</i> 1998	35.1	Crowley 1985; Gillis 1991	SW	m	d	arb
<i>Sceloporus woodi</i>	2.480	2.8*	37.0	0.25	s		Miles 1994	36.2	Bogert 1949	SW	m	d	ter
<i>Sceloporus occidentalis</i>	1.930	7.4	34.0	0.5			Garland <i>et al.</i> 1990	35.0	Brattstrom 1965	SW	m	d	arb
<i>Sceloporus jarrovi</i>	1.730	15.3*	37.0	0.25	s		Miles 1994	35.0	Brattstrom 1965	SW	x	d	sax
<i>Sceloporus merriami</i> (from Boquillas)	1.947	4.2	33.0		r		Huey <i>et al.</i> 1990	32.8	Grant, pers. comm. in Huey <i>et al.</i> 1990	SW	x	d	sax
<i>Sceloporus merriami</i> (from Grapevine Hills)	2.123	4.8	33.0		r		Huey <i>et al.</i> 1990	32.3	Huey <i>et al.</i> 1990	SW	x	d	sax

Table 1. Continued.

Species	<i>v</i>	<i>m</i>	<i>t</i>	Δs	sub	i	Reference	FBT	Reference	for	Climate	Activity	Habitat
Polychrotidae													
<i>Anolis frenatus</i>	2.718	42.7*	30.0	0.25		+	Losos <i>et al.</i> 1991	27.6	Campbell 1971	SW	t	d	arb
<i>Anolis pulchellus</i>	1.701	1.5	30.0	0.25			Losos 1990	27.5	Heatwole <i>et al.</i> 1969	SW	t	d	arb
<i>Anolis krugi</i>	1.786	2.4		0.25	r	+	Losos 1990	16.8	Heatwole <i>et al.</i> 1969	SW	t	d	arb
<i>Anolis poncensis</i>	1.761	1.6	30.0	0.25		+	Losos 1990	33.0	Rand 1964	SW	t	d	arb
<i>Anolis gundlachi</i>	2.155	7.1		0.25	r	+	Losos 1990	22.8	Hertz 1992	SW	t	d	arb
<i>Anolis cristatellus</i>	2.155	8.1		0.25		+	Losos 1990	26.3	Hertz 1992	SW	t	d	arb
<i>Anolis stratulus</i>	1.488	1.9		0.25		+	Losos 1990	30.0	Heatwole <i>et al.</i> 1969	SW	t	d	arb
<i>Anolis evermanni</i>	1.825	5.6		0.25		+	Losos 1990	20.2	Heatwole <i>et al.</i> 1969	SW	t	d	arb
<i>Anolis carolinensis</i>	1.200	6.0	29.0	0.25	w	+	Irschick & Losos 1998	26.6	Brattstrom 1965	SW	t	d	arb
<i>Anolis humilis</i>	1.160	1.0				+	van Berkum 1986	26.4	van Berkum 1986	SW	t	d	arb
<i>Anolis lemurinus</i>	1.480	3.6				+	van Berkum 1986	25.6	Henderson & Fitch 1975	SW	m	d	arb
<i>Anolis limifrons</i>	1.320	0.9				+	van Berkum 1986	26.9	van Berkum 1986	SW	t	d	arb
<i>Anolis sagrei</i>	1.812	2.9		0.25		+	Losos 1990	33.1	Ruibal 1961	SW	t	d	arb
<i>Anolis lineatopus</i>	2.033	4.6		0.25	r	+	Losos 1990	27.6	Rand 1964	SW	t	d	arb
Iguanidae													
<i>Amblyrhynchus cristatus</i>	2.800	71.8	34.0	0.25			Miles <i>et al.</i> 1995	36.0	Bartholomew 1966	H	x	d	sax
Gekkota													
<i>Eublepharis macularius</i>	0.661	49.5	35.0	0.25	c		Zaaf <i>et al.</i> unpublished data	26.5*	Dial & Grismer 1992	A	x	n	ter
<i>Coleonyx variegatus</i>	1.530	4.4	34.0	0.25			Huey <i>et al.</i> 1989	28.4	Pianka 1986	SW	x	n	ter
<i>Coleonyx brevis</i>	1.490	1.8	37.5	0.25			Huey <i>et al.</i> 1989	28.6	Dial 1978	SW	x	n	ter
<i>Hemidactylus frenatus</i>	2.210	3.3	34.0	0.1			Huey <i>et al.</i> 1989	27.4	Huey <i>et al.</i> 1989	SW	t	n	arb
<i>Hemidactylus turcicus</i>	1.640	2.8	37.5	0.25			Huey <i>et al.</i> 1989	31.3	Huey <i>et al.</i> 1989	SW	x	n	arb
<i>Lepidodactylus lugubris</i>	1.540	1.1	37.5	0.1			Huey <i>et al.</i> 1989	29.2*	Huey <i>et al.</i> 1989	SW	t	n	arb
<i>Gekko gekko</i>	1.512	38.1	35.0	0.25	c		Zaaf <i>et al.</i> unpublished data	27.5*	Sievert & Hutchison 1988	SW	m	n	arb
<i>Christinus (Phyllodactylus) marmoratus</i>	0.970	3.7	30.0	0.1–0.3	f		Daniels 1983	21.9	Heatwole & Taylor 1987	SW	x	n	arb
<i>Gonatodes concinnatus</i>	1.040	2.3		0.5	h		Zani 1996	29.0	Fitch 1968	SW	t	d	arb

Table 1. Continued.

Species	<i>v</i>	<i>m</i>	<i>t</i>	Δs	sub i	Reference	FBT	Reference	for	Climate	Activity	Habitat
Scincidae												
<i>Mabuya variegata</i>	1.360	1.3	36.0	0.5	s	Huey 1982	33.6	Pianka 1986	A	x	d	ter
<i>Mabuya striata</i>	2.100	15.8	36.0	0.5	s	Huey 1982	34.1	Pianka 1986	A	x	d	ter
<i>Mabuya occidentalis</i>	1.730	13.7	36.0	0.5	s	Huey 1982	36.0	Pianka 1986	A	x	d	ter
<i>Mabuya spilogaster</i>	2.370	9.5	36.0	0.5	s	Huey 1982	34.5	Pianka 1986	A	x	d	ter
<i>Pseudemoia entrecasteauxii</i> , form A	1.180	4.7	34.9	0.5	r	Huey & Bennett 1987	33.2	Bennett & John-Alder 1986	A	t	d	ter
<i>Pseudemoia entrecasteauxii</i> , form B	0.890	3.3	34.9	0.5	r	Huey & Bennett 1987	33.2	Bennett & John-Alder 1986	A	t	d	ter
<i>Ctenotus uber</i>	1.650	5.4	39.3	0.5	r	Huey & Bennett 1987	35.3	Bennett & John-Alder 1986	A	x	d	ter
<i>Ctenotus taeniolatus</i>	1.180	4.5	39.3	0.5	r	Huey & Bennett 1987	35.3	Bennett & John-Alder 1986	A	m	d	sax
<i>Ctenotus regius</i>	0.990	5.5	34.9	0.5	r	Huey & Bennett 1987	36.4	in Heatwole & Taylor 1987	A	x	d	ter
<i>Eulamprus (Sphenomorphus) kosciuskoi</i>	1.040	8.3	34.9	0.5	r	Huey & Bennett 1987	30.3	Bennett & John-Alder 1986	A	m	d	ter
<i>Eulamprus (Sphenomorphus) tympanum</i>	1.490	14.4	34.9	0.5	r	Huey & Bennett 1987	29.8	Bennett & John-Alder 1986	A	m	d	ter
<i>Eulamprus (Sphenomorphus) quoyi</i>	1.520	21.1	30.0	0.5	r	Huey & Bennett 1987	29.8	Bennett & John-Alder 1986	A	m	d	ter
<i>Eremiascincus fasciolatus</i>	0.830	12.5	34.9	0.5	r	Huey & Bennett 1987	22.8	Bennett & John-Alder 1986	A	x	<i>n</i>	ter
<i>Hemiergis peronii</i>	0.490	1.5	30.0	0.5	r	Huey & Bennett 1987	21.9	Bennett & John-Alder 1986	A	m	<i>n</i>	ter
<i>Hemiergis decresiensis</i>	0.640	0.8	34.9	0.5	r	Huey & Bennett 1987	21.2	Bennett & John-Alder 1986	A	m	<i>n</i>	ter
<i>Egernia whitii</i>	1.090	25.1	37.3	0.5	r	Huey & Bennett 1987	34.1	Johnson 1977; Bennett & John-Alder 1986	A	m	d	ter
<i>Egernia cunninghami</i>	2.692	268	35.0			John-Alder <i>et al.</i> 1986	34.0	in Heatwole & Taylor 1987	A	m	d	ter
<i>Tiliqua scincoides</i>	1.069	438	35.0	0.5		John-Alder <i>et al.</i> 1986	33.5	in Heatwole & Taylor 1987	A	m	d	ter
<i>Scincella lateralis</i>	0.380	0.8		0.5	h	Zani 1996	28.8	Avery 1982	A	m	d	ter
<i>Eumeces skiltonianus</i>	0.760	5.2	25.0	0.1	sp.	Farley 1997	25.2	Cunningham 1966	A	m	d	ter
Teiidae												
<i>Cnemidophorus tigris marmoratus</i>	2.400	17.9		0.5		Cullum 1998	39.5	Pianka 1986	A	x	d	ter
<i>Cnemidophorus tigris punctilinealis</i>	2.646	11.2		0.5		Cullum 1998	39.5	Pianka 1986	A	x	d	ter
<i>Cnemidophorus inornatus arizonae</i>	2.265	4.2		0.5		Cullum 1998	40.1	Schall 1977	A	x	d	ter
<i>Cnemidophorus inornatus heptagrammus</i>	1.876	4.0		0.5		Cullum 1998	40.1	Schall 1977	A	x	d	ter

Table 1. Continued.

Species	v	m	t	Δs	sub i	Reference	FBT	Reference	for	Climate	Activity	Habitat
Lacertidae												
<i>Gallotia stehlini</i>	3.150	208	36.0	0.5	c	Márquez & Cejudo 1999	33.62727*	Cejudo <i>et al.</i> 1999	A	m	d	ter
<i>Gallotia simonyi</i>	2.300	230	36.0	0.5	c	Márquez & Cejudo 1999	35.4*	Cejudo <i>et al.</i> 1999	A	m	d	ter
<i>Gallotia atlantica</i>	1.820	5.4	40.0	0.25	c	Márquez & Cejudo 1999	33.60313*	Cejudo <i>et al.</i> 1999	A	m	d	ter
<i>Gallotia caesaris</i>	2.150	9.8	36.0	0.25	c	Márquez & Cejudo 1999	35.45556*	Cejudo <i>et al.</i> 1999	A	m	d	ter
<i>Psammmodromus algirus</i>	2.525	11.0	35.0	0.5	c	Bauwens <i>et al.</i> 1995	30.1	Pollo-Mateos & Pérez-Mellado 1989; Diaz 1992	A	m	d	ter
<i>Psammmodromus hispanicus</i>	1.499	1.4	35.0	0.5	c	Bauwens <i>et al.</i> 1995	30.2	Pollo-Mateos & Pérez-Mellado 1989	A	m	d	ter
<i>Lacerta bedriagae</i>	1.787	9.6	35.0	0.25	c	own data	32.0	Bauwens <i>et al.</i> 1990	A	m	d	sax
<i>Lacerta monticola</i>	1.566	7.7	35.0	0.5	c	Bauwens <i>et al.</i> 1995	33.5	Martinez-Rica 1977; Pérez-Mellado 1982	A	m	d	sax
<i>Lacerta vivipara</i>	0.900	2.8	35.0	0.5	c	Bauwens <i>et al.</i> 1995	29.9	Van Damme <i>et al.</i> 1986, 1987	A	c	d	ter
<i>Podarcis sicula</i>	1.669	7.1	35.0	0.25	c	own data	33.9	Van Damme <i>et al.</i> 1990	A	m	d	ter
<i>Podarcis (hispanica) hispanica</i>	2.027	2.5*	35.0	0.5	c	Van Damme <i>et al.</i> 1997	35.8	Arnold 1987	A	m	d	sax
<i>Podarcis hispanica atrata</i>	1.527	7.6	35.0	0.5	c	Bauwens <i>et al.</i> 1995	33.9	Castilla & Bauwens 1991	A	m	d	ter
<i>Podarcis bocagei</i>	1.421	3.3	35.0	0.5	c	Bauwens <i>et al.</i> 1995	32.3	Pérez-Mellado 1983; Pérez-Mellado & Salvador 1981	A	m	d	ter
<i>Podarcis muralis</i>	2.136	3.1	35.0	0.25	c	own data	33.8	Braña 1991; Tosini & Avery 1993	A	m	d	sax
<i>Podarcis pityusensis</i>	2.540	9.8				Avery <i>et al.</i> 1987	33.3	Pérez-Mellado & Salvador 1981	A	m	d	sax
<i>Podarcis lilfordi</i>	2.337	7.8	35.0	0.5	c	Bauwens <i>et al.</i> 1995	33.5	Bauwens <i>et al.</i> 1995	A	m	d	ter
<i>Podarcis tiliguerta</i>	2.411	4.8	35.0	0.5	c	Bauwens <i>et al.</i> 1995	31.1	Van Damme <i>et al.</i> 1989	A	m	d	sax
<i>Lacerta viridis</i>	2.679	28.4	35.0	0.25	c	own data	33.9	Arnold 1987	A	m	d	ter
<i>Lacerta schreiberi</i>	1.785	21.2	35.0	0.5	c	Bauwens <i>et al.</i> 1995	31.1	Salvador & Argüello 1987	A	m	d	ter
<i>Lacerta agilis</i>	1.679	9.1	35.0	0.5	c	Bauwens <i>et al.</i> 1995	31.5	Sveegaard & Hansen 1976	A	c	d	ter
<i>Takydromus septentrionalis</i>	0.810	5.5	32.0	0.25		Xiang <i>et al.</i> 1996	30.9	Xiang <i>et al.</i> 1996	A	t	d	ter
<i>Acanthodactylus pardalis</i>	2.617	6.7	35.0	0.25	c	own data	37.8	Duvdevani & Borut 1974	A	m	d	ter
<i>Acanthodactylus scutellatus</i>	2.795	8.1	35.0	0.25	c	own data	39.3	Duvdevani & Borut 1974	A	m	d	ter
<i>Acanthodactylus erythrurus</i>	3.130	8.9	35.0	0.5	c	Bauwens <i>et al.</i> 1995	33.2	Pollo Mateos & Pérez-Mellado 1989	A	m	d	ter
<i>Eremias lineoocellata</i>	2.630	4.2	36.0	0.5	s	Huey <i>et al.</i> 1984	36.9	Pianka 1986	A	x	d	ter
<i>Eremias lugubris</i>	1.580	4.0	36.0	0.5	s	Huey <i>et al.</i> 1984	37.7	Pianka 1986	A	x	d	ter
<i>Eremias namaquensis</i>	2.680	2.5	36.0	0.5	s	Huey <i>et al.</i> 1984	37.8	Pianka 1986	A	x	d	ter
<i>Nucras tessellata</i>	2.050	4.7	36.0	0.5	s	Huey <i>et al.</i> 1984	39.3	Huey <i>et al.</i> 1977	A	x	d	ter

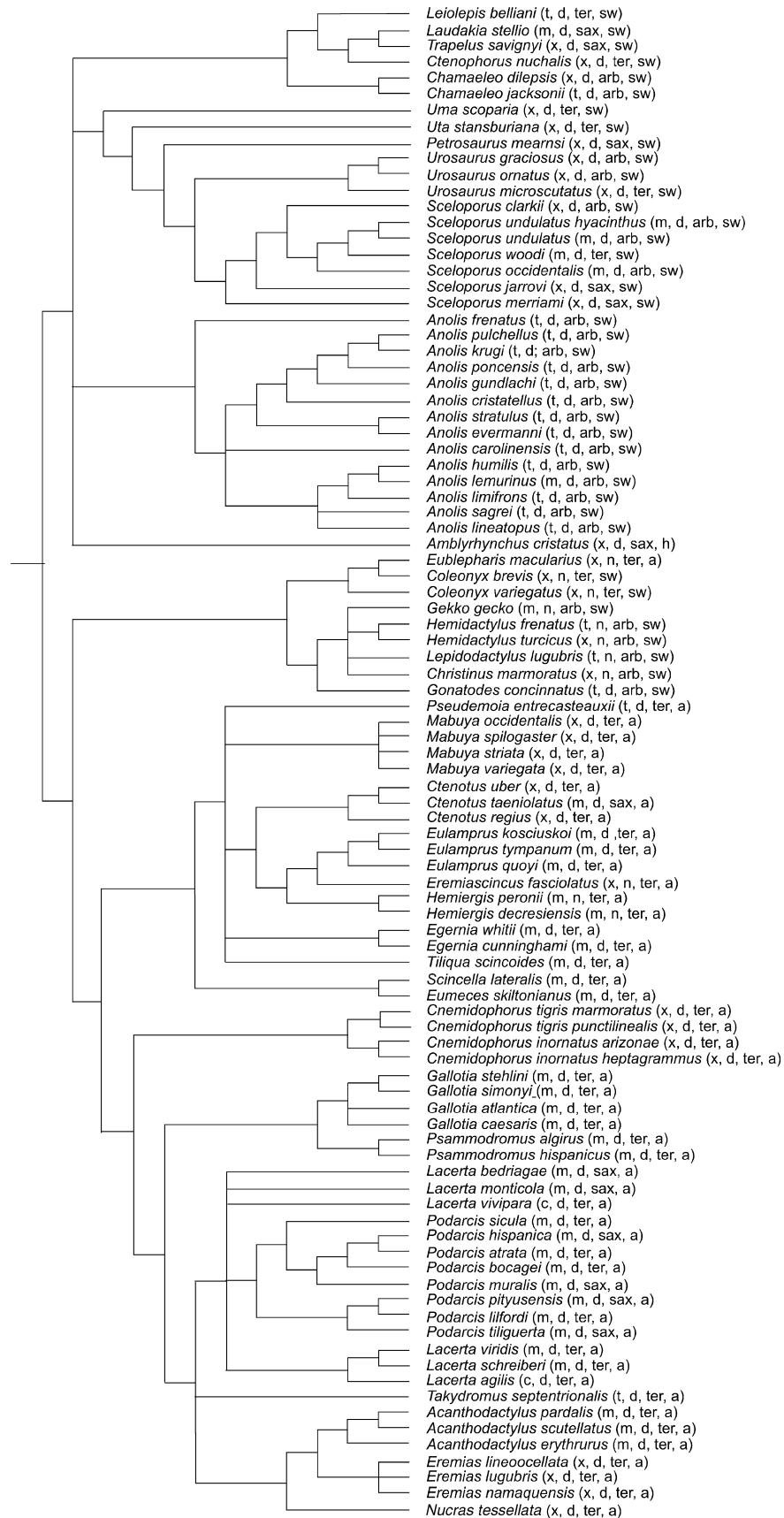


Fig. 1. Hypothesis of phylogenetic relationships for 94 species and subspecies of lizards for which sprint speed, body mass, body temperatures and phylogeny are available. Because divergence times are often unknown, all branch lengths were set to unity. Climate (t, tropical; x, xeric; m, Mediterranean; c, cool); activity patterns (d, diurnal; n, nocturnal), microhabitat use (arb, arboreal; sax, saxicolous; ter, terrestrial) and foraging mode (a, actively foraging; h, herbivorous; sw, sit-and-wait predator) of the species is indicated in parentheses. See text for references.

were used to simulate evolution of speed, mass and temperature, assuming Brownian motion as the model of evolutionary change. The means and variances were set to the means and variances of the original data. The procedure was repeated 1000 times. No limits to the simulated values of the variables were imposed. The PDANOVA program was used to perform traditional one way analyses of variance (ANOVA) on the simulated data sets. The *F*-statistics of these 1000 ANOVAs were used to set up the null distribution. The differences among sets of species were considered significant if the *F*-value exceeded the upper 95th percentile of the simulated *F*-distribution. The *F*-value at the lower end of this 95th percentile will be called 'the critical *F*-value' in the results. This procedure was repeated for each ecological variable (i.e. climate, activity, microhabitat

use, and foraging mode). The PDSIMUL program was also used to check the results obtained with regression of independent contrasts, following procedures outlined by Garland *et al.* (1999).

Both methods require input on the topology and branch lengths of the phylogenetic tree. A 'currently best' tree was compiled from literature (Fig. 1; Arnold 1983, 1989; Garland, Huey & Bennett 1991; Joger 1991; Dial & Grismer 1992; Garland 1994; Kluge & Nussbaum 1995; Reeder & Wiens 1996; Zani 1996; Irschick *et al.* 1997; Wiens & Reeder 1997; Cullum 1998; Harris *et al.* 1998; Bonine & Garland 1999). Some unresolved polytomies remain, however. This was taken into account by subtracting one degree of freedom for each unresolved node (Purvis & Garland 1993; Garland 1994). As data on the divergence times are scattered, all the branch lengths were set to unity. It has been shown that the actual length of the branches does not usually affect the outcome of the statistical analyses to a great extent (Martins & Garland 1991; Walton 1993; Irschick *et al.* 1996; Diaz-Uriarte & Garland 1998). Moreover, checks of branch lengths with the PDTREE program did not show any significant correlation between the absolute values of the standardized contrasts and their standard deviations (Garland *et al.* 1992). Because it is most likely that divergence times among the families in our data set differ strongly from those between genera and species, we also performed the phylogenetic analyses on trees of which branch lengths were proportional to the taxonomic level of the groups they connect. Divergence times were set to 5, 10, 20, 50 and 100 units for families, and to 1, 2, 3, 4 and 5 for genera (divergence times between species were always kept to 1 unit). These branch length manipulations did not alter the outcome of the tests qualitatively, and therefore only results for the tree with all branch lengths set to unity are reported.

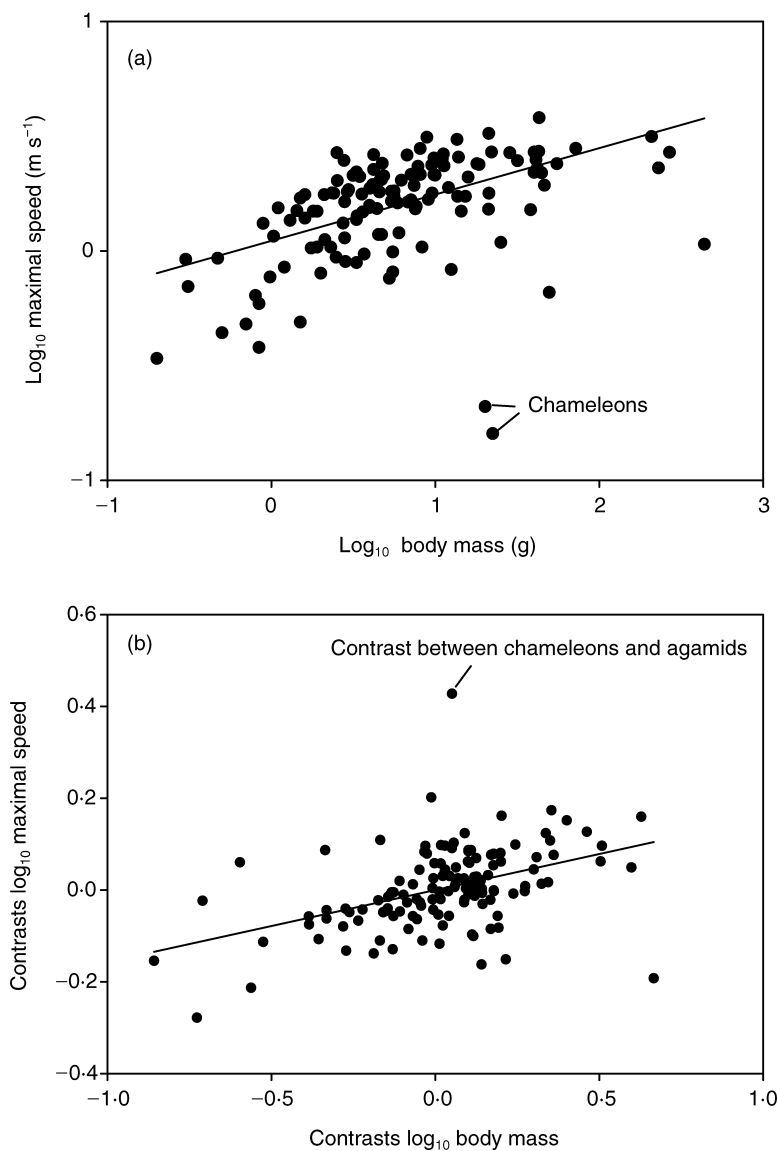


Fig. 2. Effect of body mass on maximal sprint speed in lizards. (a) Traditional analysis; the line shown is the ordinary least-squares regression line for all data, except the two chameleon species. The equation is $\log_{10}(\text{speed}) = 0.044 + 0.20 \log_{10}(\text{body mass})$, with speed expressed in m s^{-1} and body mass in g. (b) Phylogenetic analysis, using independent contrasts of body mass and sprint speed.

SELECTION OF DATA

Over 50 papers reporting sprint speeds of lizards were found. Data obtained with treadmills, and from race-tracks if the distance over which speed was calculated over more than 50 cm were disregarded. In addition, some material could not be used because data on mass and SVL or body temperature were missing, or because the phylogenetic position of the species concerned was unclear. Species used in this study are given in Table 1.

Results

EFFECTS OF BODY MASS AND BODY TEMPERATURE

Non-phylogenetic analyses

\log_{10} maximal sprint speed correlates with \log_{10} body mass (Fig. 2, $r = 0.45$). The slope of the ordinary least-squares regression line has a value of $0.177 (\pm 0.031 \text{ SE})$. Reduced major axis regression yields a slope of 0.39

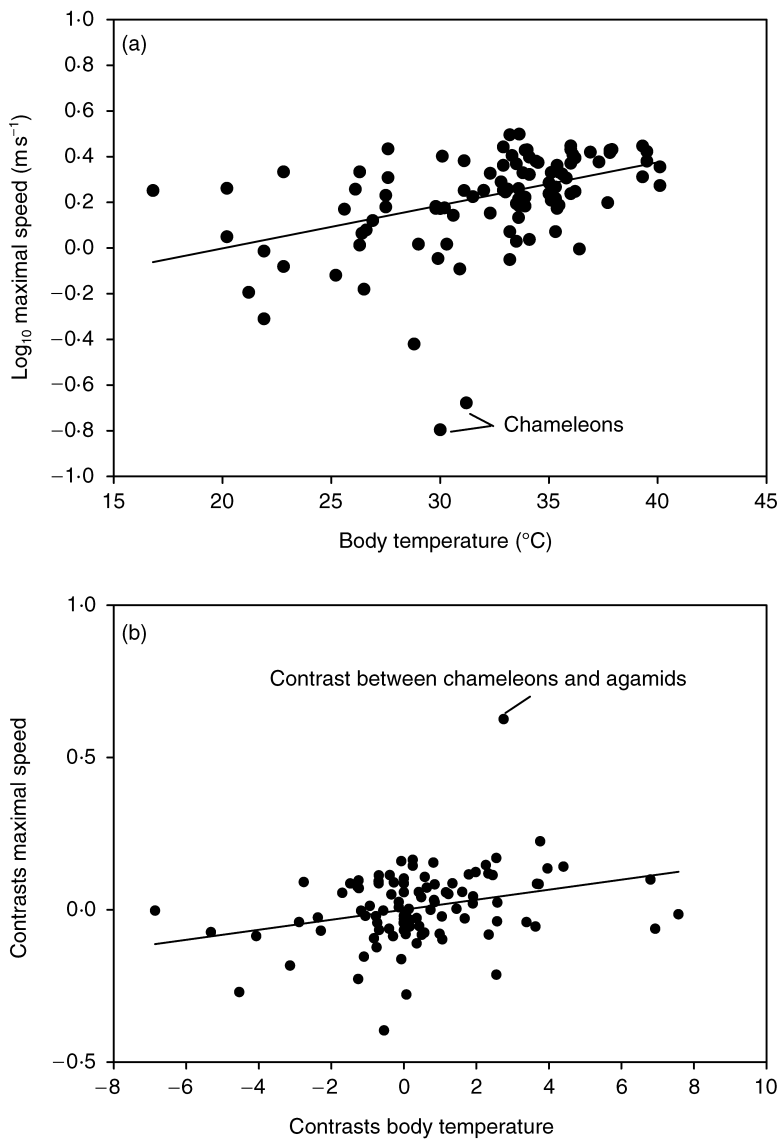


Fig. 3. Effect of body temperature on maximal sprint speed in lizards. (a) Traditional analysis; the line shown is the ordinary least-squares regression line for all data, except the two chameleon species. (b) Phylogenetic analysis, using independent contrasts of body temperature and sprint speed.

(95% confidence interval: 0.33–0.46). Inspection of the residuals of the regression reveals two outliers: the two chameleon species are obviously slow for their body size. Removing these data points improves the fit of the regression line considerably (now $r = 0.58$). Ordinary least-squares regression now produces a slope of 0.202 (± 0.025), reduced major axis regression a slope of 0.35 (95% confidence intervals: 0.30–0.40).

\log_{10} maximal sprint speed also correlates with body temperature (Fig. 3, $r = 0.52$). The estimated slopes are 0.020 (ordinary least-squares regression) or 0.037 (reduced major axis, 95% confidence interval: 0.038–0.054). Again, the chameleons stand out for having strikingly low sprint speeds for their activity temperatures. Removing them from the analysis improves the correlation ($r = 0.52$) and returns slope values of 0.019 (ordinary least-squares regression) and 0.037 (reduced major axis).

Multiple regression on all species with known speed, body mass and temperature yielded a model with a significant contribution of body temperature (partial correlation = 0.41, $P < 0.00001$), but not of body mass (partial correlation = 0.15, $P = 0.14$). However, when the two chameleon species are omitted from the analysis, both \log_{10} body mass (partial correlation = 0.28, $P = 0.001$) and body temperature (partial correlation = 0.45, $P < 0.00001$) contribute significantly to the variation in \log_{10} sprint speed (see Fig. 4a). Together, they explain 34% of the interspecific variation in sprint speed. The partial regression coefficient for \log_{10} body mass estimates the allometric scaling exponent: 0.092 (± 0.027 SE).

Phylogenetic analyses

A phylogenetic analysis on all available data indicates that standardized independent contrasts in sprint speed are positively correlated with contrasts in body mass ($r = 0.44$). Reduced major axis regression through the origin produces a slope estimate of 0.35, which is significantly different from zero ($t = 5.33$, $df = 99$ (124 spp., 21 soft polytomies), $P < 0.001$). In this data set, the contrast between the two chameleons and their sister taxon (the agamid lizards) is an obvious outlier. Removing this contrast results in a slightly higher correlation ($r = 0.46$). The reduced major axis slope is now 0.39, which is also statistically different from 0 ($t = 5.83$, $df = 97$ (122 spp., 21 soft polytomies), $P < 0.001$).

Standardized independent contrasts in sprint speed are also positively correlated with contrasts in body temperature ($r = 0.35$). The reduced major axis slope is 0.06, and differs significantly from zero ($t = 3.78$, $df = 80$ (101 spp., 19 soft polytomies), $P = 0.0003$). Here too, the contrast between the chameleons and the agamid lizards stands out. Removing it from the analysis results in a slightly higher correlation ($r = 0.36$) and a reduced major axis score of 0.02 that differs from zero ($t = 3.75$, $df = 78$ (99 spp., 19 soft polytomies), $P < 0.001$).

Multiple regression through the origin shows that both contrasts in mass (partial correlation = 0.30, $P = 0.002$) and contrasts in temperature (partial correlation = 0.32, $P = 0.002$) are significant predictors of contrasts in speed. Together, they explain 18% of the variation in the sprint speed contrasts. When the chameleons are kept out of the analysis, the contrasts in body mass (partial correlation = 0.36, $P < 0.001$) and the contrasts in temperature (partial correlation = 0.31, $P = 0.002$) together explain 21% of the variation in the sprint speed contrasts (see Fig. 4b).

EFFECTS OF CLIMATE, ACTIVITY PERIOD, FORAGING MODE AND MICROHABITAT USE

Non-phylogenetic analyses

Traditional one-way ANOVAs indicate significant effects of climate, activity period and microhabitat use on

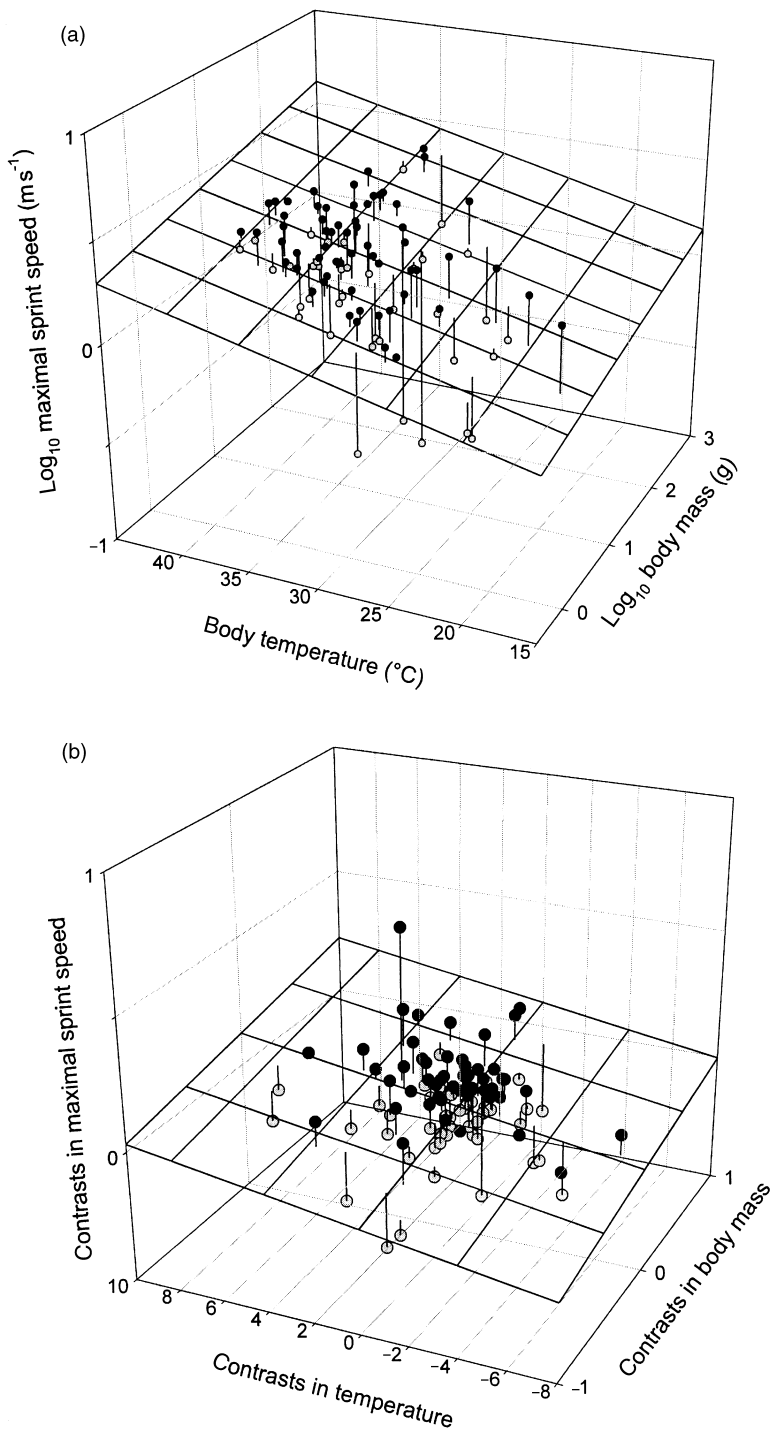


Fig. 4. Maximal sprint speed as a function of body mass and body temperature in lizards. Regression planes are calculated for all data except the chameleons: (a) traditional analysis; (b) phylogenetic analysis.

maximal sprint speed. These differences can be accounted for by differences in body mass and temperature (ANCOVA, see Table 2 for statistics). Sit-and-wait predators and actively foraging species do not differ in sprint capacity (Table 2).

Phylogenetic analyses

The effect of climate using phylogenetic simulations was reassessed. At a 0.05 significance level, the critical

F -value obtained by repeated simulation of the evolution of maximal speed was 10.81. This value is substantially above the standard tabular value for the same α and degrees of freedom ($F = 2.70$), indicating that related species tend to live in similar climates. The F -value obtained from a traditional ANOVA testing for the effect of climate on speed ($F = 5.34$) is well below the critical value obtained from the simulations, so the variation in sprint speed among lizards living in different climates reflects phylogeny, rather than ecology. That is, the effect of climate on sprint speed reported above can be explained by the fact that related species tend to have similar speeds and live in the same climatic region. A similar argument can be made about the effect of climate on body mass (critical $F = 10.89$, traditional $F = 9.48$) and on body temperature (critical $F = 11.27$, traditional $F = 10.35$).

Phylogenetic analyses also fail to find a significant difference between nocturnal and diurnal lizards in maximal sprint speed (critical $F = 22.25$, traditional $F = 6.26$), body mass (critical $F = 20.78$, traditional $F = 1.88$) or body temperature (critical $F = 16.26$, traditional $F = 10.99$).

A similar result was obtained for the effect of foraging mode on maximal sprint speed (critical $F = 84.92$, traditional $F = 0.081$), body mass (critical $F = 78.49$, traditional $F = 0.80$) and body temperature (critical $F = 94.62$, traditional $F = 0.06$).

Finally, the differences among microhabitats in maximal speed (critical $F = 27.48$, traditional $F = 4.54$), body mass (critical $F = 25.84$, traditional $F = 2.75$) and body temperature (critical $F = 22.31$, traditional $F = 10.06$) also proved not significant.

Discussion

BIGGER IS BETTER

Our results seem to refute Hill's (1950) prediction that speed would be independent of body size. The maximal sprinting speed (v) of lizards increases with body size, at least up to a certain point. There are several other predictions on the allometry of speed (elastic similarity model: $v \propto Mass^{0.25}$; static stress similarity: $v \propto Mass^{0.40}$ (McMahon 1974, 1975; Huey & Hertz 1982); dynamic similarity: $v \propto Mass^{0.17}$ (Gunther 1975; Garland *et al.* 1987)). However, because of the large amount of scatter present in the data, it cannot be decided which of these other scaling models is more fitting. The exponent obtained by ordinary least-squares regression (0.18, or 0.20 if the chameleons are omitted) is temptingly close to the value predicted by dynamic similarity theory (0.17). Garland (1983), also using ordinary least regression, obtained a highly similar value (0.165) for 106 mammal species with body masses ranging from 0.016 to 6000 kg. However, several authors have argued that in allometric studies, reduced major axis regression may be a more suitable technique than ordinary least-squares regression (e.g. Rayner 1985; McArdle 1988;

Table 2. Mean (\pm SE) maximal sprint speeds, body masses and activity body temperatures of lizards from different climatic regions and with different activity periods, foraging modes and microhabitat uses. Also shown are the results from non-phylogenetic tests for differences among lizard groups (ANOVAS, *t*-tests), and the result of ANCOVAs assessing the significance of the difference in speed when controlling for the differences in body mass and temperature

	Sprint speed (m s ⁻¹)			Body mass (g)			Body temperature (°C)		
	<i>x</i>	SE	<i>n</i>	<i>x</i>	SE	<i>n</i>	<i>x</i>	SE	<i>n</i>
Climate									
Cool	1.09	0.30	3	4.07	2.60	3	30.70	0.80	2
Mediterranean	1.95	0.11	46	38.47	12.52	45	32.51	0.56	44
Xeric	1.94	0.11	36	11.65	2.30	36	34.82	0.74	33
Tropical	1.38	0.09	44	6.61	1.70	44	27.82	0.97	23
ANOVA	$F_{3,125} = 5.77, P = 0.001$			$F_{3,124} = 10.54, P < 0.0001$			$F_{3,98} = 13.35, P < 0.0001$		
ANCOVA	$F_{3,95} = 0.43, P = 0.73$								
Activity									
Diurnal	1.86	0.07	119	21.51	5.23	108	32.62	0.47	92
Nocturnal	1.23	0.16	11	10.87	5.07	11	27.99	1.89	10
<i>t</i> -test	$t_{118} = 2.51, P = 0.01$			$t_{117} = 1.27, P = 0.21$			$t_{100} = 3.00, P = 0.003$		
ANCOVA	$F_{1,97} = 3.20, P = 0.08$								
Foraging mode									
Sit-and-wait	1.66	0.09	44	7.90	1.54	44	30.14	0.91	34
Active	1.75	0.10	67	26.08	8.73	66	33.20	0.58	54
<i>t</i> -test	$t_{109} = 0.42, P = 0.67$			$t_{108} = 1.93, P = 0.055$			$t_{86} = 2.97, P = 0.004$		
Microhabitat									
Ground-dwelling	1.65	0.10	68	25.48	8.25	68	33.42	0.60	53
Saxicolous	2.24	0.11	18	20.17	4.88	18	34.25	0.43	17
Arboreal	1.63	0.09	41	8.41	1.81	40	28.98	0.91	32
ANOVA	$F_{2,124} = 4.63, P = 0.01$			$F_{2,123} = 3.31, P = 0.04$			$F_{2,99} = 12.89, P = 0.00001$		
ANCOVA	$F_{2,96} = 1.79, P = 0.17$								

Christian & Garland 1996). The exponent obtained through reduced major axis regression on the data presented here (0.39, or 0.35 without the chameleons) is closer to that predicted by the static stress similarity model (0.40).

In mammals, none of the theoretical scaling models describe the actual relationship between speed and body mass very well (Garland 1983). Log(speed) does not increase monotonically with log(body mass), as suggested by the biomechanical models, but takes a curvilinear path, reaching an 'optimum' at a body mass of about 119 kg (Fig. 5). Following this line, a polynomial regression equation was fitted through the lizard data. It took the following form (with speed in m s⁻¹ and body mass in g; see also Fig. 5, chameleons omitted):

$$\log_{10}(\text{speed}) = -0.0129 + 0.435 \log_{10}(\text{body mass}) - 0.129 \log_{10}(\text{body mass})^2.$$

The fit was slightly higher for this curve ($r^2 = 0.28$) than for the linear regression ($r^2 = 0.20$). The equation suggests an 'optimal' body size for lizards (with regards to running ability) of 48 g. Observe, however, that our data set contains very few speeds of large species. Only seven species have body masses above the 'optimum' of 48 g. In addition, observations of lizards running in the field suggest that race track measurements may underestimate maximal performance, especially in larger lizards (Jayne & Ellis 1998). Therefore the curvilinear nature of the log(speed)–log(body mass)

relationship remains uncertain; data on the maximal velocities of truly large lizards (e.g. large varanids) are badly needed to solve the case.

Measurement error is undoubtedly one of the reasons for the large amount of scatter around the body mass–speed relationship. In spite of our attempt to restrict our data set to studies using similar techniques for measuring sprint speed, it is clear that variation among experimental set-ups and protocols (e.g. the fanaticism with which lizards are chased through the tracks) is bound to introduce some error. Interspecific variation in 'design' (morphology, physiology, biochemistry) most probably also contributes to the scatter. For instance, biomechanical models predict a positive relationship between (relative) limb length and sprint speed (see Garland & Losos 1994 and references therein), and several empirical studies have corroborated this prediction (Snell *et al.* 1988; Losos 1990; Sinervo, Hedges & Adolph 1991; Sinervo & Losos 1991; Bauwens *et al.* 1995). However, limb lengths and other design characteristics are not routinely reported in the literature, so this line of investigation could not be pursued here.

How do sprint speeds of lizards compare with those of mammals? Of course, the difficulties encountered when comparing lizard data from different studies multiply when comparing lizards with mammals. Probably even more than our lizard data set, the mammal data in Fig. 5 (taken from Garland 1983) are a varied assortment, collected using widely different techniques and degrees of accuracy. In addition, the body size ranges

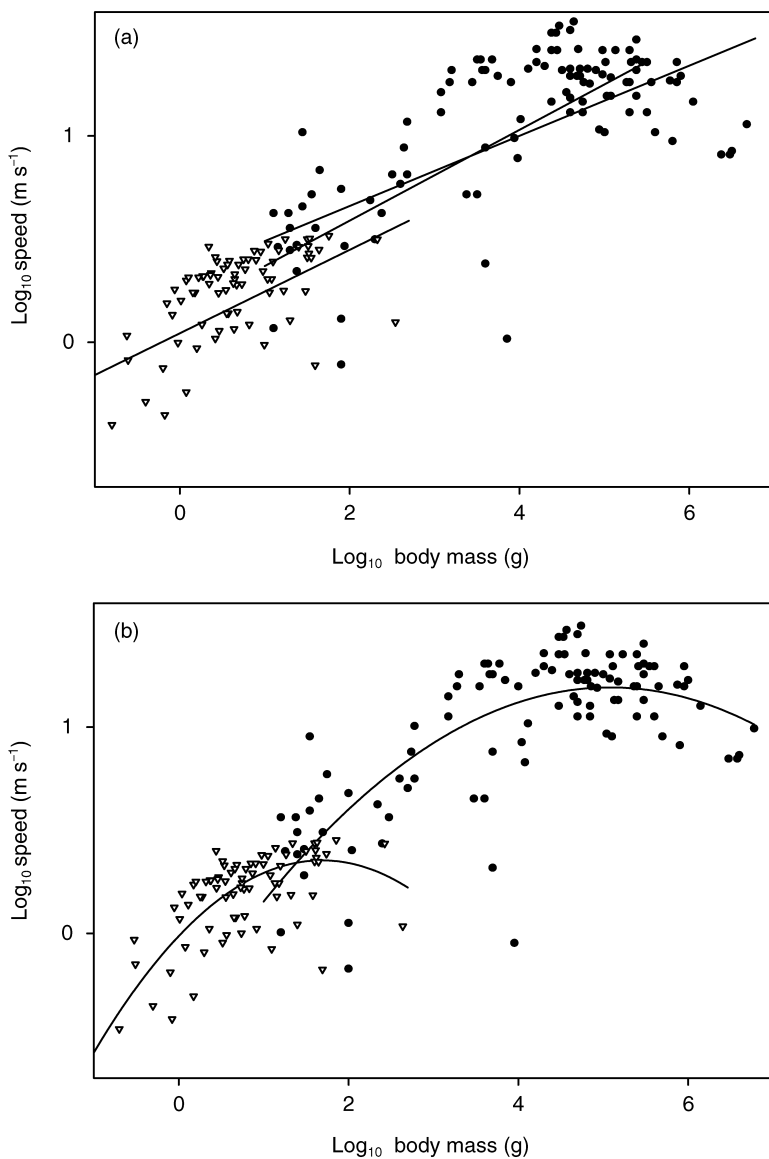


Fig. 5. Comparing maximal sprint speeds of mammals (circles, data from Garland 1985) and lizards (triangles). (a) Using linear ordinary least-squares regression. The regression line for the lizards is calculated for all species except the chameleons. Regression lines for the mammals are calculated for all data points, and for all animals weighing less than 300 kg (the latter has a closer fit, see Calder 1984). (b) Using polynomial regression.

for which speed data are available differ between the two animal groups (Fig. 5), further jeopardizing a statistical comparison. Therefore, the conclusions below must remain speculative. Moreover, the outcome of the comparison depends largely on the regression techniques used to summarize the data. When ordinary least-squares regression is used, the effect of body mass on maximal sprinting speed seems similar in lizards and mammals (Fig. 5a). As noted above, the exponents of the relationships are highly similar for the two groups. However, Fig. 5(a) also suggests that for a given body mass, lizards tend to be slower than mammals. This would corroborate the idea that, in terms of maximal attainable speed, the locomotor apparatus of lizards (sprawling gait, anaerobic fuelling, etc.) is inferior to

that of mammals (erect gait, aerobic fuelling, etc.). When polynomial regression is used, a different pattern emerges (Fig. 5b). Now, sprint speeds of lizards tend to be similar to the speeds predicted for mammals of a similar body mass. This suggests that, for small body sizes, a lizard-like type of locomotion may allow speeds comparable to those of mammals (see also Biewener 1989, 1990; Blob 2000). Speed data for small mammals and for large lizards are needed to test this unexpected finding.

HOTTER IS BETTER

Our results confirm the hypothesis that 'hotter is better' (Huey & Kingsolver 1989), at least within the temperature range considered here. Species that are active at high body temperatures run faster than species with low mean field body temperatures. Most species in this study are said to be tested near optimal body temperatures, so it seems unlikely that the correlation between speed and field body temperature is an artefact of slow lizards being tested at suboptimal temperatures. Rather, we think that our results corroborate the idea that adaptation of the thermal physiology to lower body temperatures is at the expense of performance at the optimal body temperature. The thermodynamical properties of the constituents of the cell (particularly those of water, Calloway 1976) are usually invoked to explain this phenomenon. However, this hypothesis should be tested more carefully, comparing field body temperatures, selected body temperatures and optimal temperatures with maximal performances.

ECOLOGICAL CORRELATES OF SPRINT SPEED

Traditional statistical analyses suggest that three of the four ecological variables considered (climate, time of activity, microhabitat use) explain a significant part of the variation in sprint speed among lizard species. Some of the expectations formulated in the introduction are met. Lizards from Mediterranean and xeric climatic regions sprint faster than lizards from cool or tropical climates; diurnal lizards are faster than nocturnal lizards. Non-phylogenetic analyses also indicate differences in speed among lizards from different microhabitats, but here the prediction that climbing species should have lower (horizontal) running capacities than cursorial species proved incorrect. Instead, rock-climbing lizards sprint faster than both arboreal and ground-dwelling species. Foraging strategy (sit-and-wait vs actively foraging) did not influence maximal sprint speed. Traditional analyses of covariance also suggest that the differences in sprint speed between climates, activity periods and microhabitats could be explained through differences in body mass and body temperatures.

While it is tempting to explain the variation in maximal sprint speed in terms of differences in morphology, thermal physiology and general ecology, the results of the phylogenetic analyses strongly warn against

such adaptive story-telling. When the genealogical relationships among the species considered are introduced into the analyses, the effects of the ecological factors are no longer statistically significant. This result once more stresses the importance of phylogenetic information in comparative analyses. Inspection of Fig. 1 shows that ecology and phylogeny are highly confounded within lizards, that is, phylogenetic related species tend to live in similar ecological conditions. This strongly suggests that the ecological characteristics considered are evolutionary stable. The 'clustering' of species with the same ecology reduces the statistical power of the tests to a great extent and differences among the ecological groups need to be very large to be significant (Garland *et al.* 1993; Vanhooydonck & Van Damme 1999). We conclude that the current data set and level of investigation does not allow formulating ultimate explanations of the variation in sprint speed in lizards. This will require finding a set of species for which ecology and phylogeny are not confounded. This may not be possible for the broad ecological classes used in this paper. Analyses at a more fine-grained level could be more fruitful. For instance, rather than dividing animals into such broad categories as 'sit-and-wait' and 'actively foraging', the foraging behaviour of particular species could be expressed in percentage of time spent moving, or home range size. This would allow testing the effect of the ecological parameter within a closely related group of lizards, and would circumvent the confounding effect of phylogeny.

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