

Locomotor capacity and social dominance in male lizards

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Abstract. Physiological capacities may constrain behavioural options and hence have important ecological consequences. We tested the hypothesis that social dominance is related to capacities for locomotor performance in territorial male lizards (*Sceloporus occidentalis* Baird & Girard). We first measured the maximal sprint speed and stamina of individual lizards in the laboratory. Pairs of size-matched males were then placed into a novel laboratory arena and allowed to compete for access to a basking site under a heat lamp. The lizard that physically controlled the basking site was judged the 'winner' of a dominance interaction (winner vs loser status was confirmed by quantitative scoring of behaviour). Winners of these dyadic encounters had significantly higher sprint speeds in 14 of 20 cases, with winners averaging 16.5% faster than losers. Stamina, however, did not differ between winners and losers.

Key-words: Behaviour, dominance, locomotion, performance, speed, stamina

Introduction

The behavioural options available to an animal may be limited by its physiological capacities, and these limitations can have important ecological consequences (e.g. Bennett, 1980; Christian & Tracy, 1981; Putnam & Bennett, 1981; Pough, 1983, 1989; Huey *et al.*, 1984; Taigen & Pough, 1985; Halliday, 1987; Hertz, Huey & Garland, 1988; Garland, 1990). Physiological constraints on behaviour and their functional consequences for ecology are well documented in interspecific and other intertaxa comparisons. Among vertebrate classes, for example, activity levels in nature often

correlate with, and appear to be limited by, levels of activity than can be sustained aerobically (Bennett, 1983; Pough, 1983). Physiological constraints on behaviour may exist at the level of the individual as well (Bennett, 1987), but empirical studies are rare (Wells & Taigen, 1984; Sullivan & Walsberg, 1985; Walton, 1988).

Here we use staged laboratory encounters to examine possible relationships between social dominance and locomotor capacity (maximal sprint speed and stamina) among individual male inguanid lizards (*Sceloporus occidentalis* Baird & Girard). The present study is part of a larger programme using combined field and laboratory approaches to investigate the functional ecology of natural variation in locomotor capacities in a population of western fence lizards (van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989; van Berkum *et al.*, 1989).

The dominance status of an individual lizard may profoundly influence its fitness (but see Dewsbury, 1982). For example, dominant lizards may control the largest and favourable home ranges, grow fastest and have access to the most mates (Trivers, 1976; Stamps, 1977, 1984; Ruby, 1981; Fox, 1983; Ruby & Dunham, 1987). Dominance correlates with activity levels in lizards and in most other vertebrates (Bracklin, 1978 and references therein) and activity levels are related to capacities for locomotor performance in lizards (Bennett, 1983; Bennett, Huey & John-Alder, 1984; Hertz *et al.*, 1988; Garland, 1990).

Dominance interactions in *S. occidentalis* are typically short and intense in nature, lasting a few minutes (Fitch, 1940; Schall & Sarni, 1987); however, intermittent fights lasting 45 min have been observed (Fitch, 1940). The intensity and occasionally prolonged duration of these interactions suggest that capacities for locomotion might be important in attaining or maintaining social dominance. Accordingly, we measured two different aspects of locomotor performance, maximal sprint running speed and treadmill endurance, chosen to include the range of locomotor behaviours exhibited by interacting male fence lizards. For endurance trials, we used a treadmill speed which, based on preliminary observations,

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would yield average endurance running times of a few minutes. We therefore hypothesized that dominance would correlate positively with both speed and stamina in *S. occidentalis*.

To establish dominance, we placed pairs of size-matched, adult male lizards into a novel laboratory arena and allowed them to compete for access to a localized basking site. The lizard that controlled the basking site was judged the 'winner' (cf. Bernstein, 1981). Male *S. occidentalis* are highly territorial (Tanner & Hopkin, 1972; Carpenter, 1978); they bask (sometimes in small sunflecks) to regulate body temperature, and their physiological capacities are influenced strongly by body temperature (see Fig. 6a in Huey, 1982). Thus, our criterion for judging 'winners' vs 'losers' is both behaviourally and ecologically relevant (Regal, 1971; Magnuson, Crowder & Medvick, 1979).

To determine locomotor capacities, we measured both the maximal sprint speed of lizards chased along a racetrack and their stamina on a treadmill. These measures of whole-animal performance (Huey & Stevenson, 1979; Arnold, 1983; Garland, 1990) are known or thought to be important in prey capture, escape from predators and perhaps social dominance (e.g. Christian & Tracy, 1981; Huey & Hertz, 1984; Webb, 1976; Djawdan & Garland, 1988).

Speed and stamina are supported by different metabolic pathways (Bennett, 1983; Garland, 1990) and are usually not correlated, either phenotypically or genetically, among individuals within species (Garland & Else, 1987; Garland, 1988), including *S. occidentalis* (Tsuji *et al.*, 1989). Previously, we demonstrated that individual differences in speed and stamina are heritable in this population of *S. occidentalis* (van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989). Speed and stamina may correlate rather strongly with variation in morphology, physiology and biochemistry within some species of lizards (Garland, 1984; Garland & Else, 1987; Miles, 1987; Gleeson & Harrison, 1988; Snell *et al.*, 1988), but neither correlates with individual differences in relative hindlimb span or tail length in *S. occidentalis* (Tsuji *et al.*, 1989). Presumably, speed and stamina are influenced by individual differences in behaviour as well (e.g. motivation, willingness to run to exhaustion), but we know of no study attempting to quantify such relations in lizards. In a forthcoming report we will present data concerning correlations among locomotor performance, survivorship and growth rate in this same population of lizards (Huey, Garland, van Berkum & Tsuji. in preparation).

Materials and methods

Study animals

Male lizards ($n = 42$; $\bar{x} \pm \text{SD}$, range; mass = 8.0 ± 2.92 , 4.0 to 13.2g; snout-to-vent length = 62.4 ± 7.75 , 50.0 to 74.0mm) were collected on 2–3 July 1987 at the Tuthill Ranch, Klickitat Co., Washington (collecting permit no. 153 to RBH, Department of Game, State of Washington) and transported to an environmental chamber at the University of Washington. Lizards were maintained individually in plastic shoe boxes, provided ample food (vitamin/calcium-dusted crickets) and water, kept on a cycle of 12:12 L:D (full-spectrum lights) $32:18^\circ\text{C}$. Lizards were measured (mass, snout-to-vent length) at the beginning (5 July 1987) and end (3 September 1987) of the experiment. Lizards maintained good health during the experiments ($\bar{x} \pm \text{SD}$ mass change = $-0.9 \pm 1.29\text{g}$; including lizards that lost tails during captivity, see below). Lizards were released where captured at the end of the experiment.

Locomotor capacity

We measured locomotor performance immediately after returning lizards to the laboratory. Maximal speed was determined (5–6 July 1987) by chasing lizards down the length of a 2-m long racetrack equipped with photocell stations at 0.25 m intervals (Huey *et al.*, 1984). Lizards were kept at 34°C in an environmental chamber prior to testing. This is the optimal temperature for sprinting in this species (Bennett, 1980; van Berkum, 1985) and approximately the mean body temperature of lizards from this population when active in nature (J. S. Tsuji, personal communication). Each lizard was run four times ($\geq 1\text{h}$ between trials) on each of 2 days, and we selected the single fastest 0.5 m speed (m s^{-1}) as the maximal speed for each individual. Fastest speeds on days one and two were compared to determine repeatability.

Stamina was determined (10–11 July 1987) by placing lizards on the slowly moving belt (0.5 km h^{-1}) of a treadmill and measuring the elapsed time until the lizards became exhausted (verified by checking loss of righting response; Huey *et al.*, 1984). Body temperature was again maintained at 34°C , by use of thermostatted incandescent lamps suspended above the tread belt. Each lizard was jogged on 2 days, and we selected the longer time as the measure of stamina for each individual. Times for the two trials were compared to determine repeatability.

Maximal speed and stamina of lizards are highly repeatable, even for as long as 1 year in the field (Bennett, 1980; Huey & Dunham, 1987; van Berkum *et al.*, 1989), and appear largely insensitive to effects of training or laboratory maintenance (Gleeson, 1979; Garland & Else, 1987; Garland *et al.*, 1987). Accordingly, the locomotor performance of individual lizards was probably consistent throughout these experiments.

Social dominance

We established dominance status of males 27 July–30 August 1987. We employed a paired comparison with size-matched individuals because dominance is tightly correlated to body size in lizards (Fox, 1983; Tokarz, 1985; references therein). Following Fox & Rostker (1982) and Tokarz (1985), we size matched 21 pairs of lizards by snout–vent length (measured to nearest 0.5 mm, $\bar{x} \pm \text{SD SVL} = 62 \pm 7.8$ mm; \bar{x} difference in SVL = 0.6 ± 0.71 mm, maximum difference = 3.0 mm). Because an incomplete tail is known to reduce dominance status in another sceloporine lizard (Foz & Rostker, 1982), we size matched the tails of paired lizards by artificial autotomy several days before dominance trials. Thus, for three pairs, we autotomized the tails of one individual to match that of the other that had lost its tail accidentally during prior handling. R. B. Huey & A. E. Dunham (personal communication) found that the loss of as much as two-thirds of the length of a lizard's tail does not influence sprint speed in *Sceloporus merriami* (Stejneger).

Pairs of lizards were taken quickly from the environmental chamber (at 32°C during the daytime) and placed simultaneously at opposite ends of a novel arena (52 × 113 cm) with a sand substrate and a single piece of bark in the centre. Ambient temperature was approximately 23°C, well below the thermal preference of these lizards (approximately 34°C; references in Bennett, 1980). A heat lamp was located above the bark, such that a lizard perched thereon could achieve its preferred body temperature and so that the lizards could compete for access to the basking site (Regal, 1971; Magnuson *et al.*, 1979).

One observer (EH) conducted all dominance experiments and scored the encounters with no knowledge of the relative locomotor capacities of the participants. Each pair of lizards was observed from behind a blind for 1 h. All putatively aggressive behaviour (pushup, gular flutter, lateral display, chase, displace, bite) and all putatively submissive behaviour (flee, flatten, hide in sand or

under bark) was recorded for each individual (modified from Fox & Rostker, 1982; see also Carpenter, 1978). Following Fox & Rostker (1982), pushups were assigned a weight of 0.5, whereas all other aggressive behaviours were weighted as 1.0; all submissive behaviours were weighted as –1.0. A 'behavioural score' was computed for each individual as the sum of the weights for all behaviour patterns observed during the 1 h session (Fox & Rostker, 1982). A subjective determination of the 'winner' (cf. Bernstein, 1981), based on which individual dominated the basking site, was also made. With one exception (see Results), winners always exhibited the higher behavioural score. Each lizard was tested as one member of only a single pair. We were able to score clear winners (and computed corresponding behavioural scores) for 20 of 21 pairs; subsequent analyses are based on this subset of 20 pairs.

Results

Locomotor capacity

Individual lizards showed significant and repeatable differences in locomotor performance. Two-way ANOVA indicated highly significant individual variation in both speed ($n = 42$, $F = 11.387$, d.f. = 1, 41, $P < 0.001$) and stamina ($n = 37$, $F = 3.538$, d.f. = 1, 36, $P < 0.001$). Intraclass correlations (proportion of variance among individuals) were 84.2 and 55.9%, respectively; interclass correlations (Pearson product–movement correlations between the two trials) were 0.839 and 0.568, respectively.

Two-way ANOVA also indicated that mean sprint speeds did not differ significantly ($F = 0.064$, d.f. = 1, 41, $P = 0.80$) between trial days one ($\bar{x} = 1.83$ m s⁻¹) and two ($\bar{x} = 1.84$ m s⁻¹). However, mean stamina decreased approximately 11.1% ($F = 7.939$, d.f. = 1, 36, $P = 0.01$) from trial one ($\bar{x} = 228.5$ s) to trial two ($\bar{x} = 203.1$ s).

The average maximal speed of lizards was 1.93 ± 0.054 m s⁻¹ ($\bar{x} \pm \text{SE}$; range = 1.17–2.80 m s⁻¹; $n = 43$). These speeds are virtually identical to those reported previously for this population (van Berkum *et al.*, 1989) and comparable to those obtained for adults from other northern populations of *S. occidentalis* (van Berkum, 1985), suggesting that our lizards were in good health. Log speed was not significantly correlated with log mass ($r = 0.164$, $P = 0.292$).

The average stamina of lizards was 246 ± 8.9 s ($\bar{x} \pm \text{SE}$; range = 162–414 s; $n = 43$). These values also are very similar to those reported by van

Berkum *et al.* (1989) for adult males from this population ($\bar{x} = 267$ s for males averaging 8.2 g and measured at 0.3 km h⁻¹, a speed which would be expected to yield somewhat longer running times than the 0.5 km h⁻¹ used in the present study). Log stamina was negatively correlated with log mass ($r = -0.424$, $P = 0.005$).

Speed and stamina were not correlated ($n = 43$, $r = -0.175$, $P = 0.262$). This result suggests that speed and stamina, as measured herein, represent two different aspects of individual variation in locomotor performance (cf. Bennett, 1980; Garland & Else, 1987).

Social dominance

When first placed in the arena, lizards initially remained motionless. After about 10 min, one of the lizards typically appeared to move spontaneously; this was inevitably followed almost immediately by movement of the other lizard. Both lizards then slowly explored the arena until one climbed onto the bark basking site. The other lizard usually displayed (e.g. performed a pushup) at the basking individual at this point. Thereafter, lizards displayed at each other until one occupied the basking site and the other usually moved to a corner of the arena.

Competitive encounters were typically brief. Most lasted 1 or 2 min, but a few lasted as long as 15 min. In all trials, the subjective 'winner' was judged as the individual which was on the bark under the light at the end of the trial. The subjective 'loser' always ended the trial in a less favourable position for basking. Often, the loser retreated to a corner of the arena, buried itself in the sand or crawled under the bark by the end of the trial.

Behavioural scores of subjective winners ($\bar{x} \pm$ SE = 4.7 ± 0.49 , range = $0.0-8.5$) averaged much higher than those of losers (-0.1 ± 0.44 , -3.0 to 3.5 ; Table 1), and this difference was highly significant (paired $t = -7.08$, d.f. = 19, two-tailed $P < 0.001$). In all but one trial, the subjective winner also had the higher behavioural score (Table 1). For pair 24-15, the former climbed onto the bark, after which no. 15 tried to chase him off three times without success. Thus, no. 24 was judged the winner, even though it had a lower behavioural score (1.5 vs 3 , Table 1). Pair 4-11 exhibited no discernible agonistic behaviour; no. 4 was judged the winner because he climbed onto the bark whereas no. 11 buried himself in the sand.

Relationships between dominance and performance

Social dominance was related positively to max-

imal sprint speed (Table 1). In 14 of 20 trials the individual judged the winner was also faster. Paired t -tests indicated that winners ($\bar{x} \pm 95\%$ confidence interval = 2.03 ± 0.132 m s⁻¹) were significantly faster than losers (1.81 ± 0.183 m s⁻¹; $t = -2.62$, d.f. = 19, two-tailed $P = 0.017$). Computed for each pair individually, the difference between speeds of winners and losers averaged $+0.22$ m s⁻¹ (range = -0.30 to $+1.01$ m s⁻¹), which equals an average of $+16.5\%$ of the loser's speed (range = -16.6 to $+87.0\%$).

Social dominance was not significantly related to stamina in these experiments (Table 1). The individual with higher stamina was judged the winner in only 12 of 20 trials. Stamina of winners ($\bar{x} \pm 95\%$ CI = 252 ± 29.1 s) and losers (247 ± 26.2 s) did not differ significantly ($t = -0.26$, d.f. = 19, two-tailed $P = 0.795$).

Qualitatively identical results were obtained with analysis of covariance, using body mass or snout-to-vent length as the covariate (as noted above, stamina was negatively correlated with body size). Moreover, neither body mass (paired $t = 0.00$, d.f. = 19, two-tailed $P = 1.000$) nor snout-to-vent length (paired $t = -0.64$, d.f. = 19, two-tailed $P = 0.530$) differed significantly between winners and losers. Finally, for completeness, we compared locomotor performances of winners and losers non-parametrically with Wilcoxon matched-pairs signed-rank test, and obtained similar results (for speed, $Z = -2.24$, two-tailed $P = 0.025$; for stamina, $Z = -0.34$, two-tailed $P = 0.737$).

Discussion

Our results indicate that social dominance of adult male fence lizards (*S. occidentalis*) from south-central Washington is related to maximal sprint capacities, but not to stamina. Winners of paired encounters in a laboratory arena were typically faster than were losers. The correspondence between our laboratory index of dominance and social dominance in nature remains to be determined. Nevertheless, we consider it appropriate for the paired-comparison design employed herein, in which the relative dominance status of individual lizards was related to their relative locomotor performance.

Our findings may be compared with studies of this species from central California. During 2-4 day encounters conducted in outdoor enclosures, Schall & Dearing (1987) found that males with malaria displayed less frequently to females and were also socially subordinate to males without

Table 1. Size, speed, stamina and behavioural scores for 'winners' (top entry of each pair) and 'losers' of dyadic encounters. Body size measures represent averages of values recorded at the beginning and again at the end of the experiments. Entries under 'Aggressive' and 'Submissive' are number of occurrences (modified from Fox & Rostker, 1982): P, pushups; G, gular flutters; L, lateral displays; C, chases; D, displacements; B, bites; F, flee; N, flatten; H, hide in sand or under bark (not same as flee). See text for method of calculation of behavioural score.

No.	Body mass (g)	Snout-vent length (mm)	Sprint speed (m s ⁻¹)	Stamina (s)	Score	Aggressive	Submissive
						P G L C D B	F N H
4	4.82	57.50	2.46	244	0	0 0 0 0 0 0	0 0 0
11	5.10	57.75	2.30	268	-1	0 0 0 0 0 0	0 0 1
5	4.79	53.00	1.98	202	4	0 1 0 1 1 1	0 0 0
7	4.47	52.25	1.71	392	2	0 0 2 1 0 0	1 0 0
8	4.73	55.00	1.74	271	3.5	3 0 0 1 1 0	0 0 0
1	3.73	53.25	1.36	268	-1	0 0 0 0 0 0	0 1 0
10	4.01	52.00	1.97	203	4.5	1 2 0 1 1 0	0 0 0
18	4.89	52.75	1.76	226	0	0 0 1 0 0 0	0 1 0
12	4.68	52.75	1.64	291	3.5	3 0 1 0 1 0	0 0 0
16	4.38	52.25	1.61	279	0.5	3 0 0 0 0 0	0 1 0
13	5.76	57.75	2.32	335	8.5	1 1 0 0 1 1 1	0 0 0
17	5.11	57.00	2.15	335	-2	0 0 0 0 0 0	0 2 0
14	5.44	54.50	1.52	307	4.5	5 1 0 1 0 0	0 0 0
6	4.86	55.00	1.83	190	-3	0 0 0 0 0 1	1 3 0
19	5.99	56.75	1.95	319	8.5	5 1 3 1 1 0	0 0 0
2	5.11	56.25	1.91	260	-2	0 0 0 1 0 0	0 2 1
20	10.56	70.25	1.62	268	6.5	3 2 1 1 1 1	0 1 0
37	10.58	70.50	1.81	239	3.5	3 1 1 0 0 0	0 0 0
21	9.82	69.25	2.18	229	3.5	5 0 0 0 2 0	0 1 0
25	8.17	70.00	1.82	283	2	2 0 0 0 1 1	1 0 0
23	8.63	65.50	1.82	238	5	2 2 1 1 0 0	0 0 0
34	9.82	67.00	1.18	210	0	0 0 0 0 0 0	0 0 0
24	7.10	64.00	2.02	414	1.5	3 0 0 0 0 0	0 0 0
15	6.57	61.25	1.59	175	3	0 0 0 3 0 0	0 0 0
26	9.88	67.50	2.38	181	7	6 0 2 1 1 0	0 0 0
22	8.43	67.75	1.64	207	-0.5	1 0 0 0 0 0	0 1 0
27	8.93	68.75	2.10	260	5	0 0 2 1 0 2	0 0 0
38	10.16	68.50	1.99	198	-1	0 0 1 0 0 0	0 1 1
28	6.34	59.75	2.03	278	4.5	3 1 0 1 1 0	0 0 0
3	6.09	59.50	2.05	254	-2	0 0 0 0 0 0	1 1 0
30	8.88	67.50	1.99	162	3	2 0 1 1 0 0	0 0 0
31	10.06	68.00	2.10	272	-1.5	3 0 0 0 0 0	0 3 0
33	9.05	66.75	2.53	173	7.5	1 5 0 1 1 0	0 0 0
41	9.26	66.25	2.80	206	3.5	1 6 0 0 0 0	1 1 1
35	9.49	70.75	2.30	246	6	4 0 2 1 1 0	0 0 0
44	10.03	71.75	1.39	204	-1	2 0 1 0 0 0	1 1 1
40	7.99	64.75	2.18	223	3	4 0 0 0 1 0	0 0 0
39	8.40	64.25	1.17	299	0	0 2 0 0 0 0	2 0 0
42	11.53	74.00	1.88	190	3.5	7 0 0 0 0 0	0 0 0
43	13.20	74.00	2.02	167	-2	0 0 0 0 0 0	0 2 0

malaria. Previously, Schall, Bennett & Putnam (1982) found that lizards with malaria exhibited lower distance running capacities over 30 s and 2 min (a measure of stamina) but did not show reduced maximal sprint speeds. These results might be interpreted to suggest that social dominance would correlate with stamina but not with speed. This suggestion would, however, be contrary to our finding that dominant lizards were faster, but did not have higher stamina. The apparent difference between these two studies cannot be resolved at present. Different populations of lizards were involved, different protocols for establishing dominance were employed and different time frames were used. Moreover, malaria, which does not occur in our population (J. S. Tsuji, personal communication), may have a variety of negative effects on physiology and behaviour (Schall, 1983).

Our studies were designed to test for possible correlations between dominance and locomotor performance, but not to uncover the causal links behind such relationships. Nevertheless, it is useful to consider some possible explanations for the apparent positive relationship. Whether dominance is linked directly to speed is unclear. In fact, we suspect that the relationship may be indirect, simply because the lizards studied generally did not sprint or display at high speeds while establishing dominance.

Speed might be linked indirectly with dominance if lizards use (perhaps subtle) aspects of displays (e.g. speed of headbobbing) as cues of overall quickness, speed or agility – traits that might be important in physical dominance. Alternatively, other aspects of displays might be correlated with speed and thus reflect overall health or vigour (cf. Sullivan & Walsberg, 1985). However, the fact that winners did not tend to have higher stamina may argue against this explanation.

Another possibility is that sprint speed and social dominance, as measured herein, are both correlated with a third, unmeasured variable, for example, testosterone levels. Gonadal state has been shown to influence aggression during formation of laboratory dominance hierarchies in lizards (Greenberg, Chen & Crews, 1984) and dominant individuals may have greater access to thermal resources and to food (e.g. Bels, 1974). Moore (1987a) and Moore & Marler (1987) have demonstrated that testosterone status affects components of territorial, sexual and aggressive behaviour, as well as movement rates, in free-living *Sceloporus*. Although data for reptiles are lacking, testosterone also affects muscle properties

in other vertebrates (e.g. Hooper, Brian & Bawlor, 1986; Thibert, 1986; Capaccio *et al.*, 1987). Such muscles may in turn affect sprint speed in lizards (Gleeson & Harrison, 1988; but see Garland, 1984; Garland & Else, 1987). Finally, in human children, aggression (possibly related to testosterone levels?) appears to be related to sports performance (Birrer & Levine, 1987). Based on the foregoing, we suggest the possibility that individual variation in testosterone levels might affect both agonism (but see Moore, 1987b) and sprint speed in parallel directions, leading to a correlation between dominance and speed, as found in the present study. We intend to test this hypothesis in future studies.

Few other studies have searched for correlations between capacities for physiological performance and behaviour of individual ectotherms, but three studies of toads are noteworthy. Wells & Taigen (1984) found that maximum oxygen consumption, an index of aerobic capacity and thus stamina, was uncorrelated with individual differences in calling and searching behaviour in male toads. Similarly, Sullivan & Walsberg (1985) found no correlation between maximum oxygen consumption and call rates in males of another species. Finally, Walton (1988) found no positive correlations between laboratory measures of locomotor performance and metabolism on the one hand and field behaviour on the other.

In some instances, such a lack of correlation between physiological capacities and behaviour may reflect the fact that normal activity levels, at least of ectotherms, are often well below those of which they are capable, such that physiological capacities do not generally limit behaviour (Wells & Taigen, 1984; Sullivan & Walsberg, 1985; Hertz *et al.*, 1988; Pough, 1989; Garland, 1990). However, our finding of a positive correlation between speed and dominance suggests that physiological performance capacities may sometimes correlate indirectly with ecologically important aspects of behaviour, even beyond those associated with capture of prey or escape from predators. Individual variation in locomotor performance is substantial (review in Bennett, 1987), providing opportunities for more detailed studies of the inter-relationships among physiological capacities, behaviour and ecological performance.

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