

Sexual Dimorphism in Physiological Performance of Whiptail Lizards (Genus *Cnemidophorus*)

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ABSTRACT

Numerous studies have examined sexual dimorphism in the morphology and behavior of vertebrates; very few, however, have explicitly investigated the possibility of gender differences in physiological performance, despite the observations of such differences in humans. In this study, I investigated physiological sexual dimorphism in the lizard genus *Cnemidophorus* by measuring five whole-animal traits, all of which are likely to influence fitness in these species: burst speed, endurance, maximal exertion capacity, standard metabolic rate, and evaporative water loss rate. Because at least some of these traits are known to be strongly influenced by body size, I tested for dimorphism using both absolute and size-corrected trait values. An examination of six *Cnemidophorus* species and subspecies revealed a strong trend toward higher absolute trait values in males for all variables except endurance. Most of the dimorphism in standard metabolic rate and evaporative water loss rate could be explained by differences in body mass between males and females; for the locomotor traits, however, body size explained only a small fraction of the overall sexual dimorphism. The portion of trait differences not explained by body size was likely due to gender differences in physiology, such as differences in relative muscularity and fat content.

Introduction

Differences in physiological performance between male and female humans are well documented in the literature (reviewed in Wells and Plowman [1983]; Pate and Kriska [1984]; Sanborn and Jankowski [1994]). With regard to exercise capacity, for example, male athletes typically perform short-, mid-, and long-distance running events 5%–10% faster than their female counterparts. Differences are also present in other physiological

traits, such as resting metabolic rate, with females having values 5%–10% lower than males. While such differences may be due in part to psychological and sociological effects, the major influences on performance are likely to be physiological and morphological differences between men and women (Wells and Plowman 1983; Mooradian et al. 1987; Sanborn and Jankowski 1994). For many traits, a significant portion of the difference in performance between genders is due to differences in overall body size. The remaining fraction of the difference appears to be due primarily to the effects of androgens, including testosterone, on physiology and body composition (Mooradian et al. 1987; Sanborn and Jankowski 1994; Bhasin et al. 1997). Maximal aerobic capacity ($\dot{V}O_2$ max), for example, is about 30%–40% lower on average in women than in men; about half of this difference is due to differences in overall body size, while the remainder is due to sexual differences in physiological factors and proportions of different tissue types (Pate and Kriska 1984; Sanborn and Jankowski 1994). Other physiological performance traits showing notable dimorphic trends in humans include maximal anaerobic cycling and running capacity (Vandewalle et al. 1985; Nevill et al. 1996), treadmill endurance (Wells and Plowman 1983), and the cost of transport during running (Bransford and Howley 1977).

In nonhuman animals, sexual dimorphism in morphology and behavior has been studied extensively; often, this work involves a focus on intra- or intersexual selection (e.g., Stamps 1983; Anderson and Vitt 1990). However, despite the documented influence of gender on physiological performance in humans, the possibility of similar effects in other animals has received less attention. This is unfortunate because such differences are of potential importance for a variety of reasons. For example, males and females may suffer differential mortality if sexes vary in performance traits affecting fitness (Snell et al. 1988; Jayne and Bennett 1990). Dimorphism in physiological capacities and efficiencies may also be important in sexual selection, if males compete for mates or spend considerable time searching for a receptive female (Anderson and Vitt 1990).

In this study, I examined physiological dimorphism in six species and subspecies of the lizard genus *Cnemidophorus* (Sauria: Teiidae). The use of temperate species of *Cnemidophorus* provided for a conservative test of physiological dimorphism, since these species show limited dimorphism in both morphology and behavior: no major male and female body-form differences exist (Stamps 1983; Stebbins 1985), and males are not territorial (Stamps 1983; Anderson and Karasov 1988). By examining multiple taxa simultaneously, I was able to make replicate observations and reach more robust conclusions

about patterns of dimorphism in the genus than would have been possible in a single-species study.

In order to evaluate the degree to which gender influences physiological capacities and rates, I examined five performance characters. The first three characters were locomotor traits that reflect maximal capacities: burst speed (reflecting maximal muscular and biomechanical performance), treadmill endurance (a measure of aerobic capacity), and maximal exertion (a measure of anaerobic capacity). (These traits are explained more fully under Material and Methods.) The other two characters examined are measures of maintenance values in resting animals: standard metabolic rate (SMR, which indicates energy usage by resting animals) and evaporative water loss rate (a measure of water usage by resting animals). Whole-animal traits such as these are of particular interest in the context of natural and sexual selection, since they represent the integrated aspect of an animal's physiology that actually interacts with the biotic and abiotic environment (Huey and Stevenson 1979; Arnold 1983; Bennett 1989). Since some portion of any observed differences in performance may be due to sexual dimorphism in body size, I also tested for size dimorphism in the species examined and determined what fraction of any differences in performance were due to such differences. SMR and evaporative water loss rate are known to be strongly dependent on body size (Bennett and Dawson 1976; Mautz 1982), and locomotor traits sometimes show a similar if less pronounced relationship (Garland 1993; Garland and Losos 1994).

Material and Methods

Collection and Maintenance of Animals

Lizards were collected by hand, noose, and portable drift fences in the Sonoran and Chihuahuan deserts during mid-June to mid-August of 1992–1994 (New Mexico Game and Fish Permit No. 1955, Arizona Game and Fish Permit No. CLM00000227, and Texas Parks and Wildlife Permit No. SPR-0694-692). Collection dates and localities are given in Table 1. The following species and subspecies were studied: *Cnemidophorus burti* Taylor 1938, *C. inornatus arizonae* Van Denburgh 1896, *C. inornatus heptagrammus* Axtell 1961, *C. septemvittatus* Cope 1892, *C. tigris marmoratus* Baird and Girard 1952, and *C. tigris punctilinealis* Taylor and Walker 1996 (previously *C. t. gracilis* Baird and Girard 1952). (For the sake of brevity, I will henceforth refer to these six simply as “taxa.”) This group includes the smallest (*C. inornatus* subspecies) and largest (*C. burti*) species of *Cnemidophorus* found in North America, and sexual dimorphism in overall body size also varies significantly among these taxa (see Results).

Sampling of lizard populations was conducted without regard to the sex of individuals; capture attempts were made for all individuals of or near adult size that were spotted, and the active nature of these lizards made crypsis of any sex or size class unlikely. Because female lizards were of special interest

for another study (Cullum 1997), captured males were sometimes not used, so some taxon samples are female biased. After capture, individuals were measured for snout-vent length (SVL), weighed, and sexed. Sexing involved a combination of techniques dependent on the particular taxon, including expression of hemipenes and examination of femoral pores, coloration (Stebbins 1985), head width (Anderson and Vitt 1990; C. J. Cole, personal communication), and cloacal scales (Pietruszka 1981). All individuals used in this study were judged to be sexually mature based on sexual characteristics or size (Vitt and Breitenbach [1993] and references therein). Gravid females and individuals with substantial tail loss (less than two-thirds of estimated tail length remaining) were excluded from this study. Within a day after capture, individuals were housed in plastic shoe boxes under ambient temperatures (typical daily high/low: 30°/20°C) and photoperiod (via indirect daylight). Water was provided daily, but food was withheld until SMR and evaporative water loss had been measured (see below).

Measurement of Performance Traits

The number of individuals of each sex and taxon measured is shown in Table 1. Measurements began one to three days after capture, with one locomotor trait being measured each day, followed by SMR and evaporative water loss rate after a day of rest. All trials were conducted with animals at body temperatures near 40°C (see Table 2), a temperature within the preferred range of all these taxa (Milstead 1957; Bowker and Johnson 1980; Anderson and Karasov 1988; Garland 1993; A. J. Cullum, personal observations). Testing procedures followed protocols that have become standard among comparative physiologists (e.g., Huey et al. 1984; Bennett 1989; Garland 1993). An abbreviated description of these methods is given here; further details are given in Cullum (1997), where some of the data on female *Cnemidophorus* were previously analyzed in an examination of relative performance in sexual and asexual (all-female) species of *Cnemidophorus*.

Burst Speed. Lizards were chased at full speed down a 3-m-long racetrack equipped with photocells at 25-cm intervals. A computer monitored the photocells and provided triggering times to 0.01 s accuracy. Each individual was run three times in rapid succession on two different days. The shortest time over a 50-cm interval of all six trials was used to calculate maximal speed in meters per second.

Endurance. Endurance was measured as the number of seconds an individual maintained a 1.0 km/h pace on a motorized treadmill with a 20° incline. Lizards were prompted to maintain speed by being tapped or pinched at the base of the tail. A trial ended when an individual failed to match tread speed for more than 10 s despite repeated pinching or when the righting response was lost. One measurement was made per individual.

Table 1: Abbreviations, collection dates and localities, and sample sizes for *Cnemidophorus* taxa

Taxon	Collection Dates	Collection Locality	Sample Size (Males, Females)
<i>C. burti</i>	July 12–August 11, 1993, June 14–July 31, 1994	Gaudalupe Canyon, Hidalgo Co., N.Mex.	12, 14
<i>C. inornatus arizonae</i>	July 17–27, 1993	Near Arizona 186, 6.2 km from junction with Business I-10 (Willcox). Willcox Playa, Cochise Co., Ariz.	13, 24
<i>C. inornatus heptagrammus</i>	August 2–13, 1992	Junction of frontage road east of I-25 (New Mexico 157) and College Ranch Rd., 5.8 km north of I-25's Radium Springs exit. College Ranch, Doña Ana Co., N.Mex.	6, 19
<i>C. septemvittatus</i>	June 30–July 4, 1994	Near Terlingua Ranch office, on Terlingua Ranch Rd., 29 km east of Texas 118. Brewster Co., Tex.	8, 14
<i>C. tigris punctilinealis</i>	July 25–August 9, 1993	0.8 km west of New Mexico 80 on dirt road 2.6 km north of Cienega Ranch. Hidalgo Co., N.Mex.	22, 19
<i>C. tigris marmoratus</i>	August 2–12, 1992	Along frontage road east of I-25 (New Mexico 157), 2.0 km north of I-25's Radium Springs exit. College Ranch, Doña Ana Co., N.Mex.	10, 10

Note. Because not all individuals provided useable data for every trait, sample sizes for individual traits were sometimes less than shown.

Maximal Exertion. Lizards were chased at full speed around a circular raceway of 5 m circumference. A trial ended when an individual would no longer move despite repeated pinching of the tail or when righting response was lost. Maximal exertion was defined as the number of meters the lizard had run, measured to the nearest 5 m.

SMR. Metabolic rates were measured using closed-chamber respirometry methods similar to those of Vleck (1987). Individuals were fasted for at least 5 d before testing. Trials averaging about 90 min were started between 2200 and 2130 hours, and SMR was calculated in milliliters of oxygen consumed per hour.

Table 2: Body temperatures of lizards during measurement of performance traits and significant covariates (other than body mass) used in analyses of these traits

Trait	Body Temperature (°C) (Mean ± SD and Range)	Significant Covariates
Burst speed	38.0 ± 1.4 35.0–41.0	Day of year of trial
Endurance	39.1 ± 1.0 36.5–41.5	Time of day of trial
Maximal exertion	39.1 ± .7 37.0–41.5	Time of day of trial, body temperature
SMR	40 ^a	None
Evaporative water loss rate	40 ^a	None

^a SMR and evaporative water loss rate were measured in a temperature-controlled cabinet; body temperature of individuals was not measured.

Evaporative Water Loss Rate. The rate of cutaneous and respiratory water loss was measured using a gravimetric method. For each individual, dry air was passed through a chamber housing the lizard, and then through columns of previously weighed Drierite, for a 4-h period starting between 0000 and 0130 hours. Evaporative water loss rate was calculated in milligrams of water lost per hour.

If a particular SMR or evaporative water loss rate trial for an individual had to be discarded (due to defecation in the chamber, for example), the trial was rerun the next night.

Statistical Analyses

All analyses were performed using SigmaStat 2.0 for Windows (Jandel Scientific 1995) or SYSTAT 6.0 for Windows (SPSS 1996) unless otherwise noted. Before these analyses, all traits except burst speed were \log_{10} transformed to improve normality.

Because my intention was to uncover overall trends in sexual dimorphism, I tested for differences between males and females using a two-way ANOVA, with both sex and taxon as fixed factors. In an attempt to reduce the effects of extraneous influences on performance, I tested the significance of a variety of potential covariates (e.g., time of day, time of year, and body temperature) in these ANOVAs. (Body size, another potentially important covariate, is discussed below.) Covariates were not used if they were either nonsignificant ($P > 0.05$) or if they showed heterogeneity of slopes among groups (see Sokal and Rohlf 1981, p. 522). Covariates other than body size included in the final ANOVA (now ANCOVA) are shown in Table 2. Because these tests for dimorphism involved comparisons within rather than among taxa, available phylogenetically based forms of analyses (Harvey and Pagel 1991; Garland et al. 1993) were inappropriate.

Three aspects of body size were examined for sexual dimorphism: length (log SVL), mass (log mass), and mass residuals (derived by ANCOVA of log mass with log SVL as a covariate). The allometry of size dimorphism was also determined by regressing the log of mean female SVLs and masses for each taxon on log mean male SVLs and masses, respectively; a slope of less than one indicates that females are proportionately smaller in species of greater body size. Because allometry involves interspecific comparisons, it was possible to use Felsenstein's independent contrasts (Felsenstein 1985), followed by major-axis regression through the origin, to determine the allometric slope of dimorphism (Garland et al. 1993; Abouheif and Fairbairn 1997). This analysis was carried out using PDAP 2.0 (Jones et al. 1993) and the *Cnemidophorus* phylogeny shown in Figure 1 (from Dessauer and Cole [1989], with the *C. inornatus* subspecies bifurcation estimated from data in Densmore et al. [1989])

Performance traits were tested initially for sexual dimorphism by two-way ANOVA or ANCOVA without any correction for size dimorphism (termed "absolute" analyses hereaf-

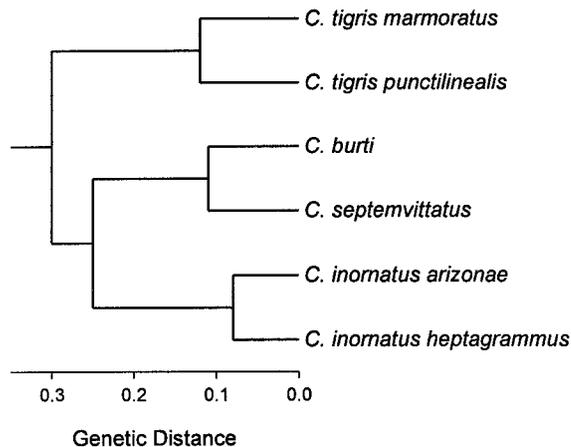


Figure 1. Phylogenetic tree used in independent contrasts analyses. Relationships and branch lengths are based primarily on Dessauer and Cole (1989), with the bifurcation of the *Cnemidophorus inornatus* subspecies estimated from Densmore et al. (1989).

ter). A second analysis was then performed for each trait, which included log mass as a covariate in the ANCOVA ("size-corrected" analyses). (Use of log SVL in place of log mass lowered the explanatory power of body size for most traits and did not significantly improve this power for any trait.) The influence of body size on performance differences between the sexes was quantified by comparing the relative performance of males and females before and after correction for body size. In the case of the four traits that were initially log-transformed, covariate-adjusted trait means were back transformed (i.e., the anti-log was taken) before calculation of the male:female ratio, in order to produce ratios based on linear values. The fractional contribution of size-dependent effects to the overall dimorphism of each trait was then calculated as $1 - [(size-corrected\ ratio - 1) / (absolute\ ratio - 1)]$.

An additional test of the influence of body size dimorphism on performance dimorphism was made using independent contrasts. For each of the five performance characters, contrasts of the male:female absolute trait ratios (described above) for each species were regressed on contrasts of male:female mass ratios using major axis regression. A slope greater than zero would suggest that sexual differences in performance were explained at least in part by sexual size dimorphism.

Results

Size Differences

Size differences between males and females of each taxon are shown in Figure 2, and the associated ANOVAs are shown in Table 3. The overall effect of sex on mass and length was significant, but the significant interaction term indicated that this difference was due primarily to the presence of very large males in some taxa (e.g., *Cnemidophorus burti*), but not others.

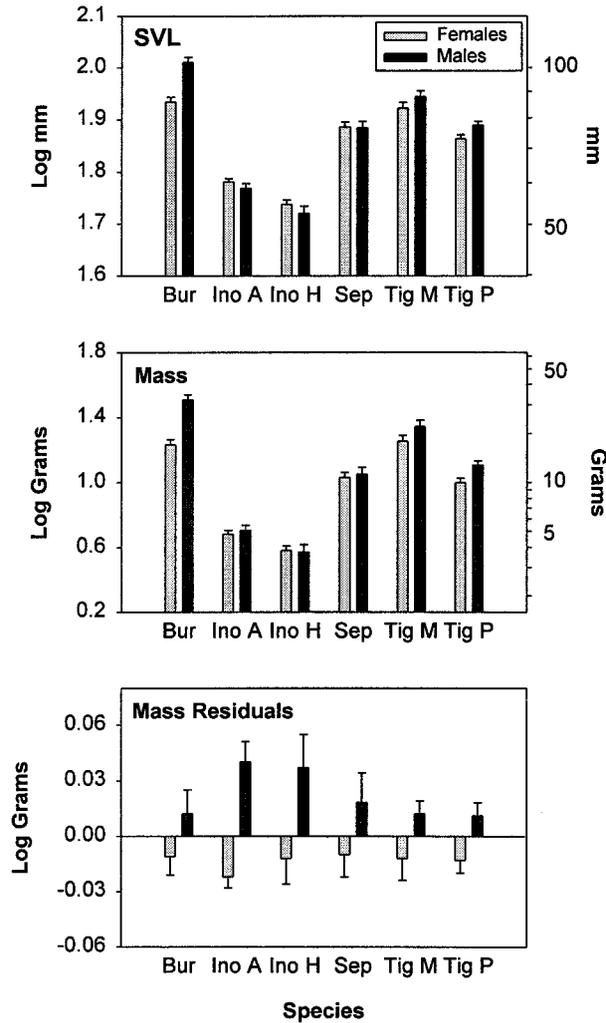


Figure 2. Size differences between males and females for the six taxa of *Cnemidophorus* studied. Calculation of mass residuals is explained in the text. Error bars are standard errors. The legend applies to all graphs. Species abbreviations: Bur, *C. burti*; Ino A, *C. inornatus arizonae*; Ino H, *C. inornatus heptagrammus*; Sep, *C. septemvittatus*; Tig M, *C. tigris marmoratus*; Tig P, *C. tigris punctilinealis*.

To determine whether differences in mass between sexes could be explained simply by differences in SVL, the ANOVA of log mass was recalculated with log SVL included as a covariate (Table 3). The still-significant difference in mass indicates that *Cnemidophorus* show sexual dimorphism in stockiness that appears consistent across all taxa examined, based on the nonsignificant interaction term. Mass residuals resulting from the ANCOVA are shown in Figure 2. The average difference in SVL-corrected mass between males and females is 9%.

The allometry of size dimorphism (as determined by major axis regression of independent contrasts; see Materials and Methods) is shown in Figure 3. The scaling coefficient was 0.68 (95% confidence interval [CI]: 0.38–0.97) for SVL and

0.71 (95% CI: 0.42–0.99) for mass, indicating that size dimorphism generally increased with increasing body size, as predicted by Rensch's rule (Rensch 1960; Abouheif and Fairbairn 1997).

Performance Differences

Absolute mean trait values (adjusted for any nonsize covariates) are shown for each sex and taxon in the left-hand graphs of Figure 4. These are the relevant data for comparison of whole-animal performance traits between males and females. Note that because body size has not been included as a covariate in any of these analyses, traits such as SMR, which were highly dependent on body size, varied greatly among taxa and sexes. The analyses associated with these absolute data are shown in the left-hand columns of Table 4. Of the five traits examined, four showed significant ($P < 0.05$) dimorphism, with only endurance showing no difference between the sexes. (Note, however, that a Bonferroni correction to these data would reduce the significance of all traits except SMR to $P > 0.05$.) For all four dimorphic traits, the trend was for males to exhibit higher trait values than females. In the case of burst speed, males were faster in all six taxa. In maximal exertion, SMR, and evaporative water loss rate, females of one or two taxa had greater values (see Fig. 4 and Table 5). This variation among taxa in dimorphism explained the significant interaction term for many of the traits.

Size-corrected trait means are shown in the right-hand graphs of Figure 4, and corresponding ANCOVAs are shown in the right-hand columns of Table 4. With the inclusion of body size (log mass) as a covariate, the differences between males and females became nonsignificant in every case, although burst speed and SMR were nearly significant, with males having higher values. Note, however, that size corrections

Table 3: Summary ANOVA results of size comparisons between male and female *Cnemidophorus*

Effect	F ratio	df	P
Log SVL:			
Sex	7.2	1, 159	.008
Taxon	168.7	5, 159	<.001
Sex × taxon	6.3	5, 159	<.001
Log mass:			
Sex	18.7	1, 159	<.001
Taxon	167.8	5, 159	<.001
Sex × taxon	4.6	5, 159	<.001
Log mass (log SVL corrected):			
Sex	27.3	1, 158	<.001
Taxon	13.6	5, 158	<.001
Sex × taxon	1.0	5, 158	.43
Log SVL	1,232.6	1, 158	<.001

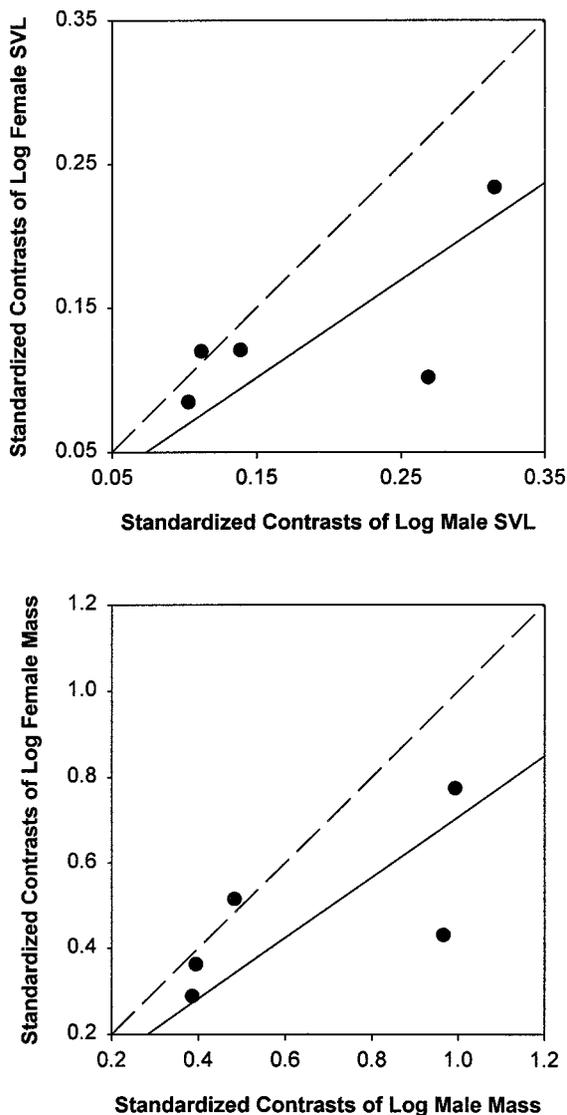


Figure 3. Allometry of sexual size dimorphism in the six taxa of *Cnemidophorus* studied. Independent contrasts (Felsenstein 1985) of female SVLs (top) and female masses (bottom) are regressed on contrasts of male SVLs and masses (respectively) using major axis regression through the origin. Dashed lines indicate the slope of 1.0 expected if males and females were similar in size; solid lines indicate the observed slope. The allometric scaling coefficients are 0.68 for SVL and 0.71 for mass.

did not change the directionality of the differences; for each taxon, whichever sex had higher absolute values also had higher size-corrected values (except for SMR for one taxon).

To check for possible correlations among traits, Pearson's correlation coefficients were calculated for all trait pairs; these analyses used residual values generated from the size-corrected ANCOVAs (i.e., differences due to sex, species, body size, and other covariates were controlled for). The only significant correlation was between SMR and evaporative water loss rate, with

the two traits having only 9% of their variation in common ($r = 0.30$, $N = 152$, $P = 0.002$).

Contribution of Size Differences to Performance Differences

The performance of males relative to females, expressed as a ratio of male : female trait values, is shown in Table 5 for each trait and taxon. Also shown is the average of this ratio for each trait. The fraction of the overall dimorphism of each trait that was due to size differences between genders is shown in the last row of Table 5. This fraction ranged greatly, from very close to zero for endurance to nearly 75% for SMR; however, for no trait did differences in body size fully explain the physiological dimorphism.

Slopes of major axis regression of male : female performance ratios on mass ratios are shown in Table 6. (Standard errors and CIs for these slopes are given since r^2 is not calculated for major axis regressions.) Only in the case of SMR did the CI of the slope exclude zero, suggesting a strong connection between body size dimorphism and SMR dimorphism.

Discussion

The six taxa of *Cnemidophorus* investigated in this study showed a general tendency to be sexually dimorphic in physiological traits. When all taxa were examined together, burst speed, maximal exertion, SMR, and evaporative water loss rate all exhibited higher average values in males than in females; however, only in the case of burst speed were male values higher for every taxon. For some traits (SMR, evaporative water loss rate), most of this physiological dimorphism could be explained by differences in body size between males and females. For other traits (e.g., burst speed), essentially none of the performance difference between sexes could be explained by body size. The effect of size on dimorphism was intermediate for maximal exertion. Despite the range in the influence of body size, the use of mass as a covariate in tests for dimorphism resulted in nonsignificant effects of gender for all traits. However, the P values for burst speed and SMR were still less than 0.09, suggesting that these traits may show size-independent dimorphism.

The results of this study are in general agreement with the limited data on physiological dimorphism available from other studies on *Cnemidophorus*. Dohm et al. (1998), using populations different than those studied here, studied performance traits in adults and juveniles of both *C. tigris punctilinealis* and *C. tigris marmoratus*, as well as in hybrids of these two taxa. As in this study, they noted differences in burst running speed between males and females, but no significant difference in endurance. Unlike this study, however, they found a significant effect of body size on burst speed and endurance, as have others (reviewed in Garland [1993]; Garland and Losos [1994]). Differences in protocols (e.g., the exclusion of juveniles in the present study) may account for these differences in allometry.

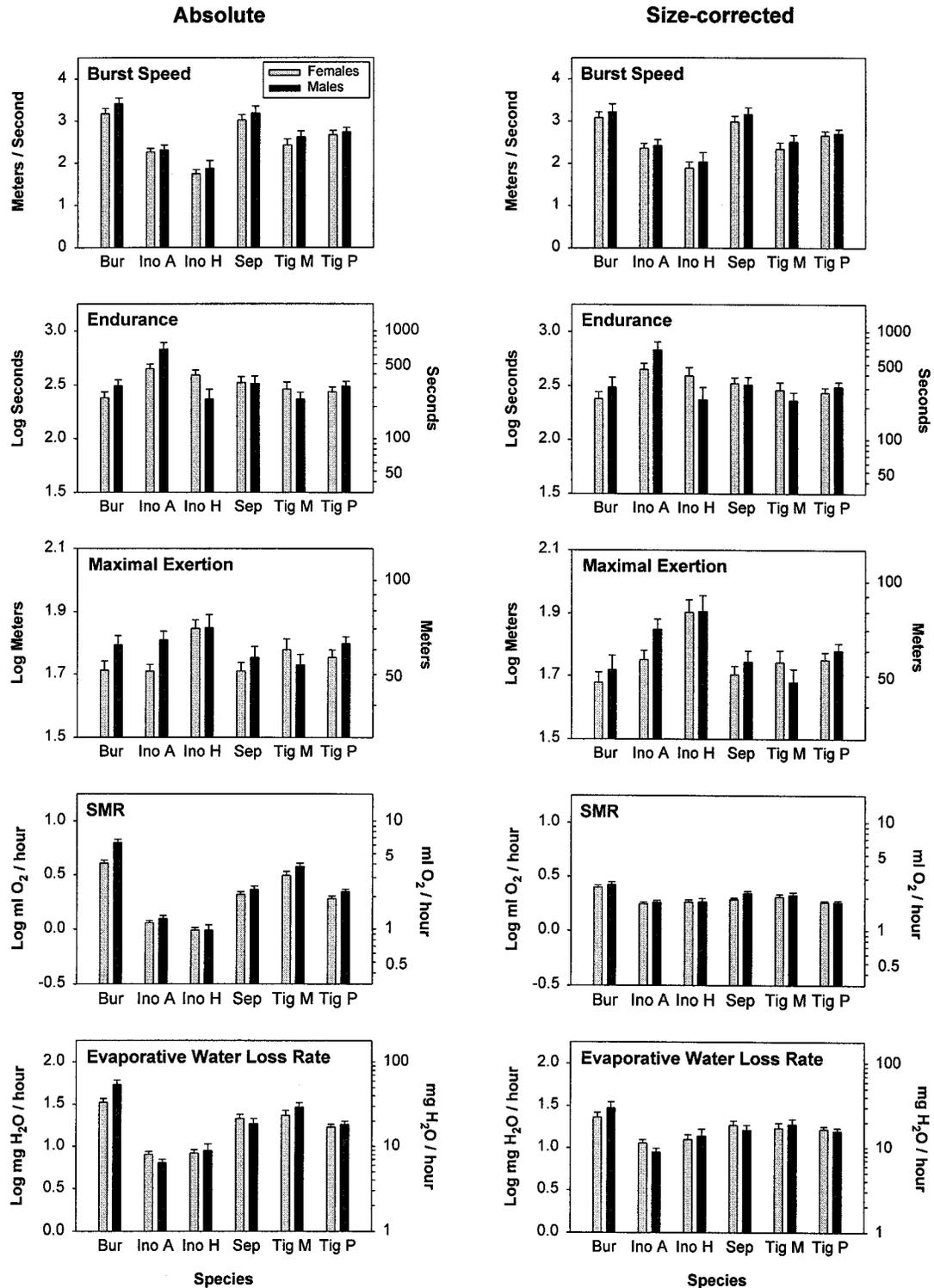


Figure 4. Trait means for males and females of each taxon of *Cnemidophorus*. Absolute trait means (adjusted for covariates other than body mass) are shown in the left-hand graphs; size-corrected trait means (with body size included as a covariate) are in the right-hand graphs. Error bars are standard errors. The legend applies to all graphs. Abbreviations are as for Figure 2.

Relevance of Physiological Dimorphism to Fitness

The most widely accepted explanation for sexual dimorphism in lizards has been sexual selection (Stamps 1983; Anderson and Vitt 1990; Censky 1995). In the case of body size, intra- or intersexual selection, or both, is thought to favor larger

Table 4: Summary of absolute and size-corrected ANOVAs and ANCOVAs

Effect	Absolute Analyses			Size-Corrected Analyses		
	F Ratio	df	P	F Ratio	df	P
Burst speed:						
Sex	4.21	1, 156	.042	2.98	1, 156	.086
Taxon	28.87	5, 156	<.001	9.15	5, 156	<.001
Sex × taxon21	5, 156	.96	.16	5, 156	.98
Log mass444	1, 156	.51
Log endurance:						
Sex01	1, 154	.92	<.01	1, 154	.93
Taxon	9.25	5, 154	<.001	5.35	5, 154	<.001
Sex × taxon	2.81	5, 154	.019	2.73	5, 154	.021
Log mass	<.01	1, 154	.99
Log maximal exertion						
Sex	4.87	1, 151	.029	1.93	1, 151	.17
Taxon	2.61	5, 151	.027	3.36	5, 151	.007
Sex × taxon	1.60	5, 151	.16	1.68	5, 151	.14
Log mass	4.34	1, 151	.039
Log SMR:						
Sex	16.23	1, 146	<.001	3.56	1, 146	.061
Taxon	158.05	5, 146	<.001	13.39	5, 146	<.001
Sex × taxon	2.33	5, 146	.045	.48	5, 146	.79
Log mass	273.18	1, 146	<.001
Log evaporative water loss rate:						
Sex	4.01	1, 140	.047	.68	1, 140	.41
Taxon	75.78	5, 140	<.001	12.08	5, 140	<.001
Sex × taxon	3.24	5, 140	.009	2.33	5, 140	.046
Log mass	20.71	1, 140	<.001

Note. Significance of main effects, interaction terms, and body-size covariates are shown; other significant covariates included in some analyses are given in Table 2.

males, with such individuals more likely to win male-male aggressive encounters and to hold territories successfully (Fitch 1981; Stamps 1983). Although *Cnemidophorus* are not territorial, males do fight for females, and large males tend to mate with more females (Anderson and Vitt 1990). If size itself is favored by sexual selection, then at least some of the sexual dimorphism seen in performance traits may have no adaptive basis, but may be due simply to correlation of some traits with body size. Such a nonadaptive explanation seems particularly likely for SMR and evaporative water loss rate, for which higher values are probably not inherently beneficial. It is possible, however, that sexual selection is acting directly on some of these performance traits, or the physiological capacities they reflect. Based on their observations of aggressive interactions among male *C. tigris*, Anderson and Vitt (1990) hypothesized that there should be sexual dimorphism for traits that influence the outcome of these interactions. The possibility that physiological capacities, rather than or in addition to body size per se, have such an influence is supported by the work of Garland et al. (1990), who found that male *Sceloporus* with higher sprint

capacities tended to win competitions for basking space in size-matched laboratory trials. The observation that male *Cnemidophorus* frequently have higher activity levels than females, especially during breeding periods (Anderson and Karasov 1988), also suggests that higher physiological capacities may be more important to males than females.

In addition to potentially affecting mating success, whole-animal physiological traits may influence the survival of individuals of both sexes. A relationship between performance and survival has been demonstrated for a variety of physiological traits, including burst speed (Miles 1989; Jayne and Bennett 1990), maximal exertion (Jayne and Bennett 1990), and drought resistance (Bradshaw 1971), of which evaporative water loss rate is a component. If such traits are important in *Cnemidophorus*, then dimorphism may have important consequences for fitness differences in males and females. Snell et al. (1988) argue that faster sprint speeds in male Galápagos lava lizards (*Tropidurus albemarlensis*) have evolved as a result of higher predation on this sex. It has even been suggested that observed sexual size dimorphism may sometimes result not

Table 5: Male : female performance ratios and the fraction of physiological dimorphism explained by size dimorphism

Taxon	Burst Speed	Endurance	Maximal Exertion	SMR	Evaporative Water Loss Rate
Absolute male : female performance ratios:					
<i>Cnemidophorus burti</i>	1.072	1.286	1.204	1.552	1.648
<i>C. i. arizonae</i>	1.021	1.521	1.258	1.094	.796
<i>C. i. heptagrammus</i>	1.073	.601	1.007	.997	1.403
<i>C. septemvittatus</i>	1.056	.976	1.103	1.109	.869
<i>C. t. punctilinealis</i>	1.029	1.138	1.107	1.159	1.148
<i>C. t. marmoratus</i>	1.080	.802	.895	1.206	1.230
Mean	1.055	1.054	1.096	1.186	1.182
Size-corrected male : female performance ratios:					
<i>C. burti</i>	1.057	1.285	1.099	1.086	1.262
<i>C. i. arizonae</i>	1.018	1.521	1.250	1.033	.762
<i>C. i. heptagrammus</i>	1.072	.601	1.007	1.007	1.422
<i>C. septemvittatus</i>	1.055	.975	1.096	1.109	.877
<i>C. t. punctilinealis</i>	1.021	1.138	1.069	1.013	1.040
<i>C. t. marmoratus</i>	1.075	.802	.866	1.042	1.112
Mean	1.050	1.054	1.064	1.048	1.079
Fraction of dimorphism explained by body size:					
<i>C. burti</i>21	.00	.51	.84	.60
<i>C. i. arizonae</i>14	.00	.03	.65	<.00
<i>C. i. heptagrammus</i>01	.00	.00	>1.00	<.00
<i>C. septemvittatus</i>02	<.00	.07	.00	.06
<i>C. t. punctilinealis</i>28	.00	.36	.92	.73
<i>C. t. marmoratus</i>06	.00	-.28	.80	.51
Overall10	<.01	.33	.74	.57

Note. The taxa-specific and overall mean ratios of male : female performance, both with and without correction for body size, are shown for each trait. The fraction of the overall dimorphism of each trait explained by differences in body size between males and females, shown in the last row, is calculated from the mean absolute ratio and mean size-corrected ratio for each trait. Note that for the last four traits, means were transformed back from log values before ratios were calculated.

from differences in growth rates or patterns, but rather from unequal age distributions in males and females due to differential mortality (Dunham 1981).

Beyond Size Differences: Physiological Effects on Dimorphism

Although overall body size accounted for some of the sexual differences in the four traits that were found to be dimorphic (Tables 5 and 6), in no case did it account for all the difference, suggesting that additional factors also influenced overall physiological performance. The most likely of these are characters influenced by androgens. For example, male *Cnemidophorus* are not only stockier than females (i.e., they have a greater mass for a given SVL; see Fig. 2), but they also have proportionately less body fat (5% vs. 10% in females in *C. tigris* [Brian et al. 1972; see also Gaffney and Fitzpatrick 1973; Dearing and Schall 1994]). Because adipose tissue is relatively inactive metabolically, this difference may account for the trend toward lower SMR in females even for size-corrected values. Such is

the case for humans, where mass-controlled differences in basal metabolic rate appear to be due primarily to differences in body composition (Sanborn and Jankowski 1994) that result from the effects of testosterone (Bhasin et al. 1997). Sexual dimorphism in body composition of *Cnemidophorus* might also explain the trend toward faster burst speeds in males, assuming that males have a higher muscle mass to body mass ratio. In mammals, testosterone has the effect of increasing both muscle size and overall strength, but apparently not strength per unit cross-sectional area of muscle (Sanborn and Jankowski 1994).

The lack of dimorphism in endurance in *Cnemidophorus* was unexpected, given the large difference in this trait in human males and females. One possible explanation for this pattern could lie in the use of an inclined treadmill to measure endurance. Walking or running up a slope requires a greater fractional increase in energy expenditure in larger animals than in smaller ones (Taylor et al. 1972); thus in species dimorphic for mass, the 20° treadmill slope may have had a greater impact on endurance in males than in females. For the size range of

Table 6: Major axis regressions of independent contrasts of absolute male : female performance ratios on contrasts of male : female mass ratios

Trait	Regression Slope	SE	P	95% CI
Burst speed012	.047	.81	-.118 to .142
Endurance	1.99	2.52	.49	-5.01 to 8.99
Maximal exertion183	.240	.50	-.485 to .851
SMR560	.056	.002	.404-.716
Evaporative water loss rate	1.31	.78	.19	-.86 to 3.48

Note. The sample size in each case is 5 contrasts.

species studies here, however, the effects of a 20° incline on locomotion are likely to quite small (Taylor et al. 1972; Huey and Hertz 1982) and should not have obscured any sexual dimorphism in aerobic capacity, were it present. Further evidence that no significant sexual difference in endurance capacity exists in these lizards is provided by suborganismal traits responsible for supporting oxygen delivery to tissues. While humans show dimorphism in traits such as hematocrit levels and mass-corrected heart size, Dohm et al. (1998) found no difference in heart size or hematocrit between males and females of two *C. tigris* subspecies, suggesting that at least some of the physiological effects of androgens may vary among vertebrate groups. Interestingly, however, the pattern in other lizards appears to be more similar to that in humans. John-Alder (1994) studied the effects of testosterone on *Anolis sagrei* and found, not only that testosterone-treated lizards had greater endurance than control lizards, but also that this difference was correlated with cardiac hypertrophy in the treated lizards. He and coworkers have also found that male *Sceloporus* sp. have a significantly higher hematocrit than females during these lizards' breeding season (H. B. John-Alder, personal communication).

Conclusions

Based on the results of this study and data from other research, temperate species of *Cnemidophorus* tend to show sexual dimorphism for whole-animal physiological traits, with males having higher trait values than females. However, not all traits examined showed dimorphism, and traits that show a general pattern of dimorphism may not exhibit higher male values in every taxon. Given that most of these traits are dimorphic, and that body size does not explain all of the differences between sexes, future comparative and evolutionary studies of performance traits may benefit from including gender (as well as body size) as a potential independent variable in analyses.

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