Sex-Based Differences and Similarities in Locomotor Performance, Thermal Preferences, and Escape Behaviour in the Lizard *Platysaurus intermedius wilhelmi*

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Accepted 3/4/03

ABSTRACT

Differences between sexes in physiological performance have received little attention in animals. We tested for sex differences in maximum sprint speed and maximal exertion over a range of temperatures in a population of *Platysaurus intermedius wilhelmi* lizards. We also examined sex-based differences in selected temperature range, mean field body temperatures (T_b), and thermal activity limits. Finally, we conducted field studies to quantify male and female responses to a potential predator, which may be affected by their respective performance capabilities. Males were faster than females at all temperatures, and body size had no significant effect on sprint speeds. Males and females also selected similar T_b's when placed in a thermal gradient, but in the field, male lizards' T_b's were different from those of the females. However, predicted sprint speeds for males and females at their field T_b's are similar. No significant differences were found between males and females with regard to maximal exertion. When approached in the field, adult male lizards took refuge significantly earlier than did adult females and also fled over shorter distances, suggesting that females rely on crypsis as an escape strategy.

Introduction

Studies of performance, especially sprint speed, have formed the cornerstone of physiological ecology for many years (Garland and Losos 1994). This is because performance is widely viewed as an intermediate link between the phenotype and environment. As such, it acts as a type of behavioural transducer, transforming genetic information into a trait that is both easily measurable and sensitive to the action of natural selection (Arnold 1983; Jayne and Bennett 1990; Garland and Losos 1994). One aspect of sprint speed that has been extensively studied in ectotherms is its thermal dependence (e.g., Bennett 1980; Huey and Hertz 1982, 1984; Hertz et al. 1983; van Berkum 1986; Marsh and Bennett 1989; Jayne et al. 1990; Bauwens et al. 1995; Angilletta et al. 2002). Reptiles are unable to run quickly at low and high body temperatures (T_b's) because extreme temperatures prevent their muscles from contracting rapidly (Marsh and Bennett 1989; Rall and Woledge 1990; Swoap et al. 1993). In addition to sprinting performance, the thermal environment also places similar constraints on the performance of various other reptilian physiological characters in nature (Gibson and Falls 1979; Bennett 1980; Huey et al. 1989; Huey 1991). Intrinsic physiological characteristics, such as muscle composition and structure, may also modify or constrain realised limits of velocity in living animals (Abu-Ghalyun et al. 1988). One such characteristic that has been largely overlooked in the past is sex.

Intersexual differences in behaviour and morphology have been widely studied in animals (Stamps et al. 1997), often in the context of sexual selection. However, while a large body of literature has documented the influence of gender on physiological performance in humans (e.g., Wells and Plowman 1983; Mooradian et al. 1987; Sanborn and Jankowski 1994), studies of sex differences in physiological performance in nonhuman animals are fewer (but see Snell et al. 1988; Herrel et al. 1999; Miles et al. 2001; Shine and Shetty 2001 for examples). In a study of six species of sexually dimorphic *Cnemidophorus* lizards, Cullum (1998) found that males were always faster than females at T_b's within their preferred range, even after controlling for body size. Cullum (1998) hypothesised that this difference was due to some inherent physiological characteristic associated with sex. If female lizards are constrained to run slower than males, then females facing predation threat may favour behavioural escape strategies that do not depend on speed, such as crypsis (see Bauwens and Thoen 1981). In turn, we might then expect that a behavioural strategy of crypsis would also influence preferred body temperature; for example, females may be free to select a lower T_b if that T_b is preferable

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Physiological and Biochemical Zoology 76(4):511–521. 2003. © 2003 by The University of Chicago. All rights reserved. 1522-2152/2003/7604-2048$15.00

Table 1: Summary ANOVA results of body size, sex, and temperature effects on performance in *Platysaurus intermedius wilhelmi*

Effect	*F* Ratio	df	*P*
Sprint:			
Sex	12.676	1, 25	.002
T_b	83.919	5, 125	<.001
Sex × T_b	2.39	5, 125	.038
Exertion:			
Sex	.242	1, 27	.627
T_b	45.08	4, 108	<.001
Sex × T_b	.035	4, 108	.998

for other activities, such as digestion, or is energetically less expensive. Consequently, integrated laboratory and field data on sprint speed, thermoregulation, and the effects of temperature on performance in males and females could shed light on the evolution of thermal preferences in lizards.

We therefore tested whether a sex difference in locomotor performance exists over a range of body temperatures in a population of flat lizards, *Platysaurus intermedius wilhelmi*. We also tested whether male and female *P. intermedius wilhelmi* selected different T_b's by examining lizards in both the lab and the field. Finally, we looked at behavioural differences between the two sexes and tested the hypothesis that males and females utilise different antipredatory strategies by measuring approach and flight distances of individual *P. intermedius wilhelmi* when exposed to a potential predator in nature.

Material and Methods

Platysaurus intermedius wilhelmi is a small, diurnal cordylid lizard (maximum snout-vent length [SVL] = 83 mm) restricted to rocky outcrops in the Mpumalanga and Kwazulu-Natal Provinces, South Africa, and to limited areas in Mozambique and Swaziland (Broadley 1978; Branch 1998). Males and females are sexually dimorphic for coloration; males have a dull olive-green to brown back with a blue belly and a red tail, becoming straw-coloured towards the tip, while females and juveniles are black with three buff stripes and are sometimes spotted (Branch 1998). Body size is also sexually dimorphic; males are larger than females (S. P. Lailvaux and M. J. Whiting, unpublished data). A dorsally compressed body (± 5 mm trunk thickness) allows lizards to squeeze into rock crevices and ensures that body temperature is usually very similar to the substrate temperature (McKinon and Alexander 1999). Dissections of museum specimens suggest an omnivorous diet (Broadley 1978), and some investigations into the digestive physiology of this species have been conducted (McKinon and Alexander 1999; Alexander et al. 2001), but little else is known about its physiology, ecology, or behaviour.

All experimental procedures used were cleared by the Animal Ethics Screening Committee of the University of the Witwatersrand under numbers 00/78/2a, 00/79/2a, 00/80/2a, 00/81/3, and 01/45/3. Lizards were collected from Pullen Farm (24°35′S, 31°11′E) in the Kaapmuiden district of Mpumalanga Province, South Africa, during November 2000. The area is hilly and consists of numerous exfoliating granite domes in moist savannah. Rock outcrops vary in size because of vegetation encroachment and are structurally simple; they comprise loose, free-standing rocks or exfoliating sheets of granite ringed with dense grass clumps and woody vegetation. In the laboratory, lizards were individually marked with Pentel gold paint pens and housed communally in enclosures with newspaper substrate and rocks. Lizards were fed commercial dog food and *Tenebrio* larvae twice a week, and water was provided ad libitum. A 12L : 12D photoperiod and a constant temperature of 25°C were maintained in the room. No gravid females were used in this study.

Sprint Speed

To determine the thermal sensitivity of sprint speed, we chased lizards down a 2-m rubberised-surface racetrack equipped with photocells at 25-cm intervals. The photocells were linked to a computer, which recorded the times at which the lizards crossed the light beams. A single-photocell design was used opposed to stacks; however, the flatness of these reptiles meant that the beam was wide in relation to the lizards, and the lizards invariably broke the light beams with their snout. Sprint trials were carried out in a constant temperature room maintained at the trial temperature. All trials were conducted within 2 wk of capture. Lizards were run at 15°, 20°, 25°, 30°, 35°, and 40°C but did not all experience the same sequence of temperatures. Lizards were randomly assigned to groups of approximately six individuals. On the first day, group 1 was run at 25°C; on the second day, group 1 and group 2 were run at 20°C, and so on, until all individuals in a group had been run at each temperature. Thus, each group was run at different T_b's in a different order, and that order was determined in a random fashion. This was done so that temperature effects could be separated from effects that were a result of order (i.e., habituation). Groupings of individuals were necessary because only six trial temperatures were measured. Lizards were placed in the environmental chamber set to the trial temperature for at least 1 h before measurement to allow the animals to reach thermal equilibrium with the air in the chamber. Each individual lizard was raced three times at each temperature with a 1-h rest between trials and a day's rest between temperatures. Consistent with previous studies (e.g., Irschick and Losos 1998) and on the basis of similar criteria, sprints were subjectively rated as either good or poor; only good trials were used in the analysis. The fastest speed over a 25-cm interval was considered the estimate of maximal sprinting ability for each lizard. After com-

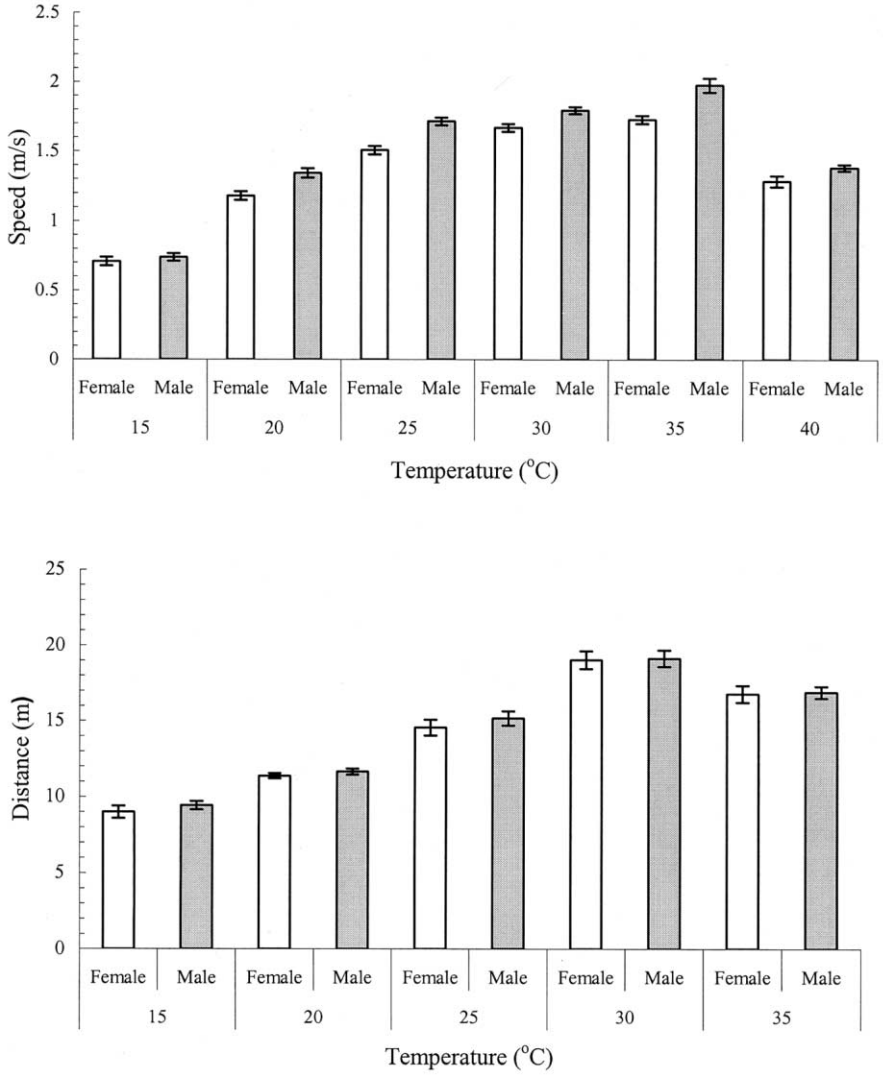

Figure 1. Absolute (i.e., not corrected for body size) performance values for male and female *Platysaurus intermedius wilhelmi* at all temperatures. *Top*, Sprint speed; *bottom*, maximal exertion. Error bars represent SE.

pletion of measurements at all trial temperatures, lizards were run again at their initial trial temperature to check for loss of condition or habituation. If a lizard declined more than 15% in speed between the two runs at the starting temperature, declined in mass more than 15% by the end of the trials, or broke a tail, it was excluded from the analysis. Fourteen males and 13 females were included in the final analysis (two males and one female were excluded). SVL and mass were also measured for each lizard.

Maximal Exertion

Maximal exertion was measured as the distance an individual ran at maximum speed before the onset of exhaustion when chased around a circular raceway 1 m in circumference. The raceway was marked such that distance run could be measured to the nearest 0.1 m even if the animal changed direction. We motivated individuals to run by lightly pinching their tails. An animal was considered exhausted when it refused to move despite repeated pinching or had lost its righting response. Lizards were run at 15°, 20°, 25°, 30°, and 35°C, and temperature sequences were randomised for each individual for the measurement of maximal sprint speed. In contrast to sprint speed measures, lizards were not run at 40°C because field and laboratory data on thermal preferences obtained subsequent to the sprinting trials indicated that such an extreme T_b is never approached by these animals, and running lizards to exhaustion at such a high temperature may cause unnecessary physiological

Table 2: Relative sprint performance breadth measures and the thermal limits of performance capacities for adult male and female *Platysaurus intermedius wilhelmi*

	T_o	B_{95}	B_{80}	CT_{min}	LRR
Males	31.95 (.78)	4.87 (.87)	13.52 (.59)	8.76 (.79)	45.48 (1.08)
Females	31.88 (.79)	6.52 (.99)	15.12 (1.03)	8.94 (.55)	44.06 (1.08)
P	.95	.22	.19	.49	**.001**

Note. Values shown are means ± SE ($F_{1,24} = 1.193$; $n = 13$ males, 14 females). *P* values for Tukey HSD post hoc ANOVA tests comparing males and females are given for each variable. Significant *P* values are in bold. LRR = loss of righting response.

stress. We placed the lizards in the environmental chamber set to the trial temperature for at least 1 h before measurement to allow the animals to reach thermal equilibrium with the air in the chamber. All individuals were run once (consistent with Cullum [1998]) at each temperature, with at least a day's rest between temperatures. Fourteen males and 15 females were measured in this manner. SVL and mass of each lizard were also measured for sprint speed. Exclusion from analysis was based on similar criteria to those employed in the sprint trials.

To carry out the minimum-polygon analyses, measures of 0 speed were needed. We thus determined the critical thermal minimum (CT_{min}) and the highest temperature at which loss of righting response (LRR) occurs for male and female *P. intermedius wilhelmi*. We measured LRR rather than CT_{max} (Lutterschmidt and Hutchison 1997) because LRR is appropriate in performance studies. To determine CT_{min}, we placed the lizards in an environmental chamber and lowered the temperature by 1°C/min until the lizard was unable to right itself. The temperature at which LRR occurred was noted as the CT_{min}. Lizard T_b's were monitored by a thermocouple inserted in the cloaca once loss of righting was achieved.

To determine LRR, we placed the lizards in a plastic container with a packed gravel substrate underneath which a copper heating plate (connected to a water bath) was located. This allowed us to control the temperature of the substrate by changing the temperature of the plate. This method is well suited to *P. intermedius wilhelmi* because of their dorsally compressed body shape. T_b was raised at approximately 1°C/min until loss of righting occurred in the lizard. Fifteen lizards of each sex were measured for both CT_{min} and LRR at high temperatures. Average CT_{min} and LRR for all males and females were used in the minimum-polygon analyses.

Selected T_b *Range*

The selected temperature ranges (equivalent but used in preference to preferred T_b range [see Currin and Alexander 1999]) of male and female *P. intermedius wilhelmi* were measured in a thermal gradient. Because *P. intermedius wilhelmi* is heliothermic, heat sources were provided by 250-W infrared lamps placed at one end of a 1.5 × 0.5 × 0.5-m wooden enclosure. A copper cooling plate connected to a water bath set at −10°C was placed underneath the compact sand substrate at the opposite end such that one end was cooler than the other, creating a thermal gradient from 46° to 5°C (measured at the surface of the sand). This range was selected because it extends above and below the T_b range that the lizards experience in nature. Fluorescent lights in the lab resulted in even lighting along the length of the gradient. The gradient was partitioned into five 0.2 × 1.5-m runways, each with its own infrared lamp. Each lizard was measured in a runway on its own.

We placed the lizards in the gradient 1 h before measurements began to allow them to habituate. Measurements began at 0900 hours every day. Lizards were captured in the gradient, and their cloacal temperatures were immediately measured using a thermocouple probe. Each lizard's T_b was sampled in this manner over a 6-h interval each day, with a 20-min interval between measurements to ensure the independence of data points. We determined this interval by sampling the T_b of one lizard for an entire day, with different time intervals between measures, and comparing the observed sequence of temperatures thus obtained to a randomised version of those same temperatures. If the differences between sequential temperatures were not significantly different from the differences between randomly selected measured T_b's, then the data points were considered independent. This method is similar to that employed by Wills and Beaupre (2000). This 6-h interval also coincided with the normal time of activity in this species. Four-

Table 3: Relative exertion performance breadth measures and the thermal limits of exertion performance capacities for adult male and female *Platysaurus intermedius wilhelmi*

	T_o	B_{95}	B_{80}
Males	30.94 (.79)	3.66 (.57)	10.26 (.79)
Females	31.02 (.55)	4.16 (.89)	10.78 (.98)
P	.93	.64	.68

Note. Values shown are means ± SE ($F_{1,25} = 0.0838$, $n =$ 14 males, 15 females). *P* values for Tukey HSD post hoc ANOVA tests comparing males and females are given for each variable.

Table 4: Summary of mean T_b's and range of T_b's

Sex	Gradient	Minimum	Maximum	Field	Minimum	Maximum
Females	30.99 (2.05)	25.64	34.12	27.05 (2.95)	20.4	35
Males	31.48 (1.66)	28.45	34.57	30.62 (2.09)	27	33.2

Note. Mean T_b's and range of T_b's were selected by males and females in the thermal gradient ($n = 14$ males, 17 females) and by active males and females in the field ($n = 19$ males, 24 females). All means are ± 1 SD.

teen adult male and 17 adult female lizards were sampled in this manner. Each lizard was thus measured for one trial, and analysis of males versus females was based on individual average temperatures. Measurements were taken at the same time every day to control for any influences of time of day on temperature selection. Before sampling began, each lizard was placed in the gradient for 1 h to habituate.

Field T_b*'s*

All fieldwork was carried out in the Kaapmuiden district of Mpumalanga Province, South Africa (24°35′S, 31°11′E), during the last week of October and the first week of November 2000, which is the end of the breeding season in this species (ca. September–October). Additional field T_b measures were collected during the last week of October 2001; these were pooled with the 2000 data. Lizards were captured in the field by using either sticky traps or a slip noose. The traps were observed continuously, and immediately after capture, the lizards' T_b's were measured using a thermocouple probe inserted into the cloaca. T_b's of lizards caught on traps fell within the range of those of lizards caught by noose. Lizards were caught at different times of the day over a period of 4 d, and temperature measures were made from only lizards that were judged to be active. A total of 19 male and 24 female lizards were sampled. Similar numbers of male and female lizards were captured in the morning and afternoon. Previous studies have shown that lizards exhibit daily rhythms with regard to T_b selection (Sievert and Hutchison 1989), a potentially confounding variable that was not controlled for when using this sampling method. However, these measurements allow us to test Hertz et al.'s (1988) hypothesis that most lizard species maintain field T_b's conducive to maximum locomotor performance.

Field Measures of Escape Behaviour

Two sets of trials were conducted wherein individual lizards were approached in the field to determine their response to a potential predator. Quantification of lizard responses when approached by a researcher is a standard method for study of antipredatory behaviour in lizards (Rand 1964; Cooper 2000 and references therein) and is appropriate for *P. intermedius wilhelmi*, which flees when approached by human beings. All trials were conducted by the same individual (S.P.L.) wearing the same clothing. The first set of trials (males $n = 20$; females $n = 20$) quantified approach and flight distances. Approach distance was defined as the straight-line distance between the observer and the lizard when the lizard began moving, and flight distance was the straight-line distance from the lizard's initial stationary position to when it stopped moving. S.P.L. approached the lizards slowly to ensure that they were aware of his presence. Once a lizard moved a minimum of 100 mm from its initial position, S.P.L. dropped a marker to indicate his position. A second marker was dropped at the lizard's initial position, and after 5 s, the lizard's final position (visible in open or concealed in rock or vegetation) was scored and indicated with a third marker. Previous studies have shown 5 s is sufficient time for a lizard to make an escape "decision" (Whiting 2002; Whiting et al. 2003). Finally, if the lizard was still visible, it was approached again until it took refuge (this was done only to force a refuge choice, and no measures of distance or time were taken). The type of refuge was scored, and whether the lizard had a choice of refuge type (rock vs. vegetation) was noted. We defined approach distance as the distance between markers 1 and 2 and flight distance as the distance between markers 2 and 3. Approach and flight distances were measured with a 3-m tape to the nearest 100 mm.

Table 5: Predicted relative and absolute sprint speeds and exertion distances for males and females at both selected and field body temperatures

	Males		Females	
	Selected	Field	Selected	Field
Sprint speed (% maximum)	93.2	92.4	95.8	90.7
Sprint speed (m/s)	1.67	1.66	1.59	1.44
Exertion distance (% maximum)	91	93.3	93.7	89
Exertion distance (m)	17.34	17.77	17.95	15.32

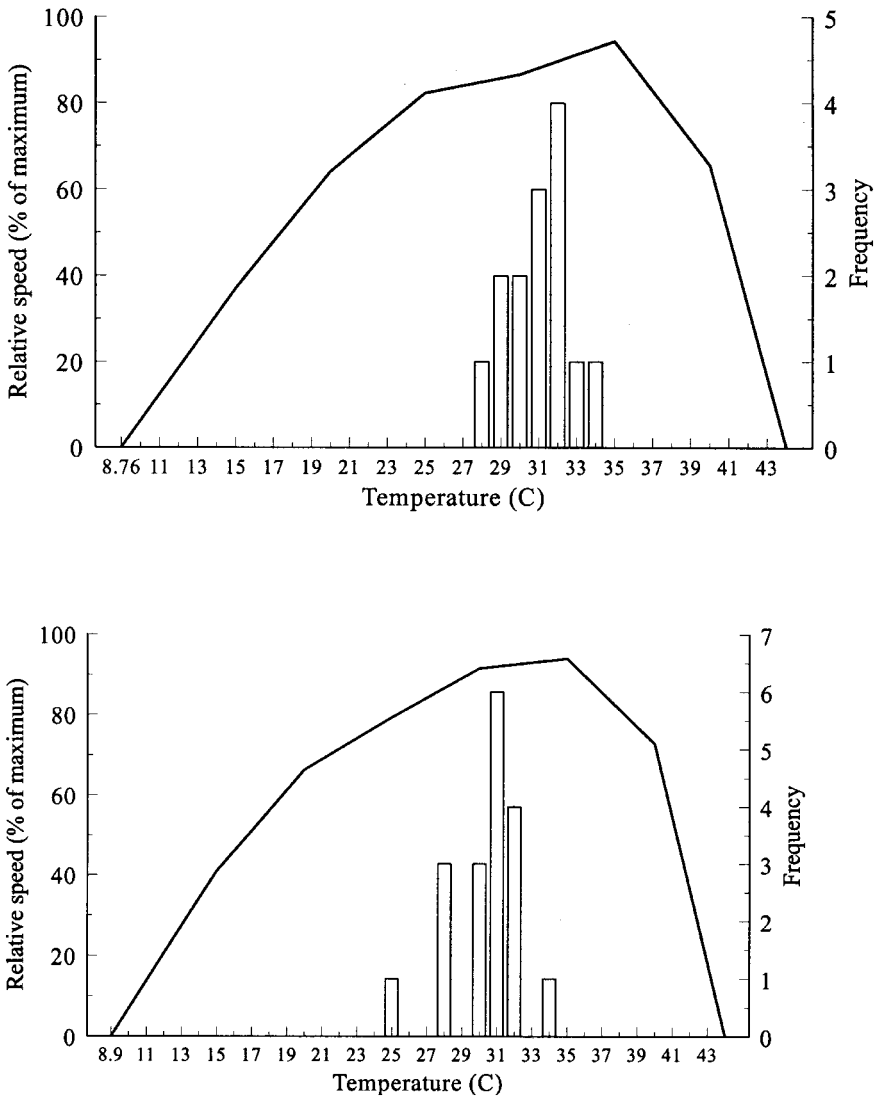

Figure 2. Superposition of the distribution of selected T_b's on the thermal sensitivity function for (*top*) males (mean selected T_b was not significantly different from T_o [$F_{1,24} = 1.193$, $P = 0.593$]) and (*bottom*) females (mean selected T_b was not significantly different from T_o [$F_{1,24} = 1.193$, $P = 0.225$]).

In the second set (males $n = 20$; females $n = 20$), we recorded several variables: (1) the time from when a lizard first moved because of S.P.L.'s approach until it found cover, (2) whether lizards took refuge in rock or vegetation, and (3) whether lizards had a choice between rock and vegetation as a refuge. In addition, we noted whether lizards ran directly into a refuge or whether they first stopped in the open. All lizards were approached at a constant speed until they took refuge. Lizards were classed as males or females primarily on the basis of colouration. Because subadult males often retain a female-like appearance, museum specimens of female *P. intermedius wilhelmi* lizards were dissected and examined in the laboratory before this study to determine the minimum size (SVL = 65 mm; S. P. Lailvaux, unpublished data) for egg laying in this species. Only females visually judged to have an SVL > 65 mm were included.

To quantify sex-specific behaviours, we performed 15-min focal observations on adult males and females. Lizards sometimes disappeared from view before 15 min. Focal samples had a mean duration of 13.08 min (±3.32, 1 SD). Of the 18 focal samples (males $n = 9$; females $n = 9$), 66.7% were for the full duration, while none was <5 min. All successful prey captures and prey capture attempts, as well as all movements >100 mm, were recorded. Because of the difficulty of distinguishing suc-

cessful and unsuccessful prey capture attempts, these were combined for analysis. Observations were recorded on a dictaphone and were transcribed. The number of prey capture attempts per minute, number of moves per minute (MPM), percentage of time spent moving (PTM), and time in refuge (RT; described as a percentage of the focal time) were calculated.

Statistical Analyses

All analyses were performed using Statistica 5.5 and SPSS 10.5 for Windows. Before analyses, all data were tested for normality using a Lillifores test. No data transformations were carried out. All tests were two tailed and were considered significant at $\alpha < 0.05$. Male and female SVL sizes were compared using *t*-tests. Two-way repeated-measures ANOVA tests with sex and temperature as fixed factors were performed on absolute (i.e., non-size-corrected) data to test for sexual dimorphism in sprint performance and exertion over the trial temperatures. ANCOVA, with SVL as a covariate, was used to test for significance of SVL.

A modified minimum-polygon algorithm (see van Berkum 1986 for detailed description) and several estimated descriptive measures were used to describe the thermal dependence of sprint speed and exertion. Zero speed was assigned to temperatures at which loss of righting occurred. For each lizard, the B_{95} (temperature range over which performance was no less than 95% of maximum), B_{80} (temperature range over which performance was no less than 80% of maximum), and the optimal performance temperatures (T_o, the midpoint of the B_{95} range) were calculated for both its sprint and exertion performance curves. The breadths of these ranges (i.e., the means) were compared between males and females and were also compared with selected T_b's in the lab and mean field T_b's using one-way ANOVAs. We carried out *t*-tests on T_b data to evaluate differences in selected T_b's between sexes, and differences within sexes (i.e., between lab and field data) were assessed using paired *t*-tests. The use of paired *t*-tests results in the exclusion of several data points, which is not desirable. However, the nature of the data set (resulting from the opportunistic sampling method we employed) precludes the use of repeated-measures ANOVA. For behavioural trials, all comparisons between the sexes with regard to approach and flight distance and time to refuge were evaluated using Mann-Whitney *U*-tests where the normal approximation continuity correction was applied. Raw data from focal studies were analysed using *t*-tests; PTM and RT are presented here as percentages.

Results

Performance Differences

In both performance studies, males were significantly larger than females (for sprint speed trials, $n = 14$ males [mean SVL $\pm$ SD $= 74.7 \pm 3.2$ mm] and $n = 13$ females [mean SVL $= 67.3 \pm 2.7$ mm], $t_{25} = 6.102$, $P = 0.001$; for exertion trials, $n = 14$ males [mean SVL $= 75.6 \pm 2.4$ mm] and $n = 15$ females [mean SVL $= 67.7 \pm 1.6$ mm], $t_{27} = 7.94$, $P = 0.001$). As expected, temperature had a significant effect on both sprint speed and exertion (Table 1). Sex also had a significant effect on sprint speed but not on exertion (Table 1); visual inspection of mean sprint speeds shows that males are always faster than females (Fig. 1, *top*), while exertion values appear the same in both sexes (Fig. 1, *bottom*). The interaction

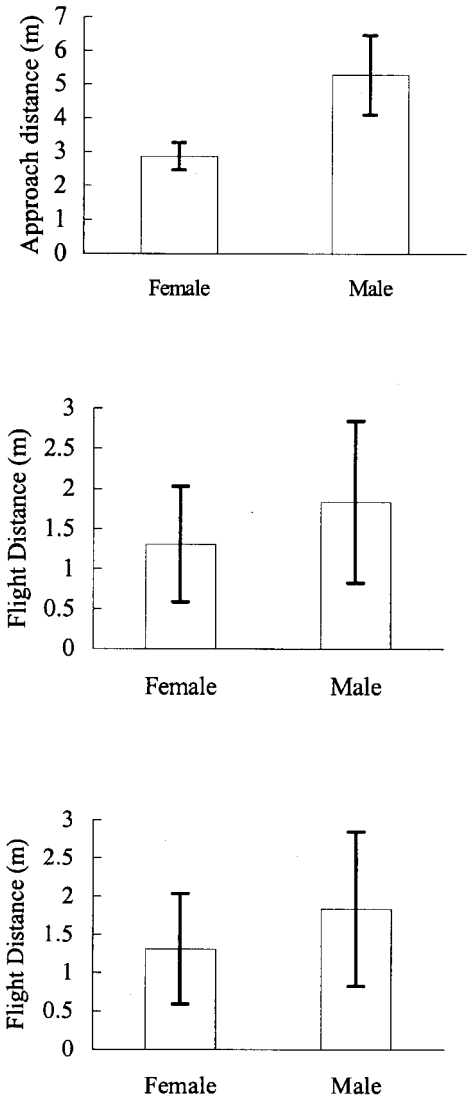

Figure 3. Results of field escape behaviour trials. *Top*, Approach distances for adult males and females. Females allowed significantly closer approach distances than did males. *Middle*, Flight distances for adult males and females. No significant differences existed. *Bottom*, Times to refuge for adult males and females. Males disappeared from view significantly faster than did females. All graphs are shown as means $\pm$ SD.

between sex and temperatures was weakly significant for sprint speed and not significant for exertion (Table 1). SVL had no significant effect on sprint speed ($F_{1,25} = 0.049$, $P = 0.827$) or exertion ($F_{1,25} = 0.208$, $P = 0.998$).

Measures of sprint performance breadth, as well as loss of righting T_b's, are presented in Table 2. All sprint performance breadth measures were found to be similar for males and females. LRR, however, was significantly higher for males. Similarly, exertion performance breadth measures (Table 3) did not differ significantly between the sexes.

T_b *Ranges*

The mean T_b's selected by male *Platysaurus intermedius wilhelmi* in the gradient were not significantly different from those selected by females ($t_{29} = 0.724$, $P = 0.48$; Table 4). Field T_b's, however, were different, with males maintaining significantly higher mean field T_b's than did females ($t_{42} = 3.636$, $P < 0.001$; Table 4). Mean field T_b's in males were not significantly different from selected T_b's ($t_{13} = 1.48$, $P = 0.22$; Table 4), but in females, mean field T_b's were significantly lower than selected T_b's ($t_{15} = -2.648$, $P = 0.02$; Table 4). Predicted sprint speeds and exertion distances at the average selected and field T_b's for each individual lizard were interpolated from the thermal sensitivity curves (after Bauwens et al. 1995) and are presented in Table 5.

Optimal Sprint T_b*'s and Selected* T_b *Ranges*

Comparison of T_o in males and females with their respective mean selected T_b's in the laboratory and measured mean field T_b's showed that T_o was not significantly different from laboratory T_b's in either males ($P = 0.59$; Fig. 2, *top*) or females ($P = 0.23$; Fig. 2, *bottom*). However, T_o was different from mean field T_b's in females ($F_{1,29} = 10.74$, Tukey HSD $P = 0.001$) but not in males (Tukey HSD $P = 0.24$).

Optimal Exertion T_b*'s and Selected* T_b *Ranges*

T_o was not significantly different from mean selected T_b in either males ($F_{2,25} = 0.388$, Tukey HSD $P = 0.56$) or females (Tukey HSD $P = 0.59$). However, T_o was significantly higher than mean field T_b in females ($F_{1,30} = 7.116$, Tukey HSD $P = 0.001$) but not in males (Tukey HSD $P = 0.72$).

Field Measures of Escape Behaviour

Female lizards allowed significantly closer approach distances than did males (Mann-Whitney $Z = 4.23$, $n = 40$ [20 females, 20 males], $P = 0.001$; Fig. 3, *top*). Although male and female flight distances were not significantly different (Mann-Whitney $Z = 0.863$, $n = 40$ [20 females, 20 males], $P = 0.87$; Fig. 3, *middle*), times to refuge were; males disappeared from view faster than did females (Mann-Whitney $Z = 4.288$, $n = 40$ [20 females, 20 males], $P = 0.001$; Fig. 3, *bottom*). In total, 95% of males ($n = 19$) and 90% of females ($n = 18$) took refuge in or under rocks when approached. When only those lizards with a choice of refuge were included in the analysis, the results were the same (95% of males, 95% of females). When approached but not forced to take refuge, 85% of males ($n = 17$) sought refuge immediately without stopping, while only 35% ($n = 7$) of females did so ($\chi^2_1 = 4.85$, $P < 0.05$). No individuals of either sex were visible after the lizards sequestered themselves, and only 2.5% ($n = 2$) of all lizards sampled, both of which were females, reemerged within 30 s of entering a refuge.

The number of MPM observed during focal observations was not significantly different for male and female *P. intermedius wilhelmi* ($t_{16} = 0.83$, $n = 18$, $P = 0.42$). Similarly, the RT for male and female lizards was not significantly different ($t_{16} = 1.35$, $n = 18$, $P = 0.19$). However, PTM was significantly different between the sexes, with females spending a greater percentage of time moving than did males ($t_{16} = 8.69$, $n = 18$, $P = 0.002$). Because of the low instances of prey capture attempts, no statistics were performed on these data, but the means are presented in Table 6.

Discussion

Our study is the first to test explicitly for sex differences in maximum sprint speeds over a range of body temperatures in a lizard species. Consistent with previous studies on lizard performance (see Angilletta et al. 2002 for review), body temperature was found to significantly affect sprinting performance in *Platysaurus intermedius wilhelmi*. Sex was also found to have a significant effect on sprinting performance, and we found a significant (although not highly significant) interaction between sex and temperature, suggesting that changes in body temperature affect sprinting in males and females differently over the examined thermal range; Figure 1 (*top*) shows that males exhibited higher average sprint speeds than did females at all temperatures. Surprisingly for such a dimorphic species, body size had no significant effect on sprinting performance. Thus, our study supports the findings of Cullum (1998), who reported that body size explained only a small proportion of the sex differences in sprinting performance in six species of *Cnemi-*

Table 6: Summary of means (±1 SD) for moves per minute (MPM), percentage of time spent moving (PTM), time in refuge (RT), and prey capture attempts for males and females

Sex	MPM	PTM	RT	Prey Capture Attempts
Females	.82 (.45)	5.75 (3.42)	30.32 (29.27)	.11 (.2)
Males	.63 (.73)	1.39 (1.39)	15.6 (14.36)	.006 (.2)

dophorus (but see Garland and Losos 1994 for a review of body size effects on sprint speed).

While differences in sprinting ability between the sexes are evident in the laboratory, these differences may not be manifest under field conditions. Males sampled in the field maintained higher body temperatures than did females; however, when relative sprint speeds at these temperatures are predicted from the thermal sensitivity function, females are predicted to be capable of moving at approximately 91% of their maximum speed (1.44 m/s) as opposed to males, who exhibit predicted sprinting capabilities of approximately 92% (1.66 m/s) of their maximum speed. The biological significance of these estimates is difficult to evaluate. Christian and Tracy's (1981) study on predation in hatchling Galapagos land iguanas (*Conolophus pallidus*) suggests that slight performance differences may have disproportionate effects on fitness; however, without precise measures of sprinting performance in the field, no predictions can be made as to the relationship between sprinting and survival in *P. intermedius wilhelmi*. Nevertheless, these rough predictions are consistent with Hertz et al.'s (1988) assertion that most reptile species maintain body temperatures conducive to maximal performance.

Our evaluation of antipredatory behaviour in this species does, however, allow us to draw some tentative conclusions. Female lizards allowed closer approach of a potential predator than did males (Fig. 3, *top*), which also disappeared from view significantly faster than did females (Fig. 3, *bottom*). This result suggests that females may rely on immobility and their cryptic colouration to mask their presence from a predator (Bauwens and Thoen 1981). Indeed, a stationary female on a rock outcrop is surprisingly difficult to see (at least for humans) as opposed to the more brightly coloured males. Cooper (1997) showed that relatively inconspicuous *Eumeces laticeps* lizards allow closer approach of a potential predator than do relatively conspicuous ones, and Martin and Lopez (1999) found that the conspicuousness of *Psammodromus algirus* lizards to potential predators in different microhabitats determines when flight is initiated. Rand (1964) reported a similar result in *Anolis lineatopus*, as did Heatwole (1968). Thus, the conspicuously coloured male *P. intermedius wilhelmi* may be at greater predation risk and may consequently opt for early flight as opposed to the more cryptically coloured females, who rely on immobility as an escape strategy. However, Whiting (2002) found that colouration is unlikely to affect male survival relative to female survival in the sexually dichromatic *Platysaurus broadleyi* and found no male behavioural compensation. A previous study also looked at escape behaviour in adult and juvenile *P. intermedius wilhelmi* (Whiting et al. 2003) and found no differences between males and females in escape strategy, although their sample size of adult males versus adult females was much smaller than it was in this study and was conducted in April as opposed to October–November for this study. Further research may therefore be required to unambiguously demonstrate female crypticity in this species.

Our field studies of *P. intermedius wilhelmi* were carried out at the end of or soon after the breeding season. This raises the possibility that some of the females included in the escape and behaviour components of this study were gravid. We reject this suggestion because all lizards used in the laboratory studies and sampled for field body temperatures were captured in the field at the same time as the escape study was conducted, and none of these was gravid or became pregnant at any time subsequent to capture. It may then be argued that nongravid lizards are more likely to be captured; however, we used two methods (sticky traps and noosing) to capture lizards. Continuously moving lizards that avoided the noose were caught on sticky traps, whereas noosing was more effective for lizards that made frequent stops when moving. Thus, we sampled a number of lizards over a spatial and behavioural continuum and found no pregnant females. We therefore consider it unlikely that any of the females included in the behavioural components of the study were gravid. No gravid lizards were included in the laboratory components either (see "Material and Methods").

In contrast to sprinting performance and escape behaviour, all other physiological variables measured showed remarkable similarity. Maximal exertion, thermal breadth measures for sprinting and exertion, and selected temperature ranges in the laboratory did not differ significantly between the sexes. Only LRR was significantly different, with males exhibiting a higher LRR than did females (Table 2). Behaviour observed during the focal trials was also similar in males and females, although the focal studies revealed that females spent a significantly greater PTM than did males (Table 6). This is curious because one would expect animals relying on crypsis to move less, not more. One possible explanation is that these increased PTM times reflect an increased foraging effort to replace energy expended during reproduction, and this might be important for future studies.

In conclusion, we found a significant effect of sex on sprint speeds in *P. intermedius wilhelmi* when measured in the laboratory, although this effect does not appear to be evident once field body temperatures are taken into consideration. Integrated studies, combining both laboratory and field components, may therefore be extremely useful in the future as an aid to understanding the evolution of reptile locomotion and thermal preferences in nature.

Acknowledgments

This work was financially supported by the National Research Foundation and the University of the Witwatersrand (grants to G.J.A. and M.J.W.). Permits for capture, transport, and maintenance of *Platysaurus intermedius wilhelmi* were granted by Gauteng Nature Conservation and the Mpumalanga Parks

Board (permits MPB 10013/98, TN 8/4/4/2, MPB 5031, MPB 5032). Charles Sandrock designed and constructed the electronics for the racetrack, and Wulf Haacke generously lent us preserved *P. intermedius wilhelmi* specimens from the Transvaal Museum in Pretoria. Thanks are due to Bruce Jayne and Alistair Cullum for their advice and ideas. This article was greatly improved by comments from Duncan Irschick and three anonymous reviewers.

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