Effects of temperature on maximum acceleration, deceleration and power output during vertical running in geckos

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Summary

We studied performance and kinematics of the diurnal gekkonid lizard *Phelsuma dubia* while running vertically on a smooth surface at different temperatures. Trials were conducted at 5°C intervals from 15°C to 35°C. High-speed video recordings and digitization were used to obtain measures of instantaneous velocity, acceleration, deceleration and mass-specific power output and maximal values for each were taken as performance measures. Kinematic variables were also obtained from high-speed video recordings and included stride length and duration, step (stance phase) length and duration, and duty factor. Maximal instantaneous velocity, acceleration and deceleration increased by a factor of approximately 1.7 between 15°C and 25°C, and less so (~1.2×) between 25°C and 35°C. Mass-specific power output was more temperature-sensitive, increasing 2.5× up to 25°C and a further 1.4× above that temperature. Stride length increased 1.5× over the entire temperature interval studied, while stride duration decreased by a factor of 1.9, suggesting that velocity is modulated by changes in both stride length and duration in *P. dubia*. Duty factor was not significantly influenced by temperature. Stride length was the only kinematic measure to be influenced by stride number, with second steps from a standstill being longer than first steps. We discuss the significance of velocity and acceleration being affected in a similar manner by temperature, and that speed is modulated by both changes in stride length and duration.

Key words: performance, acceleration, power, kinematics, lizard, *Phelsuma dubia*, gecko, temperature, performance.

Introduction

Temperature has been shown to affect many aspects of vertebrate function, including muscle contraction frequency, the maximum speed of locomotion, gas exchange and digestion rate (Huey and Bennett, 1987; Huey and Kingsolver, 1989; DeNardo et al., 2002; Ishii et al., 2004; Sollid et al., 2005). The effects of temperature on steady speed locomotion have been fairly well studied, particularly in ectotherms such as lizards and fish (Huey and Bennett, 1987; Garland, Jr and Losos, 1994). Ecological studies have also linked variation in preferred body temperature with variation in some aspects of locomotor performance, such as maximal velocity, for some taxa (Pough, 1989; Bennett and Huey, 1990; Blouin-Demers et al., 2003; reviewed by Huey and Kingsolver, 1989). However, temperature effects on maximum acceleration during running and other modes of locomotion are generally poorly understood (but see Vanhooydonck et al., 2005; Vanhooydonck et al., 2006; B. Vanhooydonck, A. Herrel and D. J. Irschick, manuscript submitted).

Although prior studies have focused on maximal velocity as a key measure of locomotor performance in lizards and other animals (Bennett, 1990; Garland, Jr and Losos, 1994; Irschick and Garland, Jr, 2001), some studies have suggested that maximum speed may be less relevant than acceleration for animal fitness (Braña, 2003; see also Huey and Hertz, 1982; Huey and Hertz, 1984a). Many animals move unsteadily in nature, producing bursts of acceleration, and therefore high acceleration capacities form an important component of their escape responses (Huey and Hertz, 1982; Huey and Hertz, 1984a; Domenici and Blake, 1997; Irschick and Jayne, 1998; Vanhooydonck et al., 2005). For example, the C-starts of fish are a stereotyped escape response composed of high accelerations that are critical for effective escape from predators and capture of prey (Domenici, 2003). These unsteady movements often produce high power outputs, such as when frogs or birds jump, or when lizards start running from a standstill (Aerts, 1998; Irschick and Jayne, 1998; Wilson et al., 2000). Therefore, examination of temperature effects on acceleration also provides an opportunity to examine temperature effects on power output. Finally, frequent deceleration is another implication of intermittent locomotion as yet unexamined. The ability to quickly decelerate, as

opposed to accelerate forward, is important for high maneuverability because deceleration facilitates changes in the direction of movement (Domenici and Blake, 1997; Domenici et al., 2004), whereas acceleration facilitates movement along a chosen trajectory.

Prior work on muscles *in vitro* provides a testable framework for relating whole-organism power output with temperature. Swoap et al. (Swoap et al., 1993) found that the maximum mass-specific power output of fast-twitch muscle fibers from the lizard *Dipsosaurus dorsalis* increased substantially with temperature (from 20 W kg^{-1} at 15°C to 154 W kg^{-1} at 42°C), but we lack data for testing if this increase also occurs at the whole organism level (Askew and Marsh, 2002). Swoap et al. (Swoap et al., 1993) showed that at low temperatures, the optimal cycling frequency for producing maximum power output was attainable for the lizard *Dipsosaurus dorsalis*, whereas at higher temperatures, the optimal cycling frequency of isolated muscle was higher than maximal limb cycling frequency *in vivo* (about 20 Hz). Again, however, we lack data on how live animals modulate their kinematics (e.g. stride frequency, stride length) across a range of temperatures during unsteady burst locomotion, when they require maximal power. Furthermore, when considering the whole organism, one must also consider behavioral alterations across different temperatures (Bennett, 1980; Bennett, 1990). For example, low body temperatures in many lizards correlate with decreased velocity, but also result in increased aggressiveness and increased flight distance (Bennett, 1990).

Geckos offer an excellent opportunity to examine ideas regarding maximum power output, acceleration, deceleration and kinematics, as they will readily run both uphill and unsteadily, two conditions that should elicit high power output. Indeed, the escape movements of arboreal geckos are composed largely of brief, rapid accelerations and decelerations, and so represent an excellent model system for unsteady locomotion (Irschick et al., 2003; Vanhooydonck et al., 2005). Geckos will also often run readily across a range of temperatures. Finally, geckos are somewhat unique in that they primarily modulate speed by increasing stride frequency, but not stride length (Zaaf et al., 2001; Irschick et al., 2003), thus providing a simple system in which locomotor performance is modulated primarily by a single kinematic variable. However, these findings were conducted under a constant temperature, and it is possible that geckos will modulate both stride frequency and stride length when exposed to a variety of temperatures.

We examined how maximum velocity, acceleration, deceleration and several simple kinematic variables (e.g. stride frequency and duration) changed across a variety of temperatures when a small diurnal gecko (*Phelsuma dubia* Boettger) ran uphill. This species was appropriate for study because it is an agile animal that moves by burst locomotion on vertical surfaces. We induced the same group of lizards to accelerate uphill from a standstill on a smooth vertical surface at body temperatures ranging from 15–35°C and filmed all movements using a high-speed digital camera. From these data, we asked two specific questions. (1) How do acceleration and deceleration capacity, as well as mass-specific power output, change with temperature? (2) How do geckos modulate kinematics (e.g. stride frequency, stride length) across a variety of temperatures? We then discuss our findings in the context of previous work investigating relationships between temperature and power output in single muscle fibers (e.g. Swoap et al., 1993).

Materials and methods
Specimens examined

Data were obtained from 19 specimens of the diurnal gekkonid *Phelsuma dubia* Boettger. Specimens included in the analyses were all of adult or sub-adult size, with a snout–vent length (*SVL*) between 42 and 65 mm (53±7 mm, mean ± s.d.) and mass between 2.1 and 6.7 g (4.1±1.4 g). All animals were obtained commercially from Strictly Reptiles (Hollywood, Florida, USA) and housed in pairs in 32 cm×18 cm×22 cm (L×W×H) plastic terraria with paper towel substrate and Petri dishes containing water. They were maintained at the Tulane laboratory in a temperature-controlled room at 28.0±1.0°C on a 12 h:12 h photoperiod supplied by fluorescent visible and UVB spectrum-emitting bulbs. Animals were fed a diet of vitamin-dusted crickets *ad libitum* on alternate days and misted with water daily. All animals were allowed a 2 week acclimatization period prior to performance trials.

We collected body mass and *SVL* measurements prior to sprinting performance trials. Subsequent to all trials, animals were euthanized with intraperitoneal nembutal injection, fixed with formalin, and preserved in 70% ethanol. All experiments were approved by the Institutional Animal Care and Use Committee at Tulane University (IACUC approval 0189-2-16-0301).

Performance trials and calculations

Sprinting ability for *Phelsuma dubia* was quantified at five different temperatures: 15, 20, 25, 30 and 35°C, and each lizard was run twice at each temperature. The temperature range was chosen because at 15°C the geckos were very sluggish and at 35°C one individual lost consciousness and was eliminated from inclusion in any trials. Temperatures outside of the chosen range were not attempted out of concern for the wellbeing of the subjects. We know of no other studies that provide information on field, preferred or optimal body temperatures for this species. Although we know of no studies that directly address the temperature ranges to which *P. dubia* are exposed to in the wild, the species lives in northwestern Madagascar, particularly centered around the Mahajanga region (Glaw and Vences, 1994), and temperatures in this area range between ~17°C and 33°C (Boisier et al., 2002). Furthermore, many diurnal and nocturnal lizards have thermal optima at about 30°C (Autumn, 1999).

Lizards were induced to run upwards on a vertically oriented custom built race track, 10 cm wide and 1.5 m long, with

Plexiglas walls (see Irschick et al., 2003). The wooden base of the race track was covered in Plexiglas, ensuring a smooth and uniform surface for running. Lizards were placed on the track, facing upward, and were induced to run with a tap on the tail base. All geckos were placed in a Tritech Research Inc. (Los Angeles, CA, USA) DigiTherm™ DT2-MP incubator set to the desired temperature 1 h prior to sprinting trials. Their body temperature was measured immediately prior to trials using a Cox Technologies DE-305 digital thermometer (Belmont, NC, USA) to ensure that it was within 1.5°C of the desired temperature. Lizards were placed back into the incubator immediately following each trial, and were allowed at least 1 h between trials to rest for their body temperature to stabilize at the desired temperature.

Sprinting trials were filmed from dorsal view using a high-speed video camera (Redlake Motionscope PCI camera; San Diego, CA, USA) at 250 frames per second (f.p.s.) and saved to computer in avi format (following Irschick et al., 2003; Vanhooydonck et al., 2005). Only sequences in which the lizard ran from a standstill were analysed because we were interested in acceleration capacity during non-steady state movements (Irschick and Jayne, 1998). Furthermore, trials were only included when the lizard ran predominantly vertically, without undue lateral movement (Farley, 1997), and when the lizard appeared to be well motivated. *Phelsuma dubia* was chosen because it moves intermittently, but this quality made it difficult to obtain trials including movement over long distances. Only trials where the subject moved greater than 0.1 m in total distance were included.

All included sequences were imported into MOTUS Peak Performance software (2000; Peak Motus® 6.0 User Manual, Peak Performance Technologies, Englewood, NJ, USA) and the tip of the snout was digitized at 250 f.p.s. The issue of frame rates is an important one for studies of acceleration due to potential effects on digitizing error (Walker, 1998). Based on simulation studies, error rates are lower at frame rates of 250 f.p.s. than at other frame rates, and we have also used this frame rate in other studies of lizard acceleration (Irschick and Jayne, 1998; Irschick et al., 2003; Vanhooydonck et al., 2005; Vanhooydonck et al., 2006; B. Vanhooydonck, A. Herrel and D. J. Irschick, manuscript submitted). Frame-by-frame digitization commenced about 20 frames prior to any movement to minimize edge effects associated with smoothing (Walker, 1998; B. Vanhooydonck, A. Herrel and D. J. Irschick, manuscript submitted), and ended when the lizard either stopped or ran from the field of view. Inter-observer digitizing error was eliminated by using only a single person for initial digitizing. Digitizing error was further minimized by frame-by-frame proof-reading and correction of initial outliers, acting to increase precision and decrease noise (Crenshaw et al., 2000). Digitizing error was quantified by digitizing a trial five times, calculating instantaneous velocities and accelerations, and calculating the coefficient of variation (CV) for maximal velocity, acceleration and deceleration.

Another important issue in studies of acceleration is the algorithm used for smoothing and filtering raw *XY* data

(Walker, 1998). The *XY* coordinates obtained from digitization were smoothed using a quintic spline processor implemented in the MOTUS software package, and instantaneous velocity and acceleration were calculated for each frame by differentiation of the quintic spline functions (Vanhooydonck et al., 2005). MOTUS implements the quitic spline using a generalized cross-validatory algorithm (GCV) (2000; Peak Motus® 6.0 User Manual). We used a quintic spline procedure because this approach is least biased and error prone, outperforming most other available methods (Walker, 1998). Although the mean square error algorithm outperforms even the GCV, this approach is not implemented in Peak MOTUS. The GCV algorithm suffers from increased error at low magnifications and very high sampling rates, so we used the 2× magnification tool in MOTUS while digitizing and a frame rate of 250 f.p.s. These settings are optimal for the GCV algorithm, resulting in estimates of velocities and accelerations on a par with the more stable mean-square error algorithm for the quintic spline (Walker, 1998).

The largest value for each of these measures, as well as maximal deceleration (highest negative acceleration), at each temperature was retained for each individual. Only the single best trial was retained for any one temperature for each individual. Mass-specific power (*MSP*) was then calculated for each trial in Microsoft Excel using the equation:

$$MSP = FV\sin90° \, / \, M \, , \qquad (1)$$

where *M* is the gecko's mass, sin90° takes into account the fact that geckos were running vertically, and *V* is the maximal instantaneous velocity calculated in Peak MOTUS. *F* is the force exerted by the gecko, calculated as:

$$F = Ma = M(A + g) \, , \qquad (2)$$

where *A* is the maximal instantaneous acceleration calculated in Peak MOTUS and *g* is acceleration due to gravity (9.81 m s^{-2}). Substituting Eqn 2 into Eqn 1 allows for the canceling out of mass and the form:

$$MSP = (A + g)V\sin90° \qquad (3)$$

in units of W kg^{-1} (Vanhooydonck et al., 2005; Vanhooydonck et al., 2006; B. Vanhooydonck, A. Herrel and D. J. Irschick, manuscript submitted). A caveat of our approach is that it assumes that movements of the center of mass are well approximated by the tip of the snout. The validity of this assumption is untested, to our knowledge, but may be justified by the observation that the snout is displaced in similar ways to the body. Calculating power from *XY* coordinates has also been done by Irschick et al. (Irschick et al., 2003), but during steady state locomotion. Power was calculated for each frame in a trial, and the maximal *MSP* in the trial selected for further analysis. This accounts for the fact that maximal acceleration and velocity, and therefore *MSP*, may not be generated at the same time during locomotion.

Finally, we calculated basic kinematic variables for the right hind limb from a dorsal view from displacement and frame number data. These included stride length and stride duration,

Table 1. *RM-ANCOVA statistics, with temperature as factor and mass as covariate, for the performance variables considered*

	d.f.$_e$	MS$_e$	*F*	*P*
Velocity	17	0.007	3.603	0.075
Acceleration	17	0.049	0.020	0.890
Deceleration	17	0.060	0.051	0.824
Mass-specific power	17	0.032	0.904	0.355

Error d.f. (d.f.$_e$), error mean squares (MS$_e$), *F*-statistics, and associated probabilities are presented.

There are no significant probabilities.

step length and step duration, and duty factor. A stride was defined from foot up until the next foot up. A step was defined while the foot was in contact with the ground (foot down until foot up). Duty factor was defined as the proportion of the step cycle that the foot is in contact with the ground (step duration divided by stride duration).

Statistical analysis

All statistical analyses were carried out using SYSTAT 10.2 (Wilkinson, 2002). Performance data (velocities, accelerations and *MSP*) were log-transformed prior to analysis because untransformed data yielded residuals that were often not normal and always heteroscedastic. Kinematic data (lengths, durations and duty factor) were not log-transformed because these data yielded residuals that were almost always normal and homoscedastic. The assumptions of normality and homoscedasticity of residuals were tested using Kolmogorov–Smirnov (KS) and F_{max} tests, respectively.

Maximal instantaneous velocity, acceleration, deceleration and *MSP* were analyzed using repeated-measures analyses of variance (RM-ANOVAs) (Farley, 1997) with temperature as a fixed factor (Model I; Sokal and Rohlf, 1995). These data were also analysed using repeated-measures analyses of covariance (RM-ANCOVA) with log-transformed mass as a covariate to evaluate the influences of mass on performance measures. Stride duration and length, step duration and length, and duty factor were analyzed using two-factor RM-ANOVAs, with temperature and step number as fixed factors. In all analyses, temperature included five treatment levels (15, 20, 25, 30 and 35°C). For two-factor ANOVAs, step included two levels:

steps one and two. This was deemed appropriate because the majority of acceleration occurs during the first two strides (fig. 7 in Irschick and Jayne, 1998), and because missing data for some individuals for the third stride would have decreased the sample size of the analysis.

Pairwise *post-hoc* tests for repeated-measures designs (Wilkinson, 2002) were used to examine specific differences in dependent variables among temperature levels, and all pairwise comparisons were run. A sequential Bonferroni correction (Rice, 1989) was applied for each analysis conducted (five treatment levels resulting in ten pairwise comparisons).

Results

In general, the assumptions of normality and homoscedasticity of the residuals were met. Only the residuals of step duration at 25°C were not normal (KS test: Diff$_{max}$=0.244, *P*<0.0001) and only residuals of duty factor were heteroscedastic (F_{max}=3.94, *P*<0.05). Hence, parametric RM-ANOVAs were conducted in all cases. When a single trial was digitized five times, displacement coordinates between trials were always within 2 pixels of one another. Coefficients of variation for maximal performance measures for these five replicates were 3.8% for velocity, 8.5% for acceleration and 11.1% for deceleration.

Maximal instantaneous velocity, acceleration, deceleration and *MSP* were unaffected by mass (Table 1) and significantly affected by temperature (Tables 2 and 3). All analyses presented henceforth are RM-ANOVAs that ignore mass because it had no significant effects. Table 2 shows mean values for each of these performance measures at each temperature and Table 3 shows RM-ANOVA results. In all cases, there was a general trend of increase in the performance measure as temperature increased (Fig. 1). However, when examined in more detail, the degree to which this trend was pronounced differed among measures. For example, *post-hoc* tests for maximal instantaneous velocity (Fig. 1A) and maximal *MSP* (Fig. 1D) showed a similar trend of significant temperature dependence at temperatures below 25°C, with a plateau at temperatures above 25°C (i.e. no significant differences). This trend is still apparent for maximal instantaneous acceleration (Fig. 1B) and deceleration (Fig. 1C), but is less pronounced, with fewer significant

Table 2. *Untransformed maximum velocity, acceleration, deceleration and mass-specific power output at various temperatures for Phelsuma dubia*

	Temperature (°C)				
	15	20	25	30	35
Velocity (m s^{-1})	0.431±0.095	0.563±0.103	0.781±0.146	0.886±0.179	0.998±0.180
Acceleration (m s^{-2})	10.158±4.805	12.642±4.692	17.302±8.872	21.939±9.881	21.733±8.105
Deceleration (m s^{-2})	8.348±2.828	11.219±4.656	14.199±7.645	17.136±11.357	14.001±5.273
Mass-specific power (W kg^{-1})	6.423±2.332	9.061±3.283	15.552±6.549	19.340±8.093	22.290±9.130

Values are means ± s.d. (*N*=19 geckos).

Table 3. *RM-ANOVA statistics, with temperature as factor, for the performance variables considered*

	d.f.$_e$	MS$_e$	F	P
Velocity	72	0.007	65.240	**<0.0001**
Acceleration	72	0.427	10.912	**<0.0001**
Deceleration	72	0.209	5.631	**0.001**
Mass-specific power	72	0.029	37.086	**<0.0001**

Treatment d.f.=4.

Error d.f. (d.f.$_e$), error mean squares (MS$_e$), F-statistics and associated probabilities are presented.

Significant probabilities are in bold.

differences between adjacent temperature levels. A lower relative significance to this increasing trend with temperature is indicated by far greater F statistics associated with RM-ANOVAs for velocity and power, than for acceleration and deceleration (Table 3). Despite the observed differences in the degree of significance between these performance measures, all show a similar increase in magnitude with increases in temperature (Table 2). Maximal velocity shows a 2.3× increase between 15°C and 35°C, while maximal acceleration shows a 2.2× increase between 15°C and 30°C and maximal deceleration shows a 2.1× increase over the same temperature range (Table 2). In contrast, maximal MSP increases 3.5× in magnitude between 15°C and 35°C.

For most of the kinematic variables considered, step number (one *versus* two) had no significant influence (Table 4). The only exception to this was stride length, in which the second stride was significantly (1.25×) longer than the first stride (Table 4). In contrast, temperature had a significant effect on almost all kinematic variables considered, except duty factor, which was unaffected by either temperature or step number, and had a mean value of 0.91 (Table 4). Although temperature had a significant effect on both step duration and step length, the trend was less pronounced, but in the same direction, as for stride duration and length (F statistics; Table 4). Therefore, only graphs for the stride data are shown (Fig. 2). Stride duration significantly decreased with increasing temperature (Fig. 2A), while stride length increased with temperature (Fig. 2B). As temperature increased, *P. dubia* took longer and faster (or higher frequency) steps. However, changes in stride duration (a 1.9× decrease between 15°C and 35°C) were more pronounced than changes in stride length (a 1.4× increase).

Discussion
Thermal dependence of performance

We have documented profound effects of body temperature on several important aspects of whole-organism locomotor performance in a gecko, including maximum mass-specific power output, acceleration and deceleration and velocity, as well as several simple kinematic variables. Our study offers an important point of comparison to prior detailed *in vitro* studies of temperature on muscle properties (i.e. power output) in
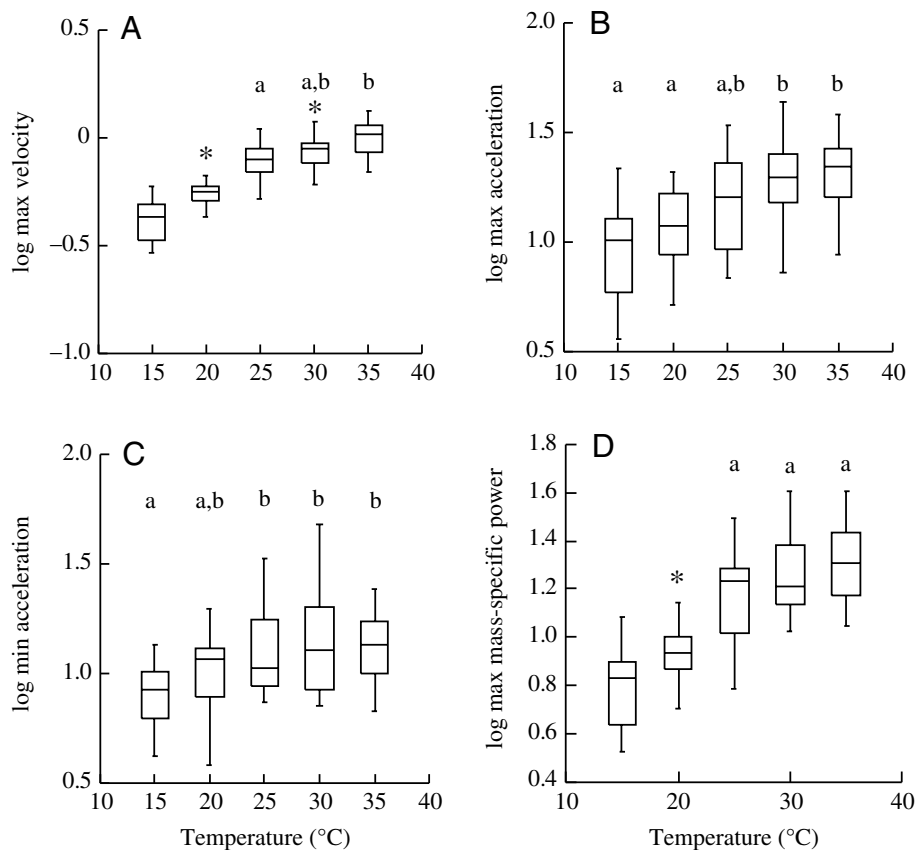

Fig. 1. Box plots for log-transformed (A) maximal instantaneous velocity (in m s^{-1}), (B) acceleration (in m s^{-2}), (C) deceleration (in m s^{-2}) and (D) mass-specific power output (in W kg^{-1}) for each experimental temperature (15, 20, 25, 30, 35°C). Values with the same letter (a,b) denote temperatures at which performance measures are not significantly different, as indicated by pairwise *post-hoc* tests. No letter indicates that a performance measure at a given temperature is significantly different for measures at all other temperatures. For each box plot, the line within the box represents the mean; the top and bottom of each box represent the 75th and 25th percentiles, respectively; the top and bottom whiskers represent the 95th and 5th percentiles, respectively; the asterisk represents an outlying datum.

Table 4. *RM-ANOVA statistics, with step number and temperature as factors, for the kinematic variables considered*

	Factor	d.f.$_e$	MS$_e$	F	P
Stride duration	Step	15	0.001	0.403	0.535
	Temperature	60	0.001	18.797	**<0.0001**
Step duration	Step	15	0.001	1.584	0.228
	Temperature	60	0.001	16.618	**<0.0001**
Duty factor	Step	15	0.015	0.794	0.387
	Temperature	60	0.013	0.300	0.877
Stride length	Step	15	43.623	78.669	**<0.0001**
	Temperature	60	60.260	17.231	**<0.0001**
Step length	Step	14	18.135	3.976	0.066
	Temperature	56	35.025	7.098	**0.0001**

Treatment d.f.=1 for step, 4 for temperature.
Error d.f. (d.f.$_e$), error mean squares (MS$_e$), *F*-statistics and associated probabilities are presented.
Significant probabilities are in bold font.

lizards (e.g. Marsh and Bennett, 1985; Marsh and Bennett, 1986; Swoap et al., 1993).

Diurnal lizards generally have high temperature preferences and optima (Huey and Bennett, 1987), and this is also the case for secondarily diurnal geckos (Autumn, 1999). This pattern was supported by our data for *Phelsuma dubia* (Fig. 1). We found that velocity increased 1.8× as temperature increased from 15°C to 25°C, and then levelled off between 25°C and 35°C (increasing only 1.2×; Fig. 1A). Such a trend, complete with a performance plateau at high temperatures, has also been found in lygosomine skinks (Huey and Bennett, 1987), a number of other disparate lizard taxa (Bennett, 1980; Marsh and Bennett, 1985), and various ectotherms in general (Huey and Kingsolver, 1989). Quantitatively, this compares quite closely with reported Q$_{10}$ values of 2–3 below 25°C and 1–1.5

above that temperature for a variety of vertebrate ectotherms (Bennett, 1990). Low but apparent thermal dependence of performance is contrasted by much higher thermal dependence of underlying physiological processes (Bennett, 1980).

Acceleration has rarely been studied from a thermal-dependence perspective (with emphasis being placed on power output instead – see below), but has been shown to be independent of incline and comparable in the phrynosomatid lizards *Callisaurus draconoides* and *Uma scoparia* (Irschick and Jayne, 1998). We find that acceleration follows a similar trend to that of velocity, increasing 1.7× as temperature increases between 15°C and 25°C, but only 1.2× above that temperature (Fig. 1B). Vanhooydonck and coworkers also found a positive correlation between maximal acceleration and
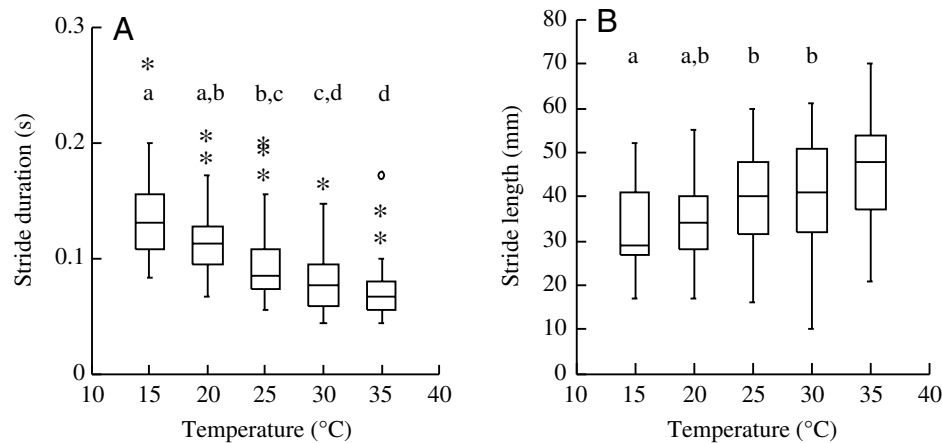

Fig. 2. Box plots for untransformed stride duration (A) and stride length (B) at each experimental temperature (15, 20, 25, 30, 35°C). Values with the same letters (a–d) denote temperatures at which kinematic measures are not significantly different, as indicated by pairwise *post-hoc* tests. No letter indicates that a performance measure at a given temperature is significantly different for measures at all other temperatures. For each box plot, the line within the box represents the mean; the top and bottom of each box represent the 75th and 25th percentiles, respectively; the top and bottom whiskers represent the 95th and 5th percentiles, respectively; asterisks represent data outlying >1.5 times the interquartile range, and circles represent data outlying >3 times the interquartile range.

velocity for the small nocturnal gecko *Hemidactylus garnoti* running on different substrates, but at a single temperature (30°C) (Vanhooydonck et al., 2005). Interspecifically, Vanhooydonck and coworkers (B. Vanhooydonck, A. Herrel and D. J. Irschick, manuscript submitted) also found that acceleration capacity correlates positively with sprint speed in *Anolis* lizards.

We observed that thermal dependence was less apparent for maximal deceleration. Although this performance measure also increased 1.7× below 25°C and 1.2× above that temperature, no significant increases were found above 20°C (Fig. 1C). Such low thermal dependence may be partially explained by the fact that the geckos were not forced to decelerate quickly. Although lizards were tapped on the tail to obtain maximal velocity and acceleration, no analogous procedure was implemented to force them to decelerate quickly, possibly contributing large variance around temperature means for deceleration (Fig. 1C). Future studies considering deceleration as a performance measure might require experimental designs forcing animals to use high degrees of manoeuvrability, such as a race track with obstacles. This design would further test whether geckos or lizards in general, can control deceleration in order to maximize manoeuvrability.

We found a highly pronounced trend of increasing mass-specific power output with increasing temperature, similar to that for maximal velocity (Fig. 1D). That is, *MSP* increased by a factor of 2.4 up to 25°C and then levelled off, increasing 1.4× up to 35°C. Such a trend is unsurprising, given that *MSP* was calculated as the product of instantaneous velocity and acceleration (see Materials and methods), and it is similar to the trend found for other *in vitro* studies of lizard muscle function, but with a lower thermal optimum (Marsh and Bennett, 1985; Marsh and Bennett, 1986; Swoap et al., 1993). For example, Swoap et al. (Swoap et al., 1993) found the power output optimum for fast glycolytic fibres of the iliofibularis muscle in *Dipsosaurus dorsalis* occurred at 42°C, and Marsh and Bennett (Marsh and Bennett, 1985) detected a very similar value of 40°C for the same muscle in the same species. Marsh and Bennett (Marsh and Bennett, 1986) also found that maximal isometric force generation in the diurnal lizard *Sceloporus occidentalis* levels off between 20°C and 35°C. Given that we found that both maximal velocity and maximal *MSP* level off above 25°C in *Phelsuma dubia*, it is possible that velocity is limited by power output at high temperatures in this species as well (see also Irschick et al., 2003).

However, the performance measures considered herein may be further influenced by the experimental setup and hence are not easily generalized to horizontal locomotion. Studying vertical locomotion in geckos is ecologically meaningful on account of their adhesive abilities (Ruibal and Ernst, 1965; Hiller, 1976; Russell, 1979), and other studies have employed a similar setup (Irschick et al., 2003; Vanhooydonck et al., 2005). However, due to the effects of gravity, velocity and acceleration are expected to be negatively influenced, while deceleration and power output are expected to be enhanced because during vertical locomotion more power must be produced than during horizontal locomotion to overcome the effects of gravity (Farley, 1997; B. Vanhooydonck, A. Herrel and D. J. Irschick, manuscript submitted).

Finally, our study, like many others, is focused on maximal instantaneous performance, which may not yield a complete picture of locomotion in animals. Specifically, further research that incorporates measures of average performance (i.e. average velocity, acceleration, etc.) would coincide more closely with our kinematic variables of stride length and duration. However, the interpretation of such data for our study may be confounded by our focus on unsteady locomotion, and would be more straightforward for studies of steady state locomotion.

Thermal dependence of kinematics

An animal's velocity is a product of its stride length and stride frequency (Biewener, 2003), and hence velocity, can be modulated by changing either or both of these kinematic variables. Most non-mammalian quadrupeds increase speed by increasing both, with an increased reliance on modulating stride length at high speeds (Biewener, 2003). Geckos are a noted exception to this rule because they primarily modulate their speed by changing stride frequency, at least under steady state locomotion (Zaaf et al., 2001; Irschick et al., 2003). We documented that as temperature increased from 15°C to 35°C, stride duration decreased (i.e. stride frequency increased) by a factor of 1.9, and stride length increased by a factor of 1.5 (Fig. 2). Hence, our findings are typical for quadrupeds, but atypical for geckos. These results underscore that changes in temperature can result in behavioural alterations that might not be observed at a single temperature (Huey and Hertz, 1982; Huey and Hertz, 1984b). However, Fig. 2 also shows that increases in speed result more through the modulation of stride duration than of stride length. A similar trend was documented by studies of the iguanid lizard *Dipsosaurus dorsalis* (Marsh and Bennett, 1985; Swoap et al., 1993; but see Fieler and Jayne, 1998). Stride length has been shown to increase with speed in horses during steady state locomotion, along with a decrease in stride duration (Hoyt et al., 2000). The stork, *Ciconia ciconia*, also increases speed primarily by increasing stride frequency, and only secondarily by increasing stride length during steady state locomotion (van Coppenolle and Aerts, 2004). Our study is somewhat unique in that we examined unsteady state locomotion, but this may also be a confounding factor, as stride length increases over the first few steps of acceleration (Irschick and Jayne, 1998) (Table 4).

Although we examined duration and length data for both strides and steps (stance phase) for *P. dubia*, stride data are emphasized because they give clearer, more significant patterns than step data. Stride and step data also show similar patterns (i.e. decreases in duration and increases in length with temperature). The importance of the stance phase should not be discounted, however, as this is the part of the stride during which all force is generated (Hoyt et al., 2000). Since the rate of force application to the substrate is inversely proportional

to step duration (Hoyt et al., 2000), the shorter steps (e.g. shorter durations) exhibited by *P. dubia* at high temperatures translate into more force being applied per unit time, even if the geckos' velocity did not increase with temperature.

Duty factor has variously been reported to change with the velocity of locomotion. In general, duty factor decreases as velocity increases, and this has been documented in animals as disparate as storks (van Coppenolle and Aerts, 2004) and horses during level and incline locomotion (Dutto et al., 2004). In contrast, duty factor increased in the newt *Taricha torosa* when walking in water relative to on land (Ashley-Ross and Bechtel, 2004). Duty factor again decreased with increased velocity in lizards: *Dipsosaurus dorsalis* (Fieler and Jayne, 1998), *Callisaurus draconoides* and *Uma scoparia* (Irschick and Jayne, 1998). Irschick et al. (Irschick et al., 2003) also found that duty factor decreased with increasing speed in two species of gecko. Our findings show a different pattern from that documented in these studies, in that duty factor did not change with increasing temperature or stride number (Table 4), although speed did increase. This has the implication that in *P. dubia* moving vertically, reductions in stride duration and step duration are coincident as speed and temperature increase. These findings are surprising because Irschick et al. (Irschick et al., 2003) also examined geckos and forced them to run vertically. However, they varied loading of the geckos, as opposed to temperature, which may contribute to observed differences between the two studies.

An increasing number of studies are examining acceleration and power output during different modes of locomotion in various animals. Jumping has received considerable attention in this regard in cats (Harris and Steudel, 2002), frogs (Wilson et al., 2000) and *Anolis* lizards (Toro et al., 2003). Similar considerations have also arisen for flight in quail (Askew and Marsh, 2001; Askew and Marsh, 2002), escape response in lobster (Nauen and Shadwick, 1999), and in fishes (Ellerby et al., 2001; Domenici, 2003; Domenici et al., 2004). Our study is one of relatively few to consider acceleration and power output in lizards (but see Huey and Hertz, 1982; Huey and Hertz, 1984a; Farley, 1997; Vanhooydonck et al., 2005; Vanhooydonck et al., 2006; B. Vanhooydonck, A. Herrel and D. J. Irschick, manuscript submitted). To our knowledge, our study is the first to consider deceleration ability, which may be correlated with manoeuvrability, as a performance measure. Although velocity may be ecologically relevant when outrunning a predator (Bennett and Huey, 1990; Irschick and Garland, Jr, 2001), and acceleration may be important during prey capture or initial evading of a predator (Huey and Hertz, 1982; Vanhooydonck et al., 2005), deceleration may also be a key component of evading predators and capturing prey. While our study was not specifically designed to evaluate maximal deceleration capacity, it provides a starting point for further studies that could examine deceleration and manoeuvrability in more ecologically realistic designs (Domenici and Blake, 1997).

In general, our findings support the expected notion that lizards are faster, accelerate/decelerate better, and produce more power at higher temperatures. These findings are, at least partially, explained by modulation of both stride length and stride duration, in contrast to other studies of locomotion in geckos. However, all of our performance measures show a distinct levelling off at high temperatures (typically above 25°C). This is consistent with the assertion that evolution appears to have minimized the impact of temperature on performance (Bennett, 1980). Our findings of relatively broad temperature optima for acceleration and power output suggest that there is little cost in utilizing suboptimal body temperatures, as long as they are in the broad plateau (Huey and Hertz, 1984b; Huey and Bennett, 1987), resulting in a relatively shallow performance gradient (Arnold, 1983).

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