

Effects of temperature and sex on jump performance and biomechanics in the lizard *Anolis carolinensis*

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Summary

1. Temperature is known to affect whole-organism performance capacities significantly in ectotherms, but may potentially alter performance kinematics as well. Locomotor performance is a multivariate phenomenon, hence changes in temperature are probably reflected in multiple aspects of locomotion.
2. We studied the thermal sensitivity of several kinetic and kinematic jump variables, including acceleration and power output, in male and female green anole lizards, *Anolis carolinensis* Voigt 1832. We hypothesized that temperature would have similar effects on kinetic and kinematic variables.
3. We also tested the hypotheses that males and females would differ in jump performance, but only because of sexual dimorphism for body size, and that males and females would also differ in optimal performance temperature and body temperature (T_b) maintained in the field.
4. Both kinetic and kinematic jump variables exhibited significant temperature dependence, as expected, suggesting that overall jump dynamics are altered by temperature in green anoles. Power, in particular, increased markedly over the 15–25 °C temperature range in males.
5. Sex differences in jumping were driven largely by sexual dimorphism in body size. However, females exhibited significantly narrower thermal tolerance ranges than males, although they maintained a T_b similar to males in the field.
6. These data illustrate the necessity of carefully controlling T_b during jumping experiments at single temperatures in ectotherms, as temperature affects a suite of kinematic and biomechanical traits determining overall jump performance.

Key-words: locomotion, performance, temperature, lizard, sex

Functional Ecology (2007) **21**, 534–543
doi: 10.1111/j.1365-2435.2007.01263.x

Introduction

A central issue in ecophysiology concerns how environmental factors affect physiological performance. Previous researchers have devoted considerable effort towards quantifying environmental effects (e.g. temperature, incline, texture) on whole-organism performance capacities such as maximum velocity or endurance (Irschick & Garland 2001). In ectotherms, for example, sprint speed and other locomotor capacities typically covary with body temperature (T_b), and individual performance abilities may therefore be constrained by the thermal environment (for reviews see Huey & Kingsolver 1989; Angilletta, Niewiarowski & Navas 2002).

Previous studies of the thermal dependence of locomotor performance have focused on performance variables such as maximum velocity or endurance, on the assumption that these traits have important effects on organism fitness (John-Alder & Bennett 1981; Lailvaux, Alexander & Whiting 2003). However, in order to understand more fully the effects of temperature on locomotion, we also need to understand how changes in temperature affect the biomechanical parameters underlying performance. For example, burst movements such as jumping in lizards and frogs, or flight take-off in birds, require high-power outputs, but although previous studies have examined whether dynamic movements are limited by power (Farley 1997; Aerts 1998; Askew & Marsh 2001; Irschick *et al.* 2003; Roberts & Marsh 2003; Curtin, Woledge & Aerts 2005), and despite some excellent *in vitro* muscle work (Marsh & Bennett 1985; Swoap *et al.* 1993), we know little about

how temperature affects *both* whole-organism power output *and* associated variables, such as the angles, durations and velocities of movements (but for examples see Wakeling & Johnston 1999; Bergmann & Irschick 2006). Given the key roles of power-intensive performance variables such as acceleration in numerous ecological tasks (e.g. competitive interactions, Altshuler 2006; escape behaviour, Domenici, Staden & Levine 2004; fighting ability, Lailvaux *et al.* 2004) within various animal taxa, studying the thermal sensitivity of such variables during locomotion *in vivo* may lead us to greater understanding of how these factors interact to influence organismal fitness. A main goal of this paper is to examine the effects of temperature, not only on 'traditional' jump performance measures such as jump velocity, distance and acceleration, but also on associated kinetic and kinematic variables (e.g. force output, power output, take-off angle) that may affect individual survival or fitness using the green anole lizard (*Anolis carolinensis* Voigt 1832) as a model system.

A further reason for studying the effects of temperature on jump kinematics is that animals may use different movement-control strategies during maximal and submaximal jumps (Toro, Herrel & Irschick 2006). Previous researchers have identified two main control strategies for submaximal locomotor movements: one based on force output (kinetics, Boyd & McLellan 2002); the other based on optimization of energy expended during jump movements (kinematics, Vanrenterghem *et al.* 2004). Here we distinguish between kinematic (movement-related) and kinetic (force-related) jump variables to examine the degree to which these two control models might apply to jumping in green anoles at different T_{bs} (although we realize that all performance variables related to a dynamic action such as jumping are, in a sense, kinematic).

Previous authors have stressed that to understand how temperature affects ectotherms, one must adopt both laboratory- and field-based approaches (Hertz, Huey & Garland 1988; Huey & Kingsolver 1989; Angilletta *et al.* 2002). Of particular importance is understanding the range of temperatures that species experience in nature, as well as their preferred body temperatures, to interpret the effects of temperature on performance properly. We conducted laboratory studies to investigate the effects of temperature on jumping biomechanics, and also collected field data to provide ecological context for these results. Finally, we also examined the role of sex in determining differences in jumping biomechanics. Recent studies have shown that males and females of several animal species differ in absolute performance capacities, and these differences may persist even after correction for sexual dimorphism in body size (Cullum 1998; Krasnov *et al.* 2003; Irschick *et al.* 2005a; see also Shine & Shetty 2001; Lailvaux *et al.* 2003). These findings suggest that sex differences in performance may be affected either by intrinsic physiological differences associated with sex, such as metabolic rate (Krasnov *et al.* 2004) or

hormone levels (Cullum 1998). However, most studies of sex-based differences in whole-organism performance in ectotherms have typically been conducted either at a single trial T_b , or within a very narrow T_b range (e.g. Cullum 1998; Krasnov *et al.* 2003, 2004). An unresolved question is whether these sex differences persist over a range of T_{bs} . If the optimal body temperatures for performance ability (T_o) differ between the sexes, then males and females may select different T_b in nature, and ultimately exhibit different behaviours in any given ecological context (e.g. antipredatory behaviour; Lailvaux *et al.* 2003).

Green anoles are ideal subjects for studies examining temperature and sex effects on jumping, both because of the ease with which jumping may be quantified in this species (Bels & Theys 1989; Toro *et al.* 2003; Toro, Herrel & Irschick 2004), and because previous studies have shown that males and females differ in absolute jump performance at their preferred T_b (Irschick *et al.* 2005a). Furthermore, green anoles jump frequently in nature, are easy to maintain in captivity, and are highly sexually dimorphic in size. We tested three hypotheses, as follows. (1) Temperature will affect both kinetic (force-related) and kinematic (jump angle, contact times) jump variables, thus changing both performance and underlying jump kinematics. (2) Jump performance will not differ between males and females when normalized for body size. (3) Males and females will differ in optimal performance temperatures and, consequently, T_b maintained in the field.

Materials and methods

We captured adult *A. carolinensis* lizards by hand on the Tulane University campus in New Orleans, LA, USA during April 2005. Lizards were housed in individual 38-l terraria in the laboratory at Tulane and provided with water and food (crickets) *ad libitum*. All performance trials were conducted within 2 weeks of capture. No gravid females were used in the study. All experiments were carried out in accordance with an approved animal-use protocol (IACUC 0189-2-16-0301).

JUMP PERFORMANCE

We measured jump performance of both males and females three times at each of the six temperatures (15, 20, 25, 30, 35 and 38 °C) with an hour's rest between trials and a day's rest between temperatures. These temperatures were chosen to cover as wide a range as possible within the thermal tolerance range for males and females; below 15 °C and above 38 °C it was difficult to elicit jumps from the lizards consistently. The sequence of trial temperatures was randomized. We manipulated lizard T_b by placing the animals inside a Tritech Research Inc. (Los Angeles, CA, USA) Dig-iTherm DT2-MP incubator set to the trial temperature for 30 min prior to and in between measures. We used a copper-constantan thermocouple probe attached to

a Cox digital thermometer to verify individual T_b directly after each jump trial by measuring cloacal temperature. In total, 17 males and 14 females were measured. We induced lizards to jump off a custom-built force platform onto a horizontal board positioned at the level of the platform and out of the animals' reach (following Toro *et al.* 2003, 2004; Lailvaux *et al.* 2004; Irschick *et al.* 2005a). We used a G4 Macintosh computer and SUPERSCOPE II ver. 3 software to record the three-dimensional ground reaction forces (smoothed by a low-pass filter) generated by each jump. Jump kinetics and kinematics were calculated from the force traces as described by Toro *et al.* (2003, 2004). Briefly, the resulting force vector was calculated from the vector sum of the individual X , Y and Z forces. Division of the resulting ground reaction forces by the mass of the animal yielded acceleration of the centre of mass, and instantaneous velocity of the centre of mass was calculated by numerical integration of the acceleration profile. Instantaneous mass-specific power was calculated by multiplication of the instantaneous velocity and acceleration profiles. Integration of instantaneous velocity during take-off yielded the displacement of the centre of mass, and the horizontal ($X + Y$) and vertical (Z) ground reaction forces were used to determine the angle of take-off. We used the take-off angle, take-off velocity, and horizontal displacement of the centre of mass to calculate the horizontal jump distance (see Toro *et al.* 2003 for further details on the force plate set-up and calculations). The force plate output and calculations of jump variables were validated using high-speed recordings (250 frames s^{-1}) of seven *Anolis valencienni* individuals jumping maximally off the plate (Toro *et al.* 2003).

We motivated the lizards to jump by startling them with a handclap. Only jumps that began with all four feet planted squarely on the platform were included in the analysis. Lizards were made to jump three times at each trial temperature, with an hour's rest between jumps and a day's rest between temperatures. The best jump for each individual was used in the final jump analysis. Velocity at take-off (terminal velocity at the end of the take-off phase), peak acceleration during take-off, peak power during take-off, peak force output, jump distance, time to peak power, time to peak acceleration, displacement of the centre of mass during take-off (referred to here as contact time distance), and duration of the entire take-off phase were extracted from the force traces for each jump. Only lizards that yielded consistent, high-quality maximal jumps at each of the six trial temperatures were retained for statistical analyses. Overall, 13 males and 13 females were included in the final analysis. The experimental animals used for performance trials were a subset of those in which field T_b was measured (see below).

FIELD T_b

We measured the field T_b of 21 male and 17 female Tulane campus *A. carolinensis* lizards to determine if

males and females maintain different body temperatures in nature, and to compare optimal laboratory performance T_b (i.e. T_o) to the T_b seen in nature. We sampled adult lizards from the campus population during random walks through likely anole habitat on Tulane's campus (principally clumps of broad-leaved *Aspidistra elatior* plants) every day from 15 to 22 April 2005 between 1 and 4 pm. All lizards were caught by hand as soon as possible after sighting. The T_b was measured immediately following capture (within 5 s) by inserting a copper-constantan temperature probe into the animal's cloaca. We only collected T_b on sunny days, as previous studies have shown that cloudy conditions can have significant effects on lizard T_b (Scheers & Van Damme 2002). Furthermore, we sampled at the same times every day to account for possible circadian rhythms in selected field T_b .

THERMAL TOLERANCE

Thermal tolerance indices define the thermal limits within which ectotherms are physiologically capable of conducting ecological tasks. We estimated the upper (CT_{max}) and lower (CT_{min}) thermal tolerance ranges for 11 adult male and 10 adult female *A. carolinensis* selected randomly from the larger pool of experimental animals. We estimated CT_{min} by placing individual lizards inside an incubator and lowering T_b at approximately $1\text{ }^{\circ}\text{C min}^{-1}$. The temperature at which a lizard was unable to right itself after being placed on its back was taken to be CT_{min} (Lutterschmidt & Hutchison 1997a). We estimated CT_{max} by placing lizards inside a large, clear, water-tight plastic bag, and lowering the bag into a water bath. We raised lizard T_b at $1\text{ }^{\circ}\text{C min}^{-1}$, and carefully monitored lizards for onset of muscle spasms (Lutterschmidt & Hutchison 1997b). At the first sign of muscle twitching, we immediately removed the lizards from the bags and measured T_b , which was recorded as the estimate of CT_{max} for that individual. We carried out CT_{min} and CT_{max} estimates on separate days, with 2 days' recovery time in between. All animals recovered completely following thermal tolerance measurements and ate normally when offered food.

STATISTICAL ANALYSES

Prior to analyses, we tested for departures from normality for all variables using Lilliefors test. non-normality in field T_b data was successfully corrected by \log_{10} transformation. We used two-way repeated measures ANOVA with sex and temperature as fixed factors to test for differences between sexes over the trial temperatures, and for interactions between sex and temperature for all variables. We repeated the analyses using two-way repeated measures ANCOVA with body mass as a covariate to examine sex effects, as well as any potential interactions between sex and temperature, independent of body size. (Repeated measures MANOVA

and MANCOVA were not used due to undesirable loss of data resulting from the unbalanced multivariate data set. Similarly, using SVL in place of body mass to represent body size lowered the explanatory power of the ANCOVAs for all traits (cf. Cullum 1998). Because the assumption of sphericity required for repeated measures analyses was not met, the degrees of freedom for all analyses were adjusted downwards by multiplying the df by the Huynh–Feldt estimation of ϵ given by SPSS (von Ende 2001). All interpretations in this study are therefore based on Huynh–Feldt-adjusted *P* values.

Differences in field T_b between males and females were assessed by means of two-tailed *t*-tests. We used a minimum-polygon analysis (van Berkum 1986) to calculate three descriptive measures of thermal sensitivity for the jump performance and kinetic variables (velocity, acceleration, power, force and distance): T_o (the optimal performance temperature), B_{95} (the temperature range over which performance is no less than 95% of maximum) and B_{80} (the temperature range over which performance is no less than 80% of maximum). Predicted performance values for velocity, acceleration and distance at the T_o and field T_{bs} were interpolated from the respective thermal performance curves following Bauwens *et al.* (1995); Lailvaux *et al.*

(2003). To test for differences between sexes in jump T_o , B_{95} and B_{80} , we used a one-way MANOVA with sex as a factor. To test for differences in T_o , B_{95} and B_{80} between jump variables within sexes, we carried out separate one-way MANOVAs for each sex. We compared field T_b with optimal T_b for all jump variables in males and females using one-way ANOVAs. We used Tukey's honestly significant difference (HSD) *post hoc* tests to determine differences between individual means. We compared CT_{min} and CT_{max} values for males and females using both two-way *t*-tests (absolute values) and ANCOVA with body mass as a covariate (size-corrected). Finally, we calculated Q_{10} values for all jump variables in males and females. All analyses were performed using SPSS ver. 13.

Results

JUMP PERFORMANCE, KINETICS AND KINEMATICS

T_b had a significant effect on all measured performance and kinetic variables (Table 1; Fig. 1). In particular, power exhibited markedly higher Q_{10} values for both males and females relative to other jump variables

Table 1. Summary statistics for univariate two-way repeated measures ANOVA (absolute) and two-way repeated measures ANCOVA with SVL as covariate (size-corrected) for all performance measures

Parameter		Absolute				Size-corrected			
		ϵ	<i>F</i>	df	<i>P</i>	ϵ	<i>F</i>	df	<i>P</i>
Velocity	Temperature	0.705	159.167	5,120	<0.001				
	Sex		4.565	1,24	0.043				
	Temp*Sex	0.705	1.274	5,120	0.288	0.717	0.754	5,115	0.518
Acceleration	Temperature	0.794	233.837	5,120	<0.001				
	Sex		0.002	1,24	0.967		0.144	1,23	0.708
	Temp*Sex	0.794	4.723	5,120	0.002	0.835	3.292	5,115	0.013
Power	Temperature	0.860	231.2	5,120	<0.001				
	Sex		0.921	1,24	0.347		0.485	1,23	0.493
	Temp*Sex	0.860	2.361	5,120	0.054	0.904	1.172	5,115	0.328
Force	Temperature	0.686	122.791	5,120	<0.001				
	Sex		15.55	1,24	0.001		0.423	1,23	0.522
	Temp*Sex	0.686	5.625	5,120	<0.001	0.728	1.175	5,115	0.327
Distance	Temperature	0.896	63.573	5,120	<0.001				
	Sex		4.619	1,24	0.042		1.996	1,23	0.171
	Temp*Sex	0.896	0.624	5,120	0.664	0.908	0.772	5,115	0.561
Angle	Temperature	0.841	4.516	5,120	0.002				
	Sex		0.121	1,24	0.731		0.625	1,23	0.437
	Temp*Sex	0.841	1.167	5,120	0.33	0.893	1.648	5,115	0.160
Duration	Temperature	0.678	2.674	5,120	0.046				
	Sex		7.277	1,24	0.013		2.365	1,23	0.138
	Temp*Sex	0.678	2.769	5,120	0.041	0.699	2.643	5,115	0.047
Contact time distance	Temperature	0.656	15.066	5,120	<0.001				
	Sex		9.347	1,24	0.005		4.274	1,23	0.05
	Temp*Sex	0.656	0.579	5,120	0.645	0.668	0.884	5,115	0.507
Time to peak power	Temperature	0.578	8.966	5,120	<0.001				
	Sex		5.64	1,24	0.026		1.011	1,23	0.325
	Temp*Sex	0.578	2.99	5,120	0.039	0.579	2.801	5,115	0.048
Time to peak acceleration	Temperature	0.737	4.331	5,120	0.004				
	Sex		2.484	1,24	0.128		0.386	1,23	0.54
	Temp*Sex	0.737	3.042	5,120	0.024	0.769	3.729	5,115	0.008

Huynh–Feldt epsilons (ϵ) are presented for both ANOVA and ANCOVA. Significant values are in bold.

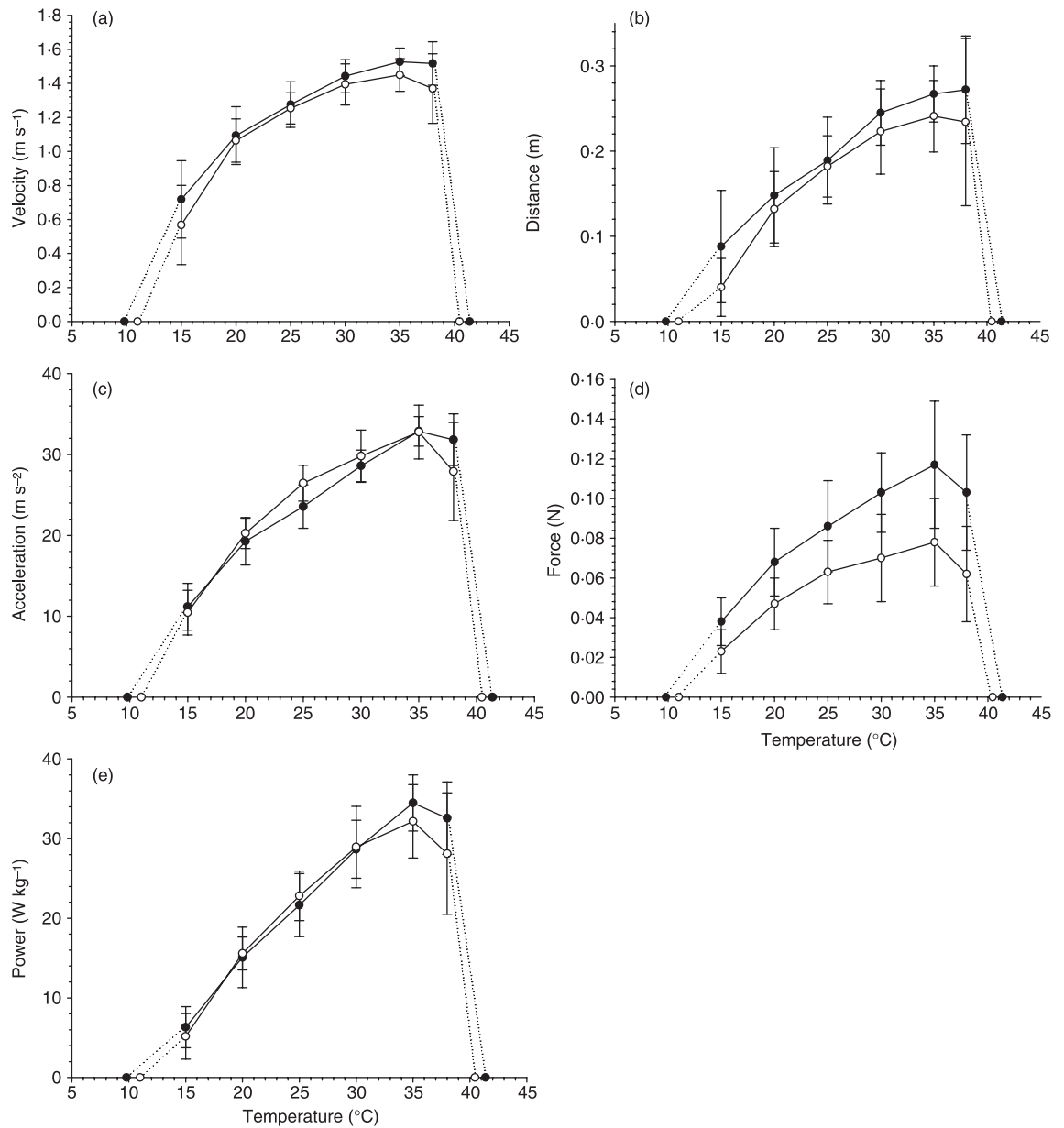


Fig. 1. Performance variables vs temperature for males (●) and females (○). CT_{min} and CT_{max} for both males and females are indicated on the x -axis for each graph. Error bars, \pm SD.

Table 2. Male and female Q_{10} values over the measured T_b range for jump velocity, acceleration, distance, force and power

Parameter	Q_{10} 15–25 °C		Q_{10} 25–35 °C	
	Males	Females	Males	Females
Velocity ($m s^{-1}$)	1.78	2.19	1.2	1.16
Acceleration ($m s^{-2}$)	2.11	2.53	2.11	2.53
Distance (m)	2.16	4.6	1.41	1.32
Force (N)	2.25	2.79	1.37	1.24
Power ($W kg^{-1}$)	3.43	1.59	4.42	1.41

(Table 2). Males exhibited higher values than females for all jump variables except for acceleration, power, jump angle and time to peak acceleration (Table 1). Significant interactions between sex and T_b were found for acceleration, force, jump duration, time to peak

power and time to peak acceleration, but not for velocity or power (although note that the interaction between sex and temperature for power was marginally non-significant; $P = 0.055$). Following correction for body size using ANCOVA, the only significant effects were those of sex on contact time distance, and the interactions between sex and T_b for acceleration and time to peak acceleration (Table 1).

The overall shapes of the (kinetic) jumping performance curves did not differ significantly between the sexes (Pillai's trace = 0.772, $F_{15,10} = 2.263$, $P = 0.098$; Fig. 1; Table 3), although females did exhibit wider ranges than males for several variables: acceleration, B_{80} ($F_{1,24} = 7.943$, $P < 0.01$); and power, B_{80} ($F_{1,24} = 4.724$, $P < 0.04$) and B_{95} ($F_{1,24} = 6.518$, $P < 0.017$). In addition, females had lower T_o for acceleration than males ($F_{1,24} = 10.057$, $P < 0.004$).

Table 3. Summary performance curve descriptive statistics for jump velocity, acceleration, power, force and distance

Parameter	Males			Females		
	T_o (°C)	B_{95} (°C)	B_{80} (°C)	T_o (°C)	B_{95} (°C)	B_{80} (°C)
Velocity	34.49 (1.78)	5.98 (2.28)	14.76 (3.11)	33.67 (1.99)	6.65 (3.31)	14.21 (2.77)
Acceleration	35.3 (1.33)*	3.98 (1.63)	10.65 (2.16)*	33.9 (0.91)*	5.34 (2.1)	12.94 (1.97)*
Power	35.25 (1.69)	3.12 (1.18)*	8.96 (1.51)*	34.03 (1.42)	5.02 (2.4)*	10.45 (1.96)*
Force	33.9 (1.33)	5.82 (2.68)	12.05 (2.69)	33.54 (1.23)	4.93 (1.84)	12.44 (1.43)
Distance	34.57 (2.97)	4.51 (3.7)	10.94 (4.24)	33.67 (3.23)	4.01 (2.99)	9.41 (3.98)

Values marked with an asterisk (*) differ between sexes. Values in bold differ among performance variables within sexes (see text for exact P values). All values are means (SD).

Table 4. Predicted performance variables at both optimal (T_o) and field T_b for males and females, as well as the percentage difference in predicted performance at field T_b relative to T_o for each sex

Parameter	Males			Females		
	T_o	Field T_b	Difference (%)	T_o	Field T_b	Difference (%)
Velocity ($m\ s^{-1}$)	1.52	1.37	-9.8	1.43	1.38	-3.5
Acceleration ($m\ s^{-2}$)	32.6	28.25	-13.3	32.25	29.75	-7.8
Distance (m)	0.265	0.241	-9	0.236	0.22	-6.8

However, the shapes of the performance curves differed significantly among performance variables within each sex (males: Pillai's trace = 0.545, $F_{12,180} = 3.328$, $P < 0.001$; females: Pillai's trace = 0.503, $F_{12,180} = 3.025$, $P = 0.001$). The B_{95} values differed within males ($F_{4,60} = 3.197$, $P = 0.019$), with force and velocity exhibiting the greatest breadth, and power the lowest (Table 3). Within males, the B_{80} variables also differed significantly ($F_{4,60} = 7.145$, $P < 0.001$), with velocity having significantly higher B_{80} values than acceleration, distance and power (Table 3). Within males, the overall velocity curve was therefore the widest (Table 3; Fig. 1a), with the curve for force being next widest (Fig. 1d), while those for acceleration (Fig. 1b), distance (Fig. 1b) and power (Fig. 1e) were largely similar, but with a narrower performance breadth for power. Within females, only B_{80} differed significantly between performance variables ($F_{4,60} = 7.33$, $P < 0.001$), with distance and power exhibiting the narrowest B_{80} ranges and velocity again showing the widest range (Table 3).

FIELD T_b AND THERMAL TOLERANCE

Males and females in the Tulane campus *A. carolinensis* population had very similar T_b (males 29.78 ± 0.412 °C, $n = 21$; females 29.77 ± 0.5 , $n = 17$; $t_{36} = -0.024$, $P = 0.981$; all values means \pm SE). Field T_b was lower than optimal performance temperatures for all jump variables in both males ($F_{5,81} = 22.653$, $P < 0.001$; Tukey's HSD $P < 0.05$) and females ($F_{5,76} = 32.506$, $P < 0.001$; Tukey's HSD $P < 0.05$). Furthermore, both males and females appear to suffer a jump performance decrement at field T_b s compared with optimal performance T_b (Table 4). Finally, males and females differed

significantly in both CT_{min} (males 9.8 ± 0.443 °C, females 11.08 ± 0.27 °C; $t_{19} = 2.338$, $P < 0.03$) and CT_{max} (males 41.38 ± 0.26 °C, females 40.46 ± 0.21 °C; $t_{19} = -2.706$, $P < 0.014$; all values means \pm SE). Thus females have an overall narrower thermal tolerance range (29.38 °C) compared with males (31.54 °C). These differences in thermal tolerance indices largely persist following correction for body size (CT_{max} , $F_{1,18} = 14.097$, $P < 0.034$; CT_{min} , $F_{1,18} = 3.295$, $P = 0.086$).

Discussion

Previous studies have demonstrated marked effects of temperature on locomotor performance abilities such as running and climbing in ectotherms (reviewed by Huey & Kingsolver 1989; Angilletta *et al.* 2002). We posited similar thermal effects on various kinetic and kinematic measures of jumping performance in green anoles. Our hypothesis is supported by the data: not only did changes in T_b affect force production (and hence jump distance, acceleration and velocity), but T_b also affected kinematic variables such as jump angle and contact time distances (Table 1). Thus, more than simply influencing overall jump performance, our findings show that changes in T_b also alter how animals jump. This study offers a valuable point of comparison for other studies dealing with temperature effects on locomotor performance and kinematics (e.g. Bergmann & Irschick 2006) and *in vitro* studies of muscle function, as well as providing data on the thermal dependence of jump kinematics, about which little is known (but cf. Wilson 2001). Our hypothesis that sex differences in jumping might be explained primarily by sexual size dimorphism was also largely supported. Finally, we

show that sex differences in thermal tolerance ranges probably affect the shape of the temperature curves for performance.

THERMAL DEPENDENCE OF KINETICS

All kinetic variables exhibited asymmetrical performance curves typical of temperature-dependent traits, with declines at low and high T_b and maximum performance at intermediate T_b (Fig. 1; Angilletta *et al.* 2002). These findings are consistent with those of Wilson (2001), who examined the thermal dependence of jumping performance in several populations of the frog *Limnodynastes peronii* (but note that Wilson 2001 did not examine temperatures higher than 35 °C). Power output, in particular, increased more than all other performance variables in *A. carolinensis* (apart from female jumping distance) over the 15–25 °C range, with Q_{10} values of 3.43 and 4.42 for males and females, respectively (Table 2). These values compare favourably with the Q_{10} value of 3.5 obtained by Bergmann & Irschick (2006) in a recent study of gecko climbing performance, and are also comparable with Q_{10} values from *in vitro* studies of muscle properties (Marsh & Bennett 1985; Swoap *et al.* 1993).

We noted several differences in the thermal sensitivity of the performance variables – in particular, the performance curves for velocity were consistently and significantly broader than those for other performance traits in both males and females (Table 3). Thus velocity appears somewhat less sensitive to temperature change than the other performance variables (acceleration, distance, power and force). Despite these differences, however, the five jump variables were similar in most other respects, including thermal performance optima (T_o ; Table 3). The thermal sensitivity of various jump performance variables therefore appears to be generally correlated in *A. carolinensis*, suggesting that there is no trade-off, from a thermal perspective, in terms of optimizing all these performance and kinetic variables simultaneously. In the only other available study on the thermal sensitivity of whole-organism jump velocity, acceleration and power, Wilson (2001) reported a similar congruence of T_o in cool-temperate (but not tropical) populations of the frog *L. peronii*, and noted a likely genetic causal basis for the difference. Unfortunately, little is known about the degree of additive genetic variation underlying the thermal sensitivity of performance in anoles.

THERMAL DEPENDENCE OF KINEMATICS

Consistent with our hypothesis, all kinematic variables were altered significantly by T_b in both male and female *A. carolinensis* (Table 1). Jump angle, for example, increased significantly with increasing T_b (Fig. 2a); at the lowest temperature (15 °C), female green anoles jumped at an average angle of 27.9°, whereas at the highest temperature (35 °C), they jumped

at an average angle of 43.4°, representing a 15.5° change in angle. The effect of T_b on jump angle is intriguing because this variable strongly influences jump performance in lizards, frogs and other animals (Marsh 1994; Toro *et al.* 2004). A recent study examining a group of 12 anole species showed that small changes in jump angle can significantly affect many aspects of jumping (Toro *et al.* 2004). For example, the optimal angle of *A. carolinensis* at its optimum temperature (given a known velocity and hindlimb length) was about 41.5° (Toro *et al.* 2004), but the authors found that green anoles (only males were examined) typically jumped at an angle of about 36.2°, resulting in only a minor loss in jump distance (–1.4%), but substantial savings in the vertical height (–17.2%) and duration (–8.3%) of the jump. Thus alterations in jump angle had only small effects on jump distance, velocity, acceleration and power, but had profound effects on the overall ‘shape’ of the jump, resulting in relatively brief, shallow jumps. In contrast to these findings, our own data set shows that T_b significantly affects both jump distance and jump angle (Figs 1b and 2a). One possible explanation for this result is that ‘obligatory’ submaximal jump performance as a result of changes in T_b , as in the present study, differs from ‘voluntary’ submaximal performance at optimal T_{bs} , as examined by Toro *et al.* (2006). In particular, whereas changes in jump angle alone have been shown to result in changes in jump kinematics as a control strategy in *A. valencienni* (Toro *et al.* 2006), our results indicate that submaximal jumps prompt changes in both force output and jump kinematics in *A. carolinensis*. Thus the performance profile of submaximal jumps caused by temperature-induced physiological impairment of muscle function may be dictated by a mixture of the two control strategies. Further studies of lizards jumping naturally (as opposed to being forced to jump) under a diversity of temperature regimes might shed light on this possibility.

EXPECTED PERFORMANCE AT FIELD T_b

Given these potentially profound effects of T_b on jump performance, one might expect green anoles in the field to maintain T_{bs} conducive to maximum performance (for a detailed discussion see Hertz *et al.* 1988). However, an intriguing result from our study was that field T_b for both males and females was significantly lower than the optimal T_b for all jump performance variables. Field T_b also appears to be lower than selected T_{bs} measured in the laboratory for male and female green anoles (Brown & Griffin 2005). Thus green anoles probably exhibit suboptimal jumping ability in the field, at least during the period that we sampled; the predicted performance decrements (the penalty for jumping at field T_b instead of T_o) for various jump variables (velocity, acceleration and distance) ranged from 3.5 to 13.3% (Table 4). Other studies have also found some evidence for a loose

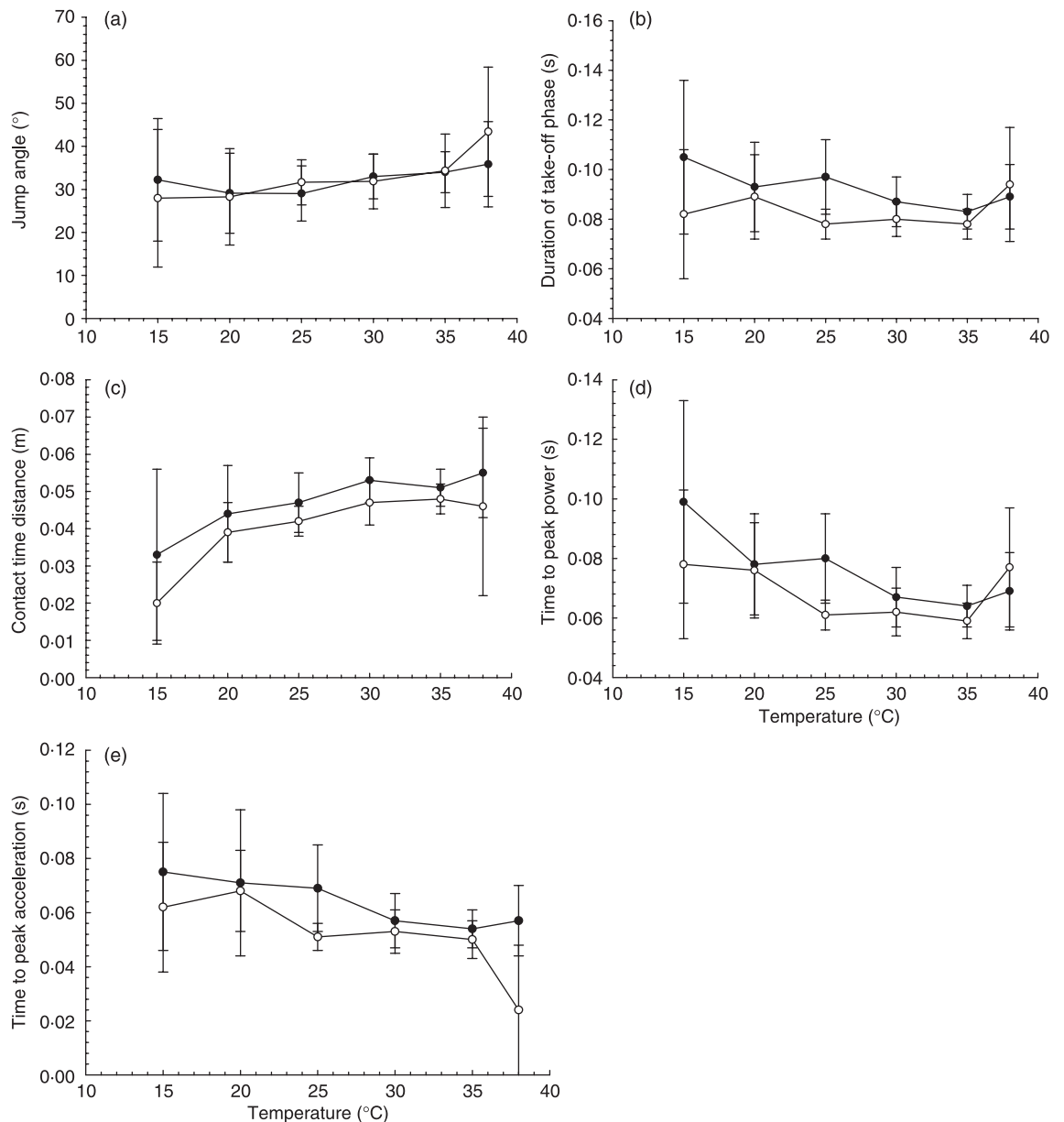


Fig. 2. Kinematic variables vs temperature for males (●) and females (○). Error bars, \pm SD.

coupling between field and optimal temperatures for whole-organism performance (e.g. sprint speed in skinks, Huey & Bennett 1987; but cf. van Berkum 1986). However, the ecological relevance of such suboptimal performance capacities is not readily apparent, but would be an interesting topic for further study (see Irschick 2000 for a discussion).

SEX AND PERFORMANCE

Several recent studies have shown that whole-organism performance capacities may differ between males and females, even after correction for sexual size dimorphism (Cullum 1998; Krasnov *et al.* 2003). Understanding such differences is important because dissimilar performance capacities in males and females may result in sex-specific behaviour in the field (Lailvaux

et al. 2003). Sex differences in several performance and kinetic variables were evident from our study (Table 1); but following correction for body size most of these differences disappeared, suggesting that scaling effects are largely responsible for the observed performance dimorphisms (see Toro *et al.* 2003 for a discussion of how size affects jump performance in anoles). These results support our hypothesis that sex differences in jump performance in *A. carolinensis* are primarily a result of sexual dimorphism in body size. Nevertheless, some kinematic differences did persist following correction for body size. For example, males exhibited longer contact time distances during take-off than did females (Table 1). Several variables also exhibited significant interactions between sex and T_b . Most notably, acceleration showed different responses to T_b manipulations over the temperature range measured,

with both overall acceleration and time to peak acceleration being significantly lower in females than in males (Fig. 1c), particularly at the high end of the temperature range (note also that the interaction between temperature and sex for time to peak power is only marginally non-significant; Table 3). Although such size-independent differences may indicate intrinsic physiological differences between males and females (Cullum 1998; Lailvaux *et al.* 2003), it is important to note that, while overall body size is controlled for in these analyses, body shape is not; therefore one possibility is that differences in body shape (e.g. relative limb length) as opposed to overall body size might affect jump kinetics and performance in *A. carolinensis*. Indeed, males have relatively longer hindlimbs than females (Irschick *et al.* 2005b), suggesting that shape effects may be important causal factors driving the observed sex-specific responses to acceleration and, potentially, power.

THERMAL TOLERANCE

Another possible explanation for these interactions between temperature and sex is that the shapes of the performance curves for acceleration and power are constrained by a relatively narrow thermal tolerance range in females. Any study of temperature effects on performance in ectotherms must take into account thermal tolerances – the upper (CT_{max}) and lower (CT_{min}) thermal limits within which performance is possible (Lutterschmidt & Hutchison 1997a, 1997b). If males and females differ in these tolerance ranges, then performance at T_{bs} close to the CT_{max} or CT_{min} might be expected to differ as well. Indeed, despite having broader curves for acceleration and power than males, we found that female *A. carolinensis* had both significantly higher CT_{min} and significantly lower CT_{max} values than males, resulting in an overall narrower thermal tolerance range for females compared with males. The thermal performance curves for both acceleration (Fig. 1c) and power (Fig. 1e) also show marked decreases as female T_b approaches CT_{max} . A parallel decrease in performance at 38 °C can also be seen for female (but not male) bite forces (unpublished data), suggesting that as CT_{max} is approached, muscle function might be compromised at a lower T_b for females compared with males. Although thermal tolerance can be affected by several factors, including acclimation regime, photoperiod, age or geography (Lutterschmidt & Hutchison 1997b), all the individuals we examined were sexually mature adults from the same population, were kept under identical conditions, and received identical treatment. A similar difference in tolerance range between males and females was also noted for *Platysaurus intermedius*, which also exhibits an interaction between sex and temperature for performance (Lailvaux *et al.* 2003). Future studies of the interactions between temperature and sex, perhaps involving experimental manipulation of CT_{min} and

CT_{max} , are needed to understand the relationship between thermal tolerance and the thermal sensitivity of performance in green anoles.

In summary, our hypothesis that manipulating T_b significantly alters all kinematic variables measured was supported, suggesting that all aspects of jump behaviour (not just force output, which directly affects jump performance) are thermally dependent. This finding underscores the need to control body temperature carefully in experimental studies of ectotherm locomotion, as movement-control strategies may also be affected by T_b . Our hypothesis that jump differences between males and females are largely attributable to body size was also supported, as male and female jumps were mostly similar following size correction. Although males and females maintained T_{bs} lower than that required for optimal jump performance, predicted jump performance is similar in both sexes. Future studies seeking to understand the constraints underlying the thermal sensitivities of complex traits in males and females might adopt Wilson's (2001) comparative approach using lizard populations or species that naturally experience different temperature regimes.

Acknowledgements

We thank J. Weaver for assisting with the collection of field body temperatures, and A. Herrel and B. Vanhooydonck for valuable discussion and comments on an earlier version of this manuscript. This study was supported by an NSF grant to D. Irschick (IOB 0421917). S. Lailvaux is a postdoctoral fellow of the Fund for Scientific Research Flanders (FWO).

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Received 15 November 2006; revised 25 January 2007;
accepted 8 February 2007
Editor: Steven Chown