

Effects of loading and size on maximum power output and gait characteristics in geckos

Duncan J. Irschick*, Bieke Vanhooydonck†, Anthony Herrel† and Anemone Andronescu

Department of Ecology and Evolutionary Biology, 310 Dinwiddie Hall, Tulane University, New Orleans, LA 70118, USA

*Author for correspondence (e-mail: Irschick@tulane.edu)

†Present address: Laboratory for Functional Morphology, University of Antwerp (UIA), Universiteitsplein 1, B-2610 Antwerp, Belgium

Accepted 21 July 2003

Summary

Stride length, stride frequency and power output are all factors influencing locomotor performance. Here, we first test whether mass-specific power output limits climbing performance in two species of geckos (*Hemidactylus garnoti* and *Gekko gecko*) by adding external loads to their bodies. We then test whether body size has a negative effect on mass-specific power output. Finally, we test whether loading affects kinematics in both gecko species. Lizards were induced to run vertically on a smooth wooden surface with loads of 0–200% of body mass (BM) in *H. garnoti* and 0–100% BM in *G. gecko*. For each stride, we calculated angular and linear kinematics (e.g. trunk angle, stride length), performance (maximum speed) and mean mass-specific power output per stride. The addition of increasingly large loads caused an initial increase in maximum mass-specific power output in both species, but for *H. garnoti*, mass-specific power output remained constant at higher loads (150% and 200% BM), even though maximum velocity declined. This result, in

combination with the fact that stride frequency showed no evidence of leveling off as speed increased in either species, suggests that power limits maximum speed. In addition, the large gecko (*G. gecko*) produced significantly less power than the smaller *H. garnoti*, despite the fact that both species ran at similar speeds. This difference disappeared, however, when we recalculated power output based on higher maximum speeds for unloaded *G. gecko* moving vertically obtained by other researchers. Finally, the addition of external loads did not affect speed modulation in either species: both *G. gecko* and *H. garnoti* increase speed primarily by increasing stride frequency, regardless of loading condition. For a given speed, both species take shorter but more strides with heavier loads, but for a given load, *G. gecko* attains similar speeds to *H. garnoti* by taking longer but fewer strides.

Key words: *Hemidactylus garnoti*, *Gekko gecko*, speed modulation, stride frequency, kinematics, mass-specific power output.

Introduction

Physiologists have long been interested in which intrinsic factors of organisms affect their maximum speed of locomotion. Among other factors, the total amount of power that animals can produce may play a central role in limiting maximum speed, but testing this hypothesis is challenging (Farley, 1997; Irschick et al., 2001). Previous authors have suggested that if the speed of an animal moving up successively steeper inclines (or moving with increasingly large loads) declines, but its power output increases, then power is not limiting (Farley, 1997; Irschick et al., 2001) (Fig. 1A). By contrast, if maximum speed on increasingly steep inclines, or with increasingly large loads, decreases, but maximum power output remains the same, then the total amount of power an animal can produce may limit maximum speed (Fig. 1B). However, it is important to consider that although Fig. 1B is consistent with a hypothesis of power limitation, another possible explanation that could explain such

a pattern is that power output covaries with some other mechanical variable. If this were the case, then the decline in speed might not be due to a lack of power. Nevertheless, studies that examine how extrinsic factors affect power output could shed light on the general issue of whether power output limits maximum speed. Here, we attempt to differentiate between the two above hypotheses by examining power output in two species of arboreal geckos climbing vertically with large loads.

Loading studies are ideal for testing hypotheses regarding limitations on power output because, relative to unloaded locomotion, moving with loads increases the amount of work expended to move a given distance for a given speed and surface, and thus necessarily increases the total power output. Moreover, many organisms move in nature with large loads, such as when females carry large eggs (Bauwens and Thoen, 1981; Vitt and Congdon, 1978), or when animals consume

large meals (Garland and Arnold, 1983). Thus, studying the effects of loads on locomotor performance has ecological relevance (Aerts, 1990; Vanhooydonck and Van Damme, 1999), although many studies (including the present work) have used loads that are generally greater than animals experience in nature. Biologists have studied the effects of adding external loads to a variety of animals, including birds (Chai et al., 1997), horses (Hoyt et al., 2000; Wickler et al., 2001) and insects (Kram, 1996). In some cases, the loads had a substantial effect on performance and kinematics (e.g. Hoyt et al., 2000; Wickler et al., 2001), whereas for other species,

particularly insects (Kram, 1996), no significant effects were found. Despite these reports, few studies have examined how loads affect power output, particularly during vertical locomotion, when one would predict that the effects of loading would be most profound.

A second factor that could influence power output during locomotion is animal size (Hill, 1950; Marden, 1987). Previous authors have suggested that large animals should produce less power than small animals per unit body mass because of the manner by which surface area (and hence force) scales with size (e.g. Wilson et al., 2000; Toro et al., 2003), although this expectation has not always been borne out (Pennycuik, 1969, 1972; Marden, 1987). While several studies have addressed the general issue of whether large and small animals differ in power output during various activities (Marden, 1987; Wilson et al., 2000), we are aware of no studies that have examined this issue for vertical locomotion, such as observed in many arboreal lizard or insect species (but see Farley, 1997). Thus, another aspect of our study concerns a comparison of power output between two gecko species that vary greatly in size (see below). While such two-species comparisons are commonplace in physiological studies, their interpretation is often controversial (Garland and Adolph, 1994), so we interpret these data cautiously.

The effects of size and loading on limb kinematics are also poorly resolved for vertical locomotion. As the amount of a load increases, one predicts that maximum speed should decrease when moving vertically, but whether animals achieve this by equally diminishing stride length or stride frequency is unknown. Furthermore, how the addition of loads affects the manner by which animals increase in speed on vertical surfaces has rarely been examined, and there are no studies on the interactive effects of size and loading on kinematics. This last issue is of particular interest to physiologists because previous work has shown that, on horizontal surfaces, small animals tend to modulate speed by changing stride frequency, whereas larger animals tend to change stride length (Gatesy and Biewener, 1991). Furthermore, a recent study has shown that a climbing gecko (*Gekko gekko*) modulates speed almost entirely by changing stride frequency, whereas a similarly sized terrestrial gecko (*Eublepharis macularius*) changes speed primarily by changing stride length (Zaaf et al., 2001). Thus, data on how size and loading affect limb kinematics during vertical climbing might shed light on these issues.

Small climbing lizards such as geckos provide an excellent opportunity for testing the effects of size and loading on locomotion. Female geckos frequently carry large eggs prior to laying, which can approximate 10–30% of their body mass (D. J. Irschick, personal observation), so geckos are accustomed to carrying large loads. Furthermore, climbing geckos differ dramatically in size among species (e.g. 1–70 g difference in mass among species) (Zaaf and Van Damme, 2001).

In the present study, we tested the effects of size and loading on the vertical locomotion of two species of geckos (*Gekko gekko* and *Hemidactylus garnoti*). Whereas *G. gekko* is the

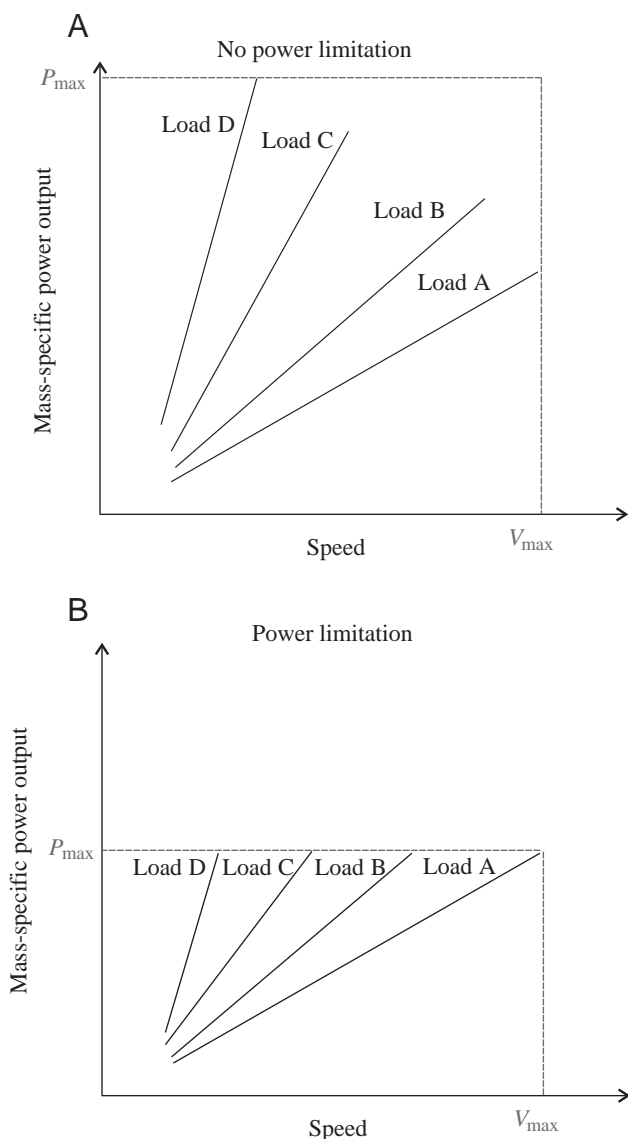


Fig. 1. Theoretical relationships between mass-specific power output (y axis) versus speed (x axis) if (A) mass-specific power output does not limit speed and (B) mass-specific power output limits speed. Different lines represent different loading conditions (Load A < Load B < Load C < Load D). V_{max} is defined as the maximal speed the animal can attain under any circumstances; P_{max} is defined as the maximal mass-specific power output the animal can attain under any circumstances.

largest extant gecko with derived toepads, and achieves a mass greater than 70 g, *H. garnoti* is a small (<5 g) climbing gecko that is more representative of the large family of geckos. However, these two species are generally similar in terms of their morphology, relative toepad dimensions and natural history, making them an excellent case study for comparison. We addressed three primary issues. First, does mass-specific power output limit locomotor performance in geckos? If the hypothesis of power limitation is correct, then as lizards are loaded with successively greater weights, speed should decrease, but mass-specific power (per unit body mass) should remain constant. Alternatively, if power is not limiting, then as successively greater weights are added, speed should decrease, but mass-specific power (per unit body mass) should increase. Second, how does loading affect the kinematics of limb movement? Third, does size affect mass-specific power output? More specifically, we predicted that larger geckos (*G. gecko*) would produce less mass-specific power (relative to size) than smaller geckos (*H. garnoti*).

Materials and methods

Trial subjects

We elicited suitable locomotion from six *Gekko gecko* L. (mass=43.3±1.5 g, mean ± S.D.) and twelve *Hemidactylus garnoti* Dumeril and Bibron (mass 2.4±0.2 g, mean ± S.D.). Geckos were maintained alone or in pairs in cages (40 cm × 100 cm × 30 cm for *G. gecko*; 15 cm × 25 cm × 20 cm for *H. garnoti*) placed in a temperature controlled room (29±2°C) illuminated for 12 h a day. They were provided crickets with a vitamin/mineral supplement three times a week, and watered once daily.

Locomotion trials

We induced geckos to run vertically up a custom-built racetrack. The racetrack had Plexiglas walls attached on either

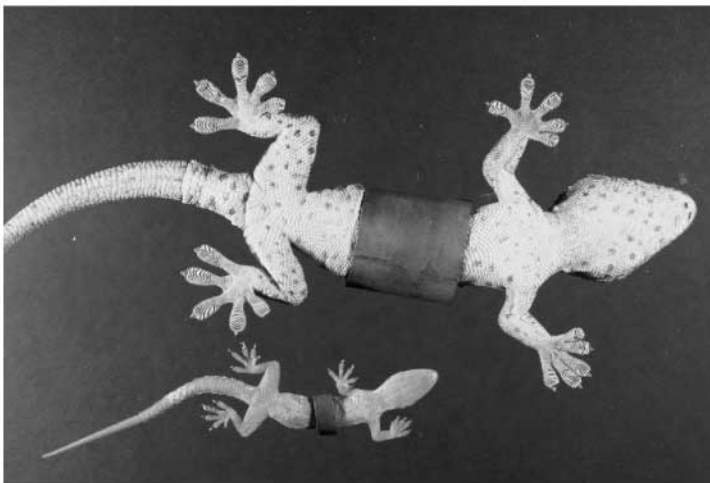


Fig. 2. Large (top, *G. gecko*) and small (bottom, *H. garnoti*) geckos with representative loads of 100% body mass. Photograph by Margarita Ramos.

side to a wooden base that was 13 cm wide and 150 cm long. We filmed the lizards from a dorsal perspective at 250 Hz with a motionscope PCI camera (Redlake, San Diego, CA, USA) attached to a PC computer. All locomotion clips were digitized using Peak performance MOTUS software.

Prior to each locomotion trial, lizards were placed either in plastic bags (*H. garnoti*) or canvas bags (*G. gecko*) inside an incubator set to 30°C for at least 30 min. We placed loads of 100–200% body mass (BM) on all individuals of *H. garnoti*, and loads of 100% BM on all individuals of *G. gecko*. For *G. gecko*, we acquired locomotion for movement uphill when unloaded and with a 100% BM load, whereas for *H. garnoti*, we acquired locomotion when moving uphill unloaded and with loads of 100%, 150% and 200% BM. We used small, thin lead weights that were wrapped approximately around the center of mass of each lizard (placed centrally between each girdle) (Fig. 2). The weights were attached to the body by placing a small piece of tape on the dorsal and ventral sides of the lizard. The width and thickness of the strips for the four load types were similar for each species, but the strips for the heavier loads were longer, and hence wrapped around the body to a greater degree. The loads did not appear to affect the overall locomotor behavior of the lizards, or the amount of lateral flexion of the back (see below). To determine whether the presence of the weight itself affected locomotion, we wrapped a piece of thin paper around the body of each *H. garnoti* that was similar in dimensions to the above weights, but only approximated 2% BM.

Each lizard was given ten opportunities to run at maximum speed with each of these weights. Loading condition was randomly assigned across days and lizards were tested on multiple, non-consecutive, days with the same loads. For each trial, we attempted to gain 2–5 strides of steady speed locomotion. We did not include any strides in which the animal was clearly accelerating or decelerating over the course of several strides. All data were analyzed on a stride-by-stride basis. We recorded footfall patterns of the hindfoot for each lizard, and defined a stride as the interval between consecutive footfalls of the right hindfoot (from a dorsal perspective). For each stride, we calculated stride length and stride frequency, and duty factor, speed and mean mass-specific power output per stride. Stride length was calculated as the displacement of the tip of the snout between consecutive footfalls; stride frequency was calculated as the reciprocal of stride duration (the time between consecutive footfalls); duty factor was calculated as the duration of foot contact (i.e. step duration) divided by stride duration; speed was calculated as stride length divided by stride duration. Since we used strides of steady speed locomotion, we only took into account gravitational forces to calculate mass-specific power output per unit body mass. Thus, mass-specific power output per unit body mass was calculated as the product of total mass m , gravitational acceleration (i.e. $F=mg$) and speed, divided by body mass. In this case, total mass equals the sum of body mass and the weight of the load.

To determine whether the addition of loads altered locomotor posture, we digitized the tip of the snout and tail, and three small evenly spaced white dots on the back, and calculated the angles of the head, trunk and tail over the whole stride cycle. The angle of the head was defined as the angle between the tip of the snout and the two dorsal points closest to the head, with angles of 180° indicating that the head was in alignment with the body, and angles greater or less than 180° indicating movement of the head towards the left or right, respectively. The angle of the trunk was defined as the angle between the three dorsal points, with angles of 180° indicating that the trunk was straight, and angles greater or less than 180° indicating lateral flexion towards the left or right, respectively. The angle of the tail was defined as the angle between the tip of the tail and the two most posterior dorsal points, with angles of 180° indicating that the tail was in alignment with the body, and angles greater or less than 180° indicating movement of the tail towards the left or right, respectively. For the same set of strides used in step (1) below, we calculated maximum and minimum values of each kinematic variable for each stride and compared loading conditions.

Statistical analyses

All values were log₁₀-transformed prior to statistical analyses. To determine whether loading affected angular kinematics, we conducted separate multivariate analyses of variance (MANOVAs) within each species, using the maximum and minimum values for each kinematic variable as dependent variables, and loading condition as the independent variable. If the MANOVA was significant within either species, we then used ANOVAs with loading condition as a factor and the different angles as dependent variables. We then used LSD *post-hoc* tests to determine where differences lie in the data structure.

We conducted several other analyses to address our primary questions. (1) For the issue of power limitation, we calculated, for each individual of each species, their maximum mass-specific power output and speed for each loading condition (based on stride-by-stride data). Because some individuals did not provide high quality runs for every loading condition, our sample sizes differ slightly among loading conditions within a species. To test for statistical differences among loading conditions for these data, we performed two one-way ANOVAs within each species using loading condition as a factor, and mass-specific power output and speed as dependent variables, respectively. We then conducted *post-hoc* tests to determine where the differences existed. (2) To address the issue of whether size affects mass-specific power output, we examined only those strides for which lizards produced the maximum amount of power for each species regardless of loading condition, and then used one-way ANOVAs to compare the two species. (3) To address the issue of whether speed modulation changes under different loading conditions, we performed bivariate linear regressions, using speed as independent variable and stride length, stride frequency and duty factor as dependent variables within each species. We

then used multiple regression analyses within each species, using stride length, stride frequency and duty factors as dependent variables, and speed and loading condition (i.e. unloaded, 2% BM, 100% BM, 150% BM and 200% BM for *H. garnoti* and unloaded and 100% BM for *G. gecko*) as independent variables to test for the effect of loading condition on stride length and stride frequency. (4) We conducted a multiple regression pooling both species (unloaded and 100% BM only), using stride length, stride frequency or duty factor as dependent variables, and speed, loading condition and species as independent variables, to test whether the two species react to the different loads in similar ways.

Table 1. Descriptive angular kinematic statistics for small (*H. garnoti*) geckos running vertically with various loads

Variable	Load	N	Angle of variable (deg.)	Speed (m s ⁻¹)
Head				
Max.	0	9	203.67±2.81	0.83±0.08
	2	7	202.30±3.18	1.45±0.19
	100	8	209.20±3.00	0.61±0.05
	150	9	205.90±2.81	0.64±0.05
	200	9	203.90±2.81	0.53±0.03
Min.	0	9	160.37±2.99	0.83±0.08
	2	7	156.91±3.39	1.45±0.19
	100	8	158.33±3.17	0.61±0.05
	150	9	159.20±3.00	0.64±0.05
	200	9	157.23±3.00	0.53±0.03
Trunk				
Max.	0	9	212.12±3.05	0.83±0.08
	2	7	208.07±3.46	1.45±0.19
	100	8	208.27±2.24	0.61±0.05
	150	9	202.27±3.05	0.64±0.05
	200	9	210.16±3.05	0.53±0.03
Min.	0	9	147.19±3.05	0.83±0.08
	2	7	155.78±3.46	1.45±0.19
	100	8	150.28±2.24	0.61±0.05
	150	9	151.41±3.05	0.64±0.05
	200	9	160.72±3.05	0.53±0.03
Tail				
Max.	0	9	209.37±6.06	0.83±0.08
	2	7	212.97±6.88	1.45±0.19
	100	8	193.78±6.43	0.61±0.05
	150	9	197.28±6.06	0.64±0.05
	200	9	205.78±6.06	0.53±0.03
Min.	0	9	149.37±4.63	0.83±0.08
	2	7	157.69±5.25	1.45±0.19
	100	8	163.14±4.91	0.61±0.05
	150	9	164.16±4.63	0.64±0.05
	200	9	165.67±4.63	0.53±0.03

N, number of individuals (one stride per individual).

Values are means ± S.E.M.

Max., maximum; Min., minimum.

Speeds are slightly different from the values in Table 3 because slightly different groups of animals were used.

Results

Angular kinematics

The MANOVA comparing loading conditions for *H. garnoti* was barely significant (Wilks' $\lambda=0.344$, $F_{24,112}=1.68$, $P=0.037$), whereas the MANOVA for *G. gecko* was non-significant (Wilks' $\lambda=0.125$, $F_{2,6}=2.334$, $P>0.30$) (Tables 1, 2). One-way ANOVAs within *H. garnoti* showed that the only variable that differed significantly among loading conditions was the minimum value of trunk angle ($F_{4,37}=2.91$, $P=0.034$), which only differed significantly between the unloaded and 200% loading conditions (*post-hoc* test, $P=0.025$). Thus, overall, loading does not substantially affect angular kinematics during vertical locomotion in either gecko species.

Power output and speed

Mean speed generally declined with the addition of increasingly larger loads for both species (Table 3). In *H. garnoti*, mean speed declined 25% between the unloaded and 100% BM conditions, and 37% between the unloaded and 200% BM conditions. In *G. gecko*, mean speed declined 31% between the unloaded and 100% BM conditions. As loads were added, mean mass-specific power output increased substantially at first for both species (Table 3), but for *H. garnoti*, power production leveled off at higher loads, (1% increase in power between the 150% and 200% BM conditions, 21% decline in velocity). The one-way ANOVAs testing for loading differences in power and speed were statistically significant for both variables within both species (Table 4). However, *post-hoc* comparisons showed that mass-specific

Table 2. Descriptive angular kinematic statistics for large (*G. gecko*) geckos running vertically with various loads

Variable	Load	N	Angle of variable (deg.)	Speed (m s ⁻¹)
Head				
Max.	0	5	198.79±5.97	0.96±0.07
	100	4	191.83±6.67	0.69±0.07
Min.	0	5	162.03±5.31	0.96±0.07
	100	4	150.44±5.93	0.69±0.07
Trunk				
Max.	0	5	203.94±6.10	0.96±0.07
	100	4	217.11±6.82	0.69±0.07
Min.	0	5	152.56±3.48	0.96±0.07
	100	4	166.84±3.89	0.69±0.07
Tail				
Max.	0	5	197.74±8.41	0.96±0.07
	100	4	213.94±9.40	0.69±0.07
Min.	0	5	154.48±10.64	0.96±0.07
	100	4	121.57±11.90	0.69±0.07

N, number of individuals (one stride per individual).

Values are means ± S.E.M.

Max., maximum; Min., minimum.

Speeds are slightly different from the values in Table 3 because slightly different groups of animals were used.

power differed between the unloaded condition and all the loaded ones (i.e. 2% BM, 100% BM, 150% BM and 200% BM; all $P<0.01$), but not among the loaded conditions in *H. garnoti* (all P values >0.05). In contrast, speed differed significantly between the control (i.e. 2% BM) and all other conditions (i.e. unloaded, 100% BM, 150% BM and 200% BM; all P values <0.05).

Analyses using only the strides that produced the maximum mass-specific power within each species (regardless of loading condition) show that mean maximum mass-specific power output is 33% greater in *H. garnoti* than in *G. gecko* (one-way ANOVA, $F_{1,1}=7.2$, $P<0.025$; Fig. 3A), whereas maximum speed is only slightly, and non-significantly, greater (19%) in *G. gecko* (one-way ANOVA, $F_{1,1}=1.6$, $P>0.20$; Fig. 3B).

Speed modulation

The bivariate regression analyses show that under all loading conditions, and in both species, stride frequency increases to a greater extent with speed than does stride length (Table 5; Fig. 4). This suggests that in all cases, the geckos modulate speed primarily by altering stride frequency. However, duty factor shows no obvious relationship with speed, with the exception of *H. garnoti* moving unloaded (Table 5). Based on multiple regression analyses, speed and loading condition

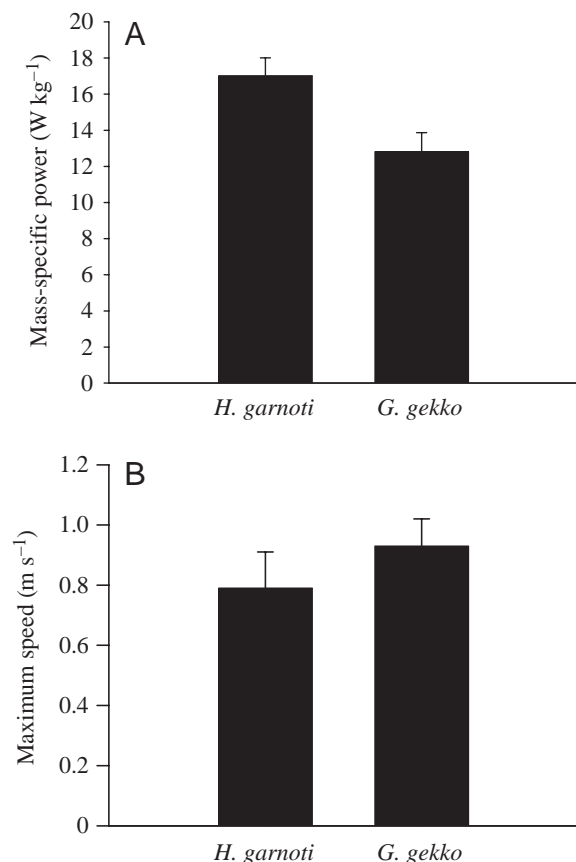


Fig. 3. Maximum values (means ± 1 S.E.M.) of mass-specific power (A) and speed (B) for small (*H. garnoti*) and large (*G. gecko*) geckos.

Table 3. Descriptive statistics for power output and speed for small (*H. garnoti*) and large (*G. gecko*) geckos running vertically with various loading conditions

	Load*	N	Mass-specific power (W kg ⁻¹)		Speed (m s ⁻¹)	
			Mean ± S.E.M.	Range	Mean ± S.E.M.	Range
<i>H. garnoti</i>	0	11	8.27±0.66	4.14–11.04	0.84±0.07	0.42–1.13
	2	11	13.01±1.47	6.06–19.96	1.30±0.15	0.61–2.00
	100	9	12.47±0.82	9.93–16.98	0.63±0.05	0.48–0.91
	150	9	15.99±1.07	12.10–22.95	0.64±0.14	0.46–0.94
	200	9	16.16±0.93	12.28–20.01	0.53±0.10	0.39–0.63
<i>G. gecko</i>	0	6	9.78±0.70	7.93–12.03	1.00±0.07	0.81–1.23
	100	4	13.61±1.30	10.07–16.32	0.69±0.07	0.52–0.83

*The loads are denoted as % body mass.

N, number of individuals (one stride per individual).

'2' condition, the paper control; '0', unloaded condition.

Table 4. Results from one-way ANOVAs using loading condition as a factor for detecting differences in mass-specific power output and speed within *H. garnoti* and *G. gecko*

	F	d.f.	P-value
<i>H. garnoti</i>			
Mass-specific power	10.75	1,4	<0.0001
Speed	14.19	1,4	<0.0001
<i>G. gecko</i>			
Mass-specific power	7.66	1,1	0.02
Speed	9.55	1,1	0.02

(independent variables) explain 70% and 89% of the variation in stride length and frequency, respectively, for *H. garnoti* (Table 6), whereas for *G. gecko*, they explain 69% and 70% of the variation, respectively. Speed and loading condition explain 58% (*H. garnoti*) and 70% (*G. gecko*) of the variation in duty factor from these multiple regressions.

With the addition of increasingly large loads, both gecko

species take smaller but more strides per unit distance for a given speed (Table 7). The multiple regression analyses with stride length or stride frequency as dependent variable, and species, loading condition and speed as independent variables, show that for a given speed and load, the two species differ in stride length and stride frequency: *G. gecko* takes larger but fewer strides than *H. garnoti* (Table 7). For a given speed and load, *G. gecko* has a greater duty factor than *H. garnoti*, which is not surprising, as larger lizards likely need more time to push off with larger loads (Table 7).

We also repeated the analyses in Table 7 by analyzing speed and stride length on a size-adjusted basis, by dividing both variables by mass, but keeping the other variables (independent variables = loading and species type; dependent variables = stride frequency and duty factor) constant (Table 8). This reanalysis shows that for a given relative speed and load, *G. gecko* takes larger relative strides at a lower frequency. At a given relative speed, both species use similar duty factors (no species effect) (Table 8).

Table 5. Results from regression analyses using stride length, stride frequency or duty factor as dependent variables, and speed as the independent variable

Load	Stride length [†]		Stride frequency		Duty factor	
	Slope	y-intercept	Slope	y-intercept	Slope	y-intercept
<i>H. garnoti</i>						
0	0.24±0.05***	-1.19±0.02***	0.76±0.05***	1.19±0.02***	-0.13±0.05**	-0.33±0.01***
2	0.19±0.04***	-1.23±0.01***	0.81±0.04***	1.23±0.01***	0.01±0.04	-0.13±0.01***
100	0.33±0.05***	-1.21±0.02***	0.67±0.05***	1.21±0.02***	-0.09±0.05	-0.27±0.02***
150	0.30±0.06***	-1.24±0.02***	0.70±0.06***	1.24±0.02***	-0.10±0.07	-0.25±0.02***
200	0.32±0.06***	-1.25±0.02***	0.68±0.06***	1.25±0.02***	-0.003±0.07	-0.21±0.03***
<i>G. gecko</i>						
0	0.34±0.15*	-0.84±0.02***	0.66±0.15***	0.84±0.02***	-0.08±0.11	-0.31±0.02***
100	0.27±0.13*	-0.95±0.04***	0.73±0.13***	0.95±0.04***	-0.02±0.07	-0.21±0.02***

Asterisks indicate significant relationships between the independent and dependent variables; * $P<0.05$, *** $P<0.0001$.

Values of stride length (cm), stride frequency (Hz), duty factor and speed (m s⁻¹) were log₁₀-transformed prior to statistical analyses.

[†]Values are ±1 S.E.M.

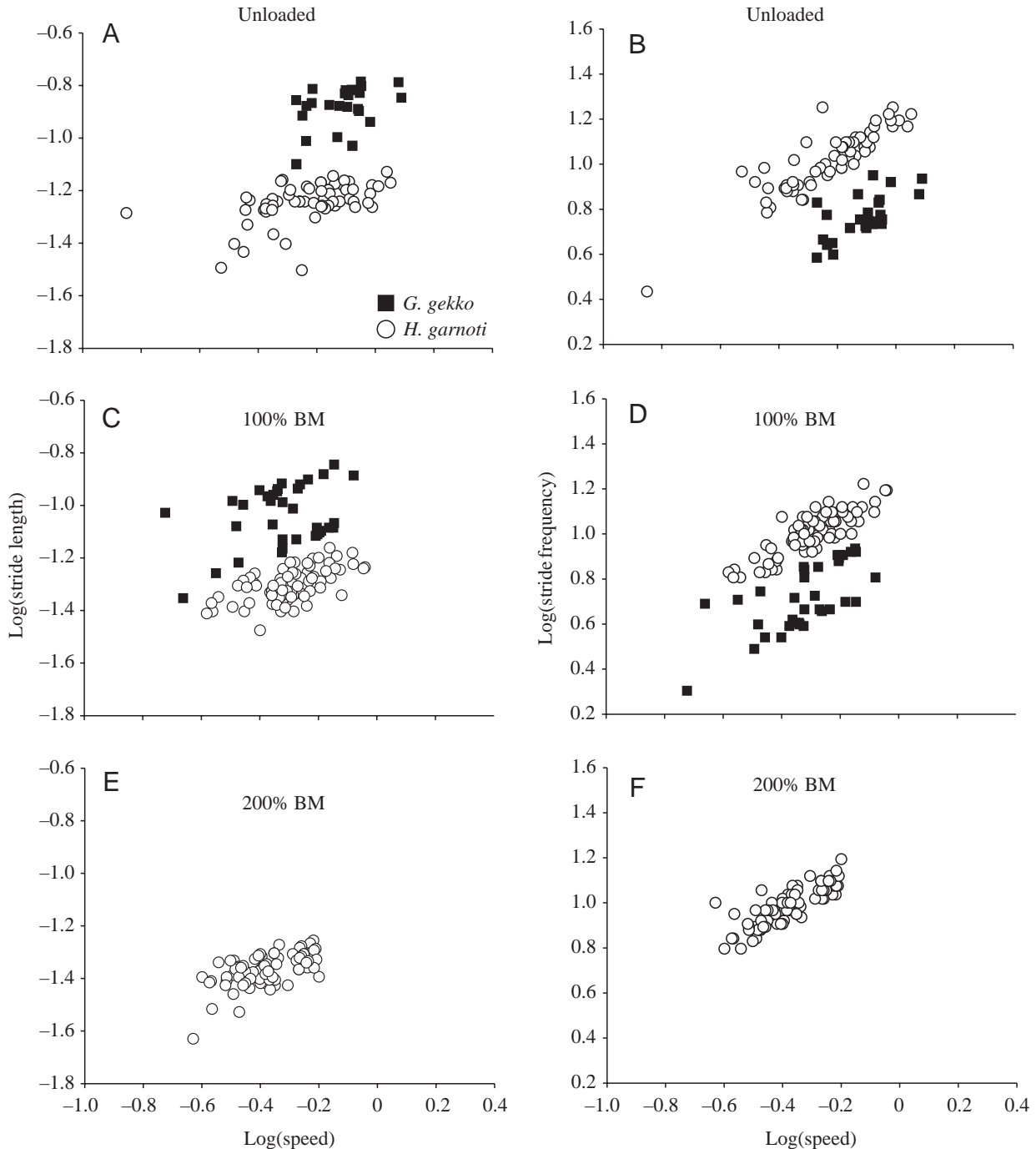


Fig. 4. Scatterplots of stride length (A,C,E) and stride frequency (B,D,F) versus speed (x axis) for various loading conditions during uphill climbing for small (open circles; *H. garnoti*) and large (filled squares; *G. gekko*) geckos. Note that in none of the plots does stride length or stride frequency level off as speed increases. Values are \log_{10} -transformed.

Discussion

Does power limit performance?

A central, yet largely unresolved, issue among physiologists interested in locomotion is which factors limit maximum speed during running, swimming or flying (Ellington, 1991; Swoap et al., 1993; Wakeling and Johnston, 1998; Irschick et al., 2001; Askew and Marsh, 2002). Some authors have suggested that mechanical power output can limit maximum speed, at

least for certain taxa such as large, flying animals (Pennycuik, 1969, 1972; Ellington, 1991). Determining whether maximum power output is limiting is difficult, but our data suggest that maximum mass-specific power output may limit maximum speed in at least one of the two gecko species (*H. garnoti*). Our results show a significant difference in mass-specific power output per unit body mass between the unloaded condition and any given loaded condition. However, one surprising result

Table 6. Results from multiple regressions within both *H. garnoti* and *G. gecko* attempting to explain variation in stride length, stride frequency and duty factor (dependent variables) using speed and the loading condition (independent variables) in each regression

Variable		<i>r</i>	<i>F</i>	<i>P</i>	Partial <i>r</i>
Dependent	Independent				
<i>H. garnoti</i>					
Stride length	Speed	0.70	175.2	<0.0001	0.50
	Load				-0.38
Stride frequency	Speed	0.89	686.5	<0.0001	0.88
	Load				0.38
Duty factor	Speed	0.58	93.4	<0.0001	-0.13
	Load				0.51
<i>G. gecko</i>					
Stride length	Speed	0.69	26.71	<0.0001	0.36
	Load				-0.63
Stride frequency	Speed	0.70	28.3	<0.0001	0.69
	Load				0.40
Duty factor	Load	0.70	56.7	<0.0001	0.70

was that speed was somewhat higher in the 'control' (2% body mass condition) compared to the unloaded condition for the small gecko (*H. garnoti*). This result is unexpected, as geckos in both conditions were run an approximately equal number of times. One possibility is that the addition of loads presented an additional stimulus to the animals that elicited higher speeds. In any case, since *H. garnoti* with the 2% load and all other loads all experienced similar conditions, any comparisons among them should be valid.

The fact that *H. garnoti* produces similar amounts of power with the 2% BM, 100% BM, 150% BM and 200% BM loads suggest a leveling-off of mass-specific power output, which may prevent them from moving with larger loads, or at faster

Table 7. Results from multiple regressions pooling all *H. garnoti* (*species*=1) and *G. gecko* (*species*=2), attempting to explain variation in stride length, stride frequency and duty factor (dependent variables) using speed, loading condition and species (independent variables) in each regression

Variable		<i>r</i>	<i>F</i>	<i>P</i>	Partial <i>r</i>
Dependent	Independent				
Stride length	Speed	0.91	307.2	<0.0001	0.50
	Load				-0.36
	Species				0.88
Stride frequency	Speed	0.91	316.6	<0.0001	0.80
	Load				0.36
	Species				-0.88
Duty factor	Speed	0.62	40.8	<0.0001	0.48
	Load				0.19
	Species				-0.22

speeds with a given load (see also Fig. 5A). However, as a cautionary note, our speeds in the unloaded condition for *G. gecko* may be slightly less than maximum speed, which is not unusual when comparing different locomotor performance studies on the same animals (Irschick and Garland, 2001). Indeed, it is important to compare maximum speeds across different data sets (Irschick and Garland, 2001). R. Van Damme and A. Zaaf (unpublished data) measured maximal speeds on a vertical incline for (unloaded) *G. gecko* of 1.44 m s⁻¹ (measured over a fixed distance of 25 cm). Extrapolation of our data results in a corresponding mass-specific output of 14.13 W kg⁻¹. This new value is similar to the maximal mass-specific power output obtained under the 100% BM loading condition (16.04 W kg⁻¹). Again, this suggests a leveling-off of mass-specific power output (see also Fig. 5B). However, more data on the maximum speeds of *G. gecko* may be necessary to determine which of the above

Table 8. Results from multiple regressions pooling all *H. garnoti* (*species*=1) and *G. gecko* (*species*=2), attempting to explain variation in relative stride length, stride frequency and duty factor (dependent variables) using relative speed, loading condition and species (independent variables) in each regression

Variable		<i>r</i>	<i>F</i>	<i>P</i>	Partial <i>r</i>
Dependent	Independent				
Relative stride length	Relative speed	0.93	449.5	<0.0001	0.30
	Load				0.07
	Species				0.79
Stride frequency	Relative speed	0.76	92.2	<0.0001	-0.28
	Load				0.05 (NS)
	Species				-0.64
Duty factor	Relative speed	0.62	40.8	<0.0001	0.33
	Load				0.44
	Species				0.07 (NS)

NS, non-significant.

Relative stride length, stride length divided by mass; Relative speed, speed divided by mass.

values more correctly estimates maximum speed in this species. Moreover, another possible explanation for the pattern observed within either species is that power does not limit maximum speed, but rather some other factor that covaries with power is responsible.

Irschick et al. (2001) examined the power output of *H. garnoti* running at submaximal preferred speeds with 30% BM and 60% BM loads on a vertical force platform, and concluded that power output did not limit maximum speed. However, that conclusion was based on submaximal running, as opposed to maximal or near-maximal running in the current study. Thus, power may not limit uphill loaded locomotion until geckos run at maximum speeds. Farley (1997) examined power output in two species of small (<10 g) terrestrial lizards when running unloaded on level and inclined surfaces (+20°, +40°) and concluded that the mechanical power required to lift the body vertically was 3.9 times greater than the external mechanical power output when moving on the level surface. By comparison, *H. garnoti* double their mean power output on changing from running unloaded uphill to running uphill with a 200% BM load. Farley (1997) found that power output continued to increase as each lizard species ran up successively steeper inclines, even though maximum speed declined, thus refuting the hypothesis that mass-specific power limits maximum speed. This difference between the work of Farley (1997) and ours can be explained by the different demands of horizontal and vertical running in lizards. When running either horizontally or on an incline when unloaded, maximum power output clearly does not limit maximum speed in lizards, but in our experiments, we forced the lizards to conduct tasks (running uphill with a load) that we knew would result in much higher total power outputs. Thus, it is possible that power output does not limit maximum speed for lizards running up relatively shallow inclines, or that move on horizontal surfaces, but power may limit vertical locomotion in lizards, particularly when moving with large loads.

A general finding emerging from comparative studies is that animals are capable of producing substantially more power than they may use for everyday activities (Askew and Marsh, 1997; Chai et al., 1997; Chai and Dudley, 1995; Farley, 1997). Activities that require high power output include take-off (quail; Askew and Marsh, 2002), running vertically with loads

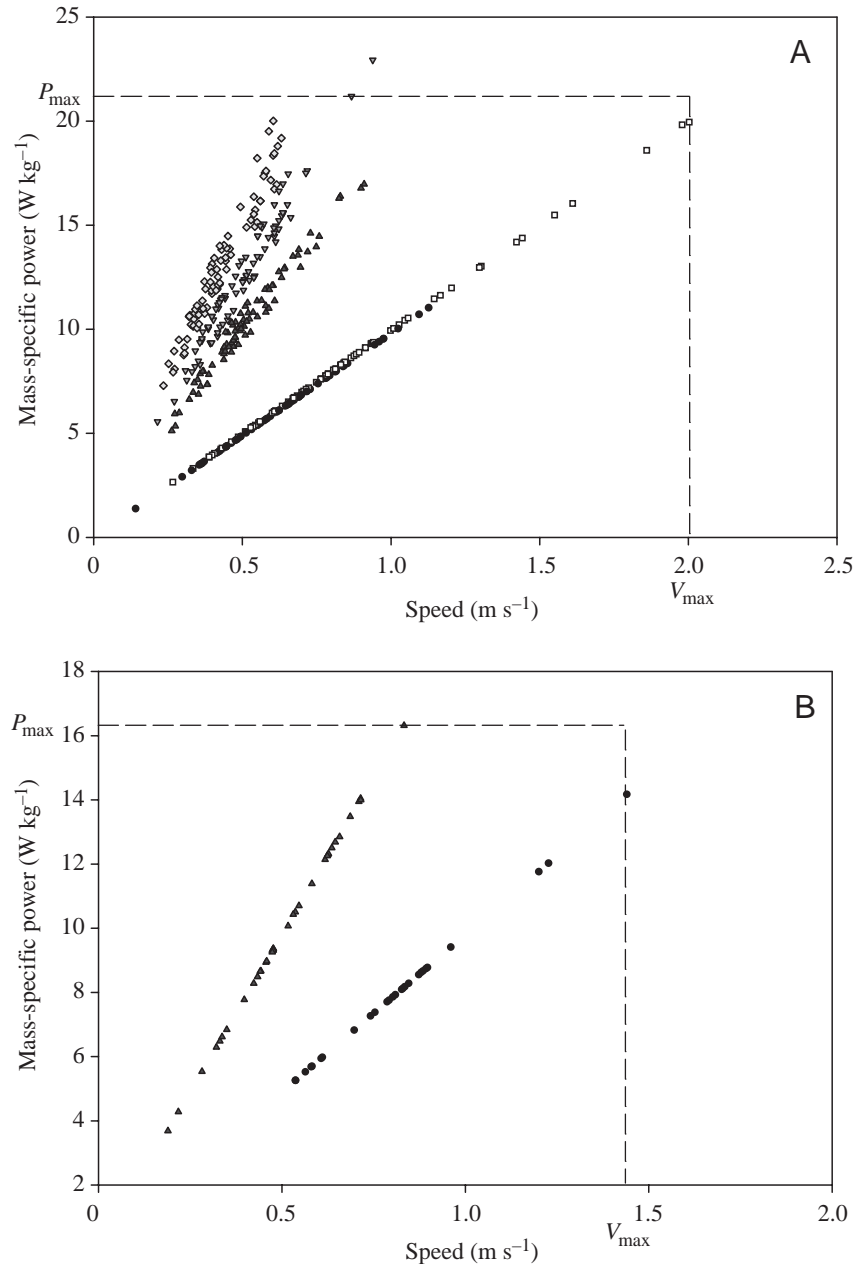


Fig. 5. Scatterplots of mass-specific power output versus speed for all strides obtained for both gecko species. (A) Mass-specific power output against speed for *H. garnoti* under five loading conditions (filled circles, unloaded; open squares, 2% BM; filled triangles, 100% BM; grey inverted triangles, 150% BM; grey diamonds, 200% BM). We obtained one extremely high value of mass-specific power output under the 150% loading condition. (B) Mass-specific power output against speed for *G. gecko* under two loading conditions (filled circles, unloaded; filled triangles, 100% BM). Extrapolation of maximal mass-specific power output to maximal speed (R. Van Damme, unpublished data) gives a value of 14.17 W kg⁻¹ (filled circles). For both species, most of the loading conditions tend to level off near P_{\max} , supporting the hypothesis that mass-specific power output limits speed in these lizards.

(present study), and hovering under high loading conditions (hummingbirds; Chai et al., 1997). However, an unresolved question for most animal groups is the ecological context in which these high power outputs are used (if at all). In the case

of geckos, one possibility is the need to run uphill effectively when carrying large loads in the form of eggs, or large food items (R. Huey, personal communication). Female geckos and other lizards (Bauwens and Thoen, 1981) can carry eggs weighing as much as 10–30% of their body mass. In the present work, we examined geckos carrying loads much greater than they are ever likely to carry in nature, but our data do indicate that the muscular and locomotor apparatus of geckos appears to be highly ‘overbuilt’ relative to their ecological requirements. An important reason for this could be the subdigital toepads used by geckos to grasp onto surfaces (Russell, 1979; Irschick et al., 1996). In a recent study of gecko setae, Autumn et al. (2000) estimated that tokay geckos (*G. gecko*) are capable of generating forces up to 100 N with one foot, while whole-organism clinging studies (Irschick et al., 1996) showed that these lizards typically achieve clinging forces of about 10 N for a single foot. Thus, if tokay geckos were able to recruit all of their setae simultaneously, they would be capable of carrying very large loads indeed. Consequently, even based on the whole-organism clinging studies by Irschick et al. (1996), the ability of the toepads to cling is not the limiting step as to why either species could not carry greater loads.

Another aspect of locomotion that requires high power output is acceleration, especially during sharp turns such as observed in the C-start escape response of fish (Wakeling and Johnston, 1998). The ability to make abrupt turns is a key part of the escape response of geckos, although few studies have examined such ‘maneuvering’ ability in lizards (but see Van Damme and Vanhooydonck, 2002; Vanhooydonck and Van Damme, 2003), and its relation to power output.

Does body size affect mass-specific power output?

Due to a lack of loading studies for animals moving uphill, the most relevant available studies for examining the effects of loading on mass-specific power output are of flying organisms such as insects, bats and birds. The dynamics of moving directly uphill and flying are similar, in that in both cases animals must work against gravity, and thus produce a substantial amount of power. Marden (1987) examined the largest load that several insect, bat and bird species could carry to understand whether species of different sizes can carry the same percentage of body mass. Contrary to theoretical predictions, the maximum lift per unit flight muscle mass was similar among taxonomic groups (54–63 N kg⁻¹). On this basis, large flying animals (e.g. birds, bats) were capable of carrying similar loads (as a percentage of body mass) to relatively small flying animals, such as insects. In addition, interspecific differences in short-duration power output were primarily related to the flight muscle ratio (ratio of the mass of flight muscles divided by all other muscles in the wing; Marden, 1987), suggesting that species with high mass-specific power outputs have evolved large amounts of flight muscle.

While our results show that *H. garnoti* has a higher maximal mass-specific power output than *G. gecko*, one should interpret this difference cautiously. Because the unloaded speeds of *G.*

gecko may be slightly less than maximum capacity, it is possible that we have underestimated their maximum power output. Extrapolation of our results to the maximal speed measured by Van Damme and Zaaf (see above) gives a mass-specific power output of 14.13 W kg⁻¹. If we replace lower values of ‘maximal mass-specific power output’ (for each individual) with this value, the difference between *H. garnoti* and *G. gecko* is not significant (one way ANOVA; $F_{1,16}=2.63$, $P=0.12$). This result corresponds to those from studies on flying animals (see above). Thus, more data on the maximum speeds of *G. gecko* as well as its relationship to power output and loading appear to be necessary before firm conclusions can be drawn.

Does loading condition affect speed modulation?

Several studies have investigated the effects of loading on energetics (Taylor et al., 1980; Herreid and Full, 1985; Kram, 1996), kinematics (Wren et al., 1998; Zani and Claussen, 1995; Hoyt et al., 2000) and performance (Zani and Claussen, 1995; Wren et al., 1998), but few studies have studied the effects of loading on mass-specific power output and kinematics when moving uphill.

First, it is clear from our results that the addition of weights does not affect the speed modulation strategy of either *H. garnoti* or *G. gecko*. Regardless of loading condition, speed increases primarily by increasing stride frequency in both species. The fact that geckos modulate their speed mainly by altering stride frequency and not stride length is in accordance with the results of Zaaf et al. (2001), who found that *G. gecko* is primarily a frequency modulator on both vertical and horizontal surfaces.

At a given speed, however, the addition of loads significantly affects both stride length and stride frequency. Both species take smaller but more strides with heavier loads and thus, the effect of loading condition seems to be the same in *H. garnoti* and *G. gecko*. It is unclear why this is the case. Smaller steps (and hence strides) with heavier loads might reflect ‘uncertainty’ on part of the animal, analogous to the hesitant small steps of humans walking on slippery surfaces, or of impaired or elderly people (Zatsiorsky et al., 1994; Grabiner, 1997; Vaughan, 1997). The increase in stride frequency when carrying a load, as observed in this study, corresponds to the results of some studies on load carrying (e.g. Cooke et al., 1991), but differs from others (e.g. Hoyt et al., 2000). The effects of loading and size on duty factor are also apparent. First, within *H. garnoti* at a given speed, duty factor increases with increased loading, while for a given load, duty factor declines with speed. Similarly, within *G. gecko* at a given speed, duty factor also increases with loading. These results make intuitive sense, as the addition of loads probably forces these lizards to spend more time pushing against the ground to generate the required forces for movement.

Problems with comparing findings from previous loading studies are not only the difference in locomotor speeds examined, but also the taxonomic diversity among studies. Some studies examined the effects of loading on animals

moving at slow preferred speeds (Hoyt et al., 2000; Wickler et al., 2001), whereas other studies examined loading effects on maximum speeds (Zani and Claussen, 1995; Wren et al., 1998). The addition of loads up to 150% BM significantly decreased maximum speed, stride length and stride frequency in turtles (Zani and Claussen, 1995; Wren et al., 1998). However, for several mammal species moving over a range of speeds, and with loads of 7–27% BM, no significant effects of loading on stride frequency were observed (Taylor et al., 1980). From the interspecific comparison, on the other hand, it is clear that, for a given load and at a given speed, *G. gecko* takes longer strides while *H. garnoti* takes more strides. Surprisingly, this does not seem to be the result of the differences in dimensions between the two species. At similar relative speeds, *G. gecko* still takes longer relative strides than *H. garnoti*. Thus, loading effects on gait characteristics seem to be both speed- and species-dependent; more comparative data for different species moving with loads on level and inclined surfaces would be welcome.

In sum, several key findings are apparent from our data. First, several lines of evidence suggest that power limits maximum speed in both gecko species. Stride frequency does not level off as speed increases for any loading condition in either species, suggesting that lizards do not reach a maximum stride frequency that they cannot exceed. Further, even though mass-specific power output increases significantly between the unloaded and any loaded condition, the small *H. garnoti* produces similar amounts of power when running with 150% and 200% BM loads, suggesting that they have reached their power limit. Second, while the large gecko produced approximately 33% less maximum power than the smaller *H. garnoti*, this difference disappeared when we used the slightly higher speeds for *G. gecko* gathered by other researchers. Finally, speed is primarily modulated by changes in stride frequency, regardless of loading condition and species. At a given speed, on the other hand, the addition of loads causes both species to take smaller, but more, strides per unit distance.

We thank Peter Aerts and two anonymous reviewers for helpful comments on previous versions of this manuscript, and especially thank Robert Full and Kellar Autumn for providing the original inspiration for this study. This work was supported by an NSF grant to D. Irschick (IBN 9983003) and generous funding from DARPA. A. Herrel and B. Vanhooydonck are postdoctoral fellows at the Fund for Scientific Research Flanders (FWO-VI).

References

- Aerts, P. (1990). Mathematical biomechanics and the 'what!', 'how?' and 'why' in functional morphology. *Neth. J. Zool.* **40**, 153-172.
- Askew, G. N. and Marsh, R. L. (1997). The effects of length trajectory on the mechanical power output of mouse skeletal muscles. *J. Exp. Biol.* **200**, 3119-3131.
- Askew, G. N. and Marsh, R. L. (2002). Muscle designed for maximum short-term power output: quail flight muscle. *J. Exp. Biol.* **205**, 2153-2160.
- Autumn, K., Liang, Y. A., Hsieh, S. T., Zesch, W., Chan, W.-P., Kenny, T. W., Fearing, R. and Full, R. J. (2000). Adhesive force of a single gecko foot-hair. *Nature* **405**, 681-685.
- Bauwens, D. and Thoen, C. (1981). Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J. Anim. Ecol.* **50**, 733-743.
- Chai, P., Chen, J. S. C. and Dudley, R. (1997). Transient hovering performance of hummingbirds under conditions of maximal loading. *J. Exp. Biol.* **200**, 921-929.
- Chai, P. and Dudley, R. (1995). Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. *Nature* **377**, 722-725.
- Cooke, C. B., McDonagh, M. J. N., Nevill, A. M. and Davies, C. T. M. (1991). Effects of load on oxygen intake in trained boys and men during treadmill running. *J. Appl. Physiol.* **71**, 1237-1244.
- Ellington, C. P. (1991). Limitations on animal flight performance. *J. Exp. Biol.* **160**, 71-91.
- Farley, C. T. (1997). Maximum speed and mechanical power output in lizards. *J. Exp. Biol.* **200**, 2189-2195.
- Garland, T., Jr and Adolph, S. C. (1994). Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol. Zool.* **67**, 797-828.
- Garland, T., Jr and Arnold, S. J. (1983). Effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* **1983**, 1092-1096.
- Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool. Lond.* **224**, 127-147.
- Grabiner, M. D. (1997). Locomotion in healthy older adults. In *Three-Dimensional Analysis of Human Locomotion* (ed. P. Allard, A. Cappozzo, A. Lundberg and C. L. Vaughan), pp. 363-374. Chichester: John Wiley and Sons.
- Herreid, C. F. and Full, R. J. (1985). Energetics of hermit crabs during locomotion: the cost of carrying a shell. *J. Exp. Biol.* **120**, 297-308.
- Hill, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Progr.* **38**, 209-230.
- Hoyt, D. F., Wickler, S. J. and Cogger, E. A. (2000). Time contact and step length: the effect of limb length, running speed, load carrying and incline. *J. Exp. Biol.* **203**, 221-227.
- Irschick, D. J., Austin, C. C., Petren, K., Fisher, R. N., Losos, J. B. and Ellers, O. (1996). A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.* **59**, 21-35.
- Irschick, D. J. and Garland, T., Jr (2001). Integrating function and ecology in studies of adaptation: Studies of locomotor capacity as a model system. *Annu. Rev. Ecol. System.* **32**, 367-396.
- Irschick, D. J., Bocchi, S. and Full, R. J. (2001). Does power limit climbing performance? Loading small climbing lizards. *Am. Zool.* **41**, 1481.
- Kram, R. (1996). Inexpensive load carrying by rhinoceros beetles. *J. Exp. Biol.* **199**, 609-612.
- Marden, J. H. (1987). Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* **130**, 235-258.
- Pennyquick, C. J. (1969). The mechanics of bird migration. *Ibis* **111**, 525-556.
- Pennyquick, C. J. (1972). *Animal Flight*. London, Arnold Press.
- Russell, A. P. (1979). Parallelism and integrated design in the foot structure of gekkonine and diplodactylid geckos. *Copeia* **1979**, 1-21.
- Swoap, S. J., Johnson, T. P., Josephson, R. K. and Bennett, A. F. (1993). Temperature, muscle power output, and limitations on burst locomotor performance of the lizard *Dipsosaurus dorsalis*. *J. Exp. Biol.* **174**, 185-197.
- Taylor, C. R., Heglund, N. C., McMahon, T. C. and Looney, T. R. (1980). Energetic cost of generating muscular force during running a comparison of large and small animals. *J. Exp. Biol.* **86**, 9-18.
- Toro, E., Herrel, A., Vanhooydonck, B. and Irschick, D. J. (2003). A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards. *J. Exp. Biol.* **306**, 2641-2652.
- Van Damme, R. and Vanhooydonck, B. (2002). Speed versus manoeuvrability: association between vertebral number and habitat structure in lacertid lizards. *J. Zool. Lond.* **258**, 327-334.
- Vanhooydonck, B. and Van Damme, R. (1999). Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evol. Ecol. Res.* **1**, 785-805.
- Vanhooydonck, B. and Van Damme, R. (2003). Relationships between locomotor performance, microhabitat use, and anti-predator behaviour in lacertid lizards. *Funct. Ecol.* **17** (in press).
- Vaughan, C. L. (1997). Neural network models of the locomotor apparatus.

- In *Three-Dimensional Analysis of Human Locomotion* (ed. P. Allard, A. Cappozzo, A. Lundberg and C. L. Vaughan), pp. 259-280. Chichester: John Wiley and Sons.
- Vitt, L. J. and Congdon, J. D.** (1978). Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* **112**, 595-608.
- Wakeling, J. M. and Johnston, I. A.** (1998). Muscle power output limits fast-start performance in fish. *J. Exp. Biol.* **201**, 1505-1526.
- Wickler, S. J., Hoyt, D. F., Cogger, E. A. and Hall, K. M.** (2001). Effect of load on preferred speed and cost of transport. *J. Appl. Physiol.* **90**, 1548-1551.
- Wilson, R. S., Franklin, C. E. and James, R. S.** (2000). Allometric scaling relationships of jumping performance in the striped marsh frog, *Limnodynastes peronii*. *J. Exp. Biol.* **203**, 1937-1946.
- Wren, K., Claussen, D. L. and Kurz, M.** (1998). The effects of body size and extrinsic mass on the locomotion of the ornate box turtles, *Terrapene ornata*. *J. Herpetol.* **32**, 144-150.
- Zaaf, A., Van Damme, R., Herrel, A. and Aerts, P.** (2001). Spatio-temporal gait characteristics of level and vertical locomotion in a ground-dwelling and climbing gecko. *J. Exp. Biol.* **204**, 1233-1246.
- Zaaf, A. and Van Damme, R.** (2001). Limb proportions in climbing and ground-dwelling geckos (Lepidosauria, Gekkonidae): a phylogenetically informed analysis. *Zoomorphol.* **121**, 45-53.
- Zani, P. A. and Claussen, D. L.** (1995). Effects of extrinsic load on locomotion in painted turtles (*Chrysemys picta*). *Copeia* **1995**, 735-738.
- Zatsiorsky, V. M., Werner, S. L. and Kaimin, M. A.** (1994). Basic kinematics of walking: step length and step frequency. A review. *J. Sports Med. Phys. Fitness* **34**, 109-134.