

Physiological Variation and Allometry in Western Whiptail Lizards (*Cnemidophorus tigris*) from a Transect across a Persistent Hybrid Zone

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A hybrid zone involving *Cnemidophorus tigris punctilinealis* (formerly *gracilis*) and *C. tigris marmoratus* in southwestern New Mexico and adjacent Arizona is narrow and characterized by abrupt and concordant change in both morphological characters and allele frequencies studied by protein electrophoresis. We compared adult *C. tigris* sampled from three locations that span the hybrid zone. Body mass was positively associated with both treadmill endurance at 1.0 km/h and maximal sprint running speed on a high-speed treadmill, although the largest individuals were not the fastest sprinters. Males and females differed significantly for maximal sprint running speed, liver mass, and kidney mass (ANCOVA with body mass as covariate). We found no statistically significant population differences for body mass, maximal sprint running speed, standard metabolic rate at 40C, blood hematocrit levels, or heart mass. Hybrids tended to have lower treadmill endurance running capacities as compared with the pure forms, but the difference was not statistically significant. *Cnemidophorus tigris punctilinealis* and the hybrids both had significantly heavier kidneys, relative to body mass, than did *C. tigris marmoratus*. Hybrid individuals also had significantly heavier livers as compared with either pure population. However, the present data cannot rule out the possibility that the observed differences in organ masses were related to reproductive status as opposed to being genetically based population differences. Thus, our results do not suggest that hybrid individuals differ from nonhybrids with respect to Darwinian fitness.

CNEMIDOPHORUS *tigris punctilinealis* (formerly *gracilis*, Taylor and Walker, 1996) and *Cnemidophorus tigris marmoratus* are widely distributed forms of the western whiptail lizard found primarily in the Sonoran and Chihuahuan deserts, respectively. They have been recognized sometimes as separate species (Hendricks and Dixon, 1986) but hybridize freely wherever their ranges meet. One contact zone in southeastern Arizona and southwestern New Mexico has been described in some detail (Dessauer et al., 1962; Zweifel, 1962; Dessauer and Cole, 1991). This hybrid zone is narrow (approximately 3 km wide) and characterized by abrupt, concordant changes in both morphological characters and allele frequencies determined by protein electrophoresis (Dessauer and Cole, 1991). Persistent, narrow hybrid zones are often interpreted as support for selection against hybrids (Endler, 1977; Barton and Hewitt, 1989; Arnold, 1992). This may arise because of a direct response to environmental dif-

ferences across the species' range (e.g., local adaptation), or it may reflect an intrinsic inferiority of hybrids. For the *C. tigris* hybrid zone, however, no support for selection against the hybrids has been found, and substantial gene exchange occurs. All individuals can be uniquely identified by their genotypes at polymorphic loci, no single individual exhibits an F_1 genotype for all polymorphic loci, and allele frequencies are in Hardy-Weinberg equilibrium (Dessauer and Cole, 1991). Clutch sizes do not differ among hybrid or parental populations and usually range from two to four (H. C. Dessauer and C. J. Cole, pers. obs.), values typical for *C. tigris* populations (Parker, 1973; Vitt and Breitenbach, 1993).

Natural selection is thought to act more directly on whole-animal performance abilities than on lower level biochemical, physiological, or morphological traits (Bennett and Huey, 1990; Garland and Losos, 1994, and references therein). We, therefore, compared individuals

from the two "pure" subspecies and hybrid forms in terms of ecologically relevant measures of locomotor performance (e.g., sprint speed, stamina) and minimum resting rate of oxygen consumption under standardized conditions (standard metabolic rate, SMR). Locomotor and metabolic capacities can be viewed as components of Darwinian fitness because these traits are thought to be causally linked to success in many activities (e.g., foraging, predator escape, social dominance) that affect fitness (e.g., Garland et al., 1990; reviewed by Bennett and Huey, 1990; Garland and Losos, 1994). By contrasting performance capacities of individuals from the pure populations with individuals sampled from the hybrid zone (e.g., see Harrison and Hall, 1993), we can determine, indirectly, whether hybrids are "fit" or "unfit" relative to the parental populations (cf. Arnold and Hedges, 1995).

We also measured several suborganismal traits because they are potentially important determinants of whole-animal locomotion or abilities and/or metabolism (see Garland, 1993). For example, heart mass (a determinant of stroke volume and, therefore, oxygen and substrate delivery to tissues) has been shown to correlate with individual variation in stamina for some species of lizards (e.g., Garland, 1984; Garland and Else, 1987; review in Garland and Losos, 1994). Similarly, liver mass is associated with intraspecific (e.g., Garland, 1984; Garland and Else, 1987) or interspecific (e.g., Else and Hulbert, 1981) differences in SMR (cf. John-Alder, 1990; John-Alder and Joos, 1991). *Cnemidophorus*, because of their active, widely foraging lifestyle (Anderson and Karasov, 1988; Garland, 1993, and references therein), are good candidates for investigation of putative links between variation in locomotor performance, metabolism, and fitness.

MATERIALS AND METHODS

We collected adults from populations of *C. tigris punctilinealis* (4 mi NE San Simon, Cochise Co., AZ), *C. t. marmoratus* (7 mi WSW Lordsburg, Hidalgo Co., NM), and the hybrids (mid-point of contact zone through Steins Pass in the Peloncillo Mountains; sample site 6 in Dessauer and Cole, 1991) by drift fence, slip noose, or excavation from burrows and brought them to the American Museum of Natural History's Southwestern Research Station (SWRS, Portal, AZ). We measured locomotor performance and metabolic rates for individuals captured during May 1992 [we also included sprint speed data for 5 *C. t. punctilinealis* in May 1990 from the

vicinity of federal highway 80 in Hidalgo, Co., NM, site described in Bulova (1994)]. At SWRS, individuals lived in glass terraria on a natural photocycle, and room temperature was 30C days, 20C nights (at Madison, WI, we used the same temperature cycle but 12:12 h photocycle). Incandescent lamps allowed behavioral thermoregulation. Water was always available, and crickets were provided three to four times per week; but we fasted lizards during intervals of locomotor performance and prior to SMR determination. Animals were in good health over the period of locomotor performance and SMR measurements. Mean (\pm SE) loss of body mass between locomotor trials conducted in Portal, Arizona, and SMR trials in Madison, Wisconsin, was approximately 4% (\pm 1.76%; n = 28).

We measured maximal sprint running speed, treadmill endurance, and standard metabolism at 40C, near the mean or modal field body temperature of *C. tigris* (Anderson and Karasov, 1988; Garland, 1993, and references therein). Lizards were preheated for two to three hours in a constant temperature cabinet prior to locomotor measurements. We measured body temperature immediately after the speed and endurance trials with a Schultheis thermometer.

We measured maximal sprint running speed and endurance of all individuals between 27 May and 5 June 1992, within one to five days of capture (the five individuals from May 1990 were also measured within five days of capture). Lizards ran on a high-speed motorized treadmill with an effective belt area of approximately 140 cm long (with Plexiglas at the front), 15 cm wide at the front and 25 cm wide at the rear (where lizards were started). Incandescent lamps and heaters kept the surface warm.

We conducted sprint speed trials as follows. When removed from their cloth bag and placed onto the stationary tread belt, individuals either began to move immediately upon release or were induced to sprint at top speed by lightly tapping the tail or posterior portion of the body. As the animal started to move, treadmill speed was increased rapidly to match the individual's apparent capacity to maintain treadmill speed. The textured rubber belt (American Star International, Brighton, MI, #IAR-PT) appeared to provide good traction. The total time animals ran on the belt was approximately five to 15 seconds. We tested each animal on two consecutive days and took the faster of the two times as the individual's maximal sprint running speed (see discussion in Garland and Losos, 1994). We used both performance values to determine whether individual variation in sprint speed was

repeatable (Pearson product-moment correlation).

We measured treadmill endurance capacity (stamina) at a relatively low speed (1.0 km/h) on the same motorized treadmill by standard techniques (Garland, 1993, 1994, and references therein). We removed lizards from their cloth bags, placed them onto the belt, and induced them to walk by gentle tapping about the posterior body and tail. If needed, tapping kept the animal walking throughout the trial, but most matched treadmill speed with little encouragement. The end point was defined as the time when an individual no longer maintained pace in response to 10 consecutive taps about the tail and/or hind limbs. Most individuals were tested on two or more different, but not necessarily consecutive, days to obtain good estimates of stamina [e.g., frantic, "bursty" activity by an individual while running on the treadmill indicated a poor trial (Garland, 1994)]. We took the longest trial as an individual's maximal endurance.

Following the locomotor measures, we transported the lizards by car to the University of Wisconsin-Madison for measures of SMR between 9 and 14 June 1992. We fasted lizards an average of 6.8 days with water always available [range 4–9 days; fasting durations of this length do not lead to metabolic depression on a mass-specific basis in reptiles (Roberts, 1968; Bennett and Dawson, 1976)]. We measured metabolic rates for 10 hours while the animals rested overnight, in the dark, in a constant temperature cabinet at 40°C. We placed them into Plexiglas metabolic chambers inside the temperature cabinet prior to 1700 Central Daylight Savings Time, allowing them to acclimate for two hours before testing. The metabolic chambers were part of an open-circuit respirometry system as described in Hayes et al. (1992). Up to seven lizards were monitored simultaneously with each lizard and one control chamber receiving dry air at 100–200 mL/min (depending on the animal's body mass) from upstream thermal mass flow controllers (Side = Track Model 844, Sierra Instruments, Inc., Monterey, CA). Drierite® removed water from the incurrent and excurrent air and Ascarite II® removed CO₂ from the excurrent air stream. Excurrent air was monitored for at least 7.5 min of each hour (more if fewer than seven individuals were being measured) by an Applied Electrochemistry S-3A/II oxygen analyzer (Ametek, Pittsburgh, PA) interfaced to a microcomputer. Air was diverted by an automated system with solenoid valves under programmed control to the oxygen sensor. We calculated $\dot{V}O_2$ for the last 5 min

of each 7.5-min interval (i.e., 10 intervals for each animal) before switching to the next chamber using equation (4a) given in Hill (1972). Flow rates and chamber volumes used ensured the clearing of the respirometry system downstream of the metabolic chamber prior to the start of the 5-min interval.

We measured hematocrit and organ masses on individuals captured from 4–23 July 1993 from the same collecting sites censused in 1992. We captured additional individuals from a second hybrid zone, near the north end of Animas Valley, 17.8 miles by road north of Lordsburg, New Mexico. (No trait differed significantly between the two hybrid populations, so we pooled values from these groups for subsequent comparisons.) We killed animals by intraperitoneal injection of 0.2 mL dilute Nembutal, weighed them, and took blood samples immediately from around the heart. Heparinized microhematocrit tubes (75 mm long, 1.1–1.2 mm i.d.) were centrifuged for 5 min in a microhematocrit centrifuge. We excised the heart, liver (excluding bile), and kidneys; blotted them with paper; and weighed them to the nearest 0.1 mg. We measured suborganismal traits three to four days after initial capture, during which the lizards were not fed or watered except to moisten the substrate.

We compared populations as follows. For each trait, we first used multiple regression analyses to perform analysis of covariance (ANCOVA) to test for effects of population, sex, and whether the individual had an intact tail. (Preliminary analyses indicated that no interaction term was statistically significant, so we report results for main effects only.) Next, we compared the two pure populations; if no statistical difference was found for a given trait, we then conducted a two-group comparison of pooled pure populations versus hybrids. If the two parental populations differed, then we conducted a second two-group comparison of pooled hybrids plus one pure population versus the other parental population. Tests for slope differences among groups were conducted as required for ANCOVA (Sokal and Rohlf, 1981). Plots of residuals from regression equations were visually inspected, and data were transformed as necessary to meet the assumptions of ANCOVA and multiple regression analyses (Sokal and Rohlf, 1981). We also used nonparametric tests (e.g., Kruskal-Wallis for one-way layout) to check results of population comparisons conducted by ANCOVA, because of the relatively small sample sizes. However, results from Kruskal-Wallis tests essentially confirmed conclusions derived from

parametric methods and, therefore, are not presented.

We also conducted allometric analyses by linear regression, polynomial regression, and change-point (two-phase) regression (Chappell, 1989; Yeager and Ultsch, 1989). Because of the small range of body masses available in this study, the regression equations presented are for descriptive purposes only; they are not meant to represent tests of general hypotheses about scaling relationships (e.g., geometric similarity, Schmidt-Nielsen, 1984; but see Garland, 1983; Garland et al., 1988). The SPSS/PC statistical package (vers. 5.0) was used for all analyses (M. J. Norusis, 1988, unpubl.), except for detection of change points in two-phase regression models, which was performed with a Visual BASIC program written by the first author (after the approach provided in Yeager and Ultsch, 1989).

RESULTS

Individual variation and effects of tail loss.—Descriptive statistics for body mass, sprint running (burst) speed, treadmill endurance, and SMR are reported for each population in Table 1. Sprint speeds of individuals were consistent between trial days (Fig. 1; $r = 0.88$, $P < 0.001$), but they tended to be slower on the second day ($\bar{x} \pm SD$: TRIAL 1 = 19.5 ± 3.64 , TRIAL 2 = 18.7 ± 3.76 , paired $t = 1.95$, $df = 26$, $P = 0.062$). Total variation among individuals in sprint running performance was approximately 16% (CV, coefficient of variation; see also Table 1). Individual treadmill endurance performances were log-normally distributed. Substantial individual variation was also evident, with a nearly 14-fold difference between the “worst” (13 min) and “best” (3 h, stopped by the observer) individuals (Table 1).

For the maximal sprint speed from either trial day, individuals missing half or more of their tail did not differ significantly from individuals with intact tails ($n = 32$ tail intact, $\bar{x} \pm SD = 20.2 \pm 3.30$; $n = 8$ tail missing, 18.1 ± 2.56 ; two-tailed $t = 1.68$, $P = 0.101$, see also Fig. 1). We chose not to exclude individuals with missing tails from population comparisons because sprint speed performances of tailless and tailed individuals overlapped substantially and a Levene's test for heterogeneity of variances (M. J. Norusis, 1988, unpubl.) was not significant ($F = 0.87$, $P = 0.358$); tailed individuals were not significantly heavier than tailless lizards (mean difference of 2.2 g, $t = 1.27$, $df = 38$, $P = 0.213$); and tailless individuals were represented about equally in all three populations (Fig. 1; three *C.*

t. punctilinealis, three hybrid, and two *C. t. marmoratus*; one *C. t. punctilinealis* and one *C. t. marmoratus* lost tails at the end of the first trial and were, therefore, dropped from calculation of repeatability). Moreover, conclusions about population comparisons held whether or not individuals with incomplete tails were included in the analyses. Finally, tail status, although included as a potential main effect in the full ANCOVAs when assessing population differences, was never statistically significant.

Mean ($\pm SD$) treadmill endurance for six tailless individuals was 44.5 ± 17.89 min as compared with 34.4 ± 33.81 min for individuals with intact tails. This difference was not statistically different ($t = -0.70$, $df = 29$, $P = 0.49$). SMR values did not differ significantly between tail groups (mean difference of 0.63 mL O₂/h, $t = 1.15$, $df = 26$, $P = 0.260$).

Population comparisons and sexual dimorphism.—For the maximal sprint speed recorded from either trial, ANCOVA indicated no statistical differences among the three populations ($F_{2,39} = 1.64$, $P = 0.209$), a significant difference between male and female sprint running speeds ($F_{1,39} = 6.31$, $P = 0.017$), and no significant difference in relation to tail status ($F_{1,39} = 2.42$, $P = 0.129$; Fig. 2). The covariate, body mass, was also not statistically significant ($F_{1,39} = 2.30$, $P = 0.142$) in the full comparison. After removing tail status from the ANCOVA, the population comparison remained statistically nonsignificant for sprint speed ($F_{2,39} = 1.50$, $P = 0.238$), whereas sex remained as a statistically significant factor ($F_{1,39} = 5.23$, $P = 0.028$) (Fig. 2B). Body mass was close to statistical significance ($F_{1,39} = 3.99$, $P = 0.054$). We obtained similar results for the comparison of hybrids versus the two pure populations considered together: no significant population differences ($F_{1,39} = 0.38$, $P = 0.541$), a marginally significant sex effect ($F_{1,39} = 3.85$, $P = 0.058$), and significant effect of body mass ($F_{1,39} = 4.28$, $P = 0.046$) on sprint speed. After dropping population from the analysis, both body mass and sex were statistically significant (see below; Fig. 2B).

For treadmill endurance, we did not find statistical differences among individuals in relation to population membership ($F_{2,28} = 3.00$, $P = 0.070$), sex ($F_{1,28} = 3.44$, $P = 0.076$), or whether the individual had a complete tail ($F_{1,28} = 1.74$, $P = 0.201$). Larger individuals tended to have greater stamina than did smaller individuals ($F_{1,28} = 4.36$, $P = 0.048$; see Fig. 3). After dropping sex and tail as main effects, population differences were also nonsignificant ($F_{2,28} = 2.59$, $P = 0.095$; body mass: $F_{1,28} = 6.75$, $P = 0.015$).

TABLE 1. DESCRIPTIVE STATISTICS FOR BODY SIZE, SPEED, ENDURANCE, AND STANDARD METABOLIC RATES (SMR) MEASURED IN *Cnemidophorus tigris punctilinealis*, *C. t. marmoratus*, AND THEIR HYBRIDS FROM SOUTHEASTERN ARIZONA AND SOUTHWESTERN NEW MEXICO, 1992.^{a,b}

		n	Mean	SD	Minimum	Maximum
Body mass (g) measured following endurance trials ^{c,d}						
<i>C. t. punctilinealis</i>	males	13	15.42	4.442	9.13	22.06
	females	4	13.89	4.737	8.43	19.97
Hybrid	males	5	18.24	1.764	15.56	20.46
	females	6	11.14	4.199	6.81	18.01
<i>C. t. marmoratus</i>	males	5	15.60	3.071	10.58	18.79
	females	5	13.05	4.250	6.80	17.02
Sprint speed (km/hr) ^d						
<i>C. t. punctilinealis</i>		17	19.7	2.93	13.5	25.5
	Hybrid	12	18.9	2.67	14.5	22.5
<i>C. t. marmoratus</i>		11	20.9	4.14	15.1	26.0
Treadmill endurance at 1.0 km/hr (min)						
<i>C. t. punctilinealis</i>		12	31.7	19.97	13.0	71.2
	Hybrid	8	26.6	13.82	13.3	47.8
<i>C. t. marmoratus</i>		9	50.1	47.70	15.3	179.8
SMR at 40 C (mL O ₂ /hr) ^c						
<i>C. t. punctilinealis</i>		9	3.65	0.729	2.84	4.71
	Hybrid	9	3.58	1.328	1.90	6.29
<i>C. t. marmoratus</i>		10	3.54	1.045	1.28	4.65

^a All whole animal measures were made at 40 C.

^b Sexes pooled for speed, stamina, and SMR.

^c Sample sizes are greater for body mass than for endurance entries because some endurance scores were excluded from analyses (e.g., individual failed to run at steady pace).

^d We used body mass measured following the endurance trials for mass at sprint speed trials, except for two individuals (one female *marmoratus*, one male *punctilinealis*) whose tails broke during speed trials. We measured these individuals plus their tails after the sprint trials and obtained a second body mass for them following the endurance trial (i.e., mean \pm SE body mass following sprint speed was male *punctilinealis* 15.51 \pm 4.353 g; female *marmoratus* 13.26 \pm 3.873 g).

^e Body mass (g) measured before SMR determination (at entry to metabolic chambers) (mean \pm SD, n): *C. t. punctilinealis* males (13.28 \pm 3.194, 5), females (14.30 \pm 4.555, 4); hybrid males (15.92 \pm 2.372, 4), females (10.85 \pm 3.388, 5); *C. t. marmoratus* males (14.81 \pm 3.201, 5), females (11.38 \pm 3.113, 5).

Similar results were obtained for the hybrid versus two pure population comparison ($F_{1,28} = 2.69$, $P = 0.113$; body mass: $F_{1,28} = 7.17$, $P = 0.013$).

Mean standard metabolic rate measured at 40C was 3.587 mL O₂/h (Table 1; mean mass of 13.30 g). Amount of time individuals were held without food (range = 4–9 days) accounted for about 5% of the variance in SMR values. As expected, SMR and body mass were highly correlated on a log-log scale ($r = 0.80$, $n = 28$, $P < 0.0001$; $r = 0.82$ after removing fasting effects). Results from the full ANCOVA indicated significant effects of body mass (positive: $F_{1,27} = 36.63$, $P < 0.001$) and total fasting time (negative: $F_{1,27} = 5.70$, $P = 0.026$) but no population ($F_{2,27} = 0.10$, $P = 0.906$) or sex ($F_{1,27} = 0.92$, $P = 0.347$) differences. We obtained similar results from all of the reduced (pooled population) analyses: significant covariation with body mass and/or fasting length but no population or sex differences.

Results from the full ANCOVAs for suborgan-

ismal traits were as follows (descriptive statistics summarized in Table 2). As expected, the covariate log-body mass was significantly positively related to organ size (all \log_{10} -transformed, all $P < 0.001$) but not to hematocrit levels ($F_{1,38} = 0.34$, $P = 0.566$). For hematocrit and log-heart mass, no significant population (Hct: $F_{2,38} = 0.07$, $P = 0.930$; heart: $F_{2,38} = 0.70$, $P = 0.503$) or sex differences (Hct: $F_{1,38} = 1.32$, $P = 0.258$; heart: $F_{1,38} = 0.70$, $P = 0.408$) were found. For log-liver and log-kidney masses, population (liver: $F_{2,39} = 3.03$, $P = 0.061$; kidney: $F_{2,39} = 8.54$, $P = 0.001$) and sex (liver: $F_{1,39} = 5.48$, $P = 0.025$; kidney: $F_{1,39} = 16.34$, $P < 0.001$) differences were statistically significant or nearly so (Fig. 4). Hybrids had significantly heavier livers than did the pure populations (pooled analysis; $F_{1,39} = 6.18$, $P = 0.018$; sex: $F_{1,39} = 5.82$, $P = 0.021$; body mass: $F_{1,39} = 85.55$, $P < 0.001$; Fig. 4A–B), whereas both hybrids and *C. t. punctilinealis* (pooled) had significantly heavier kidneys than did *C. t. marmoratus* ($F_{1,39} = 17.58$, $P <$

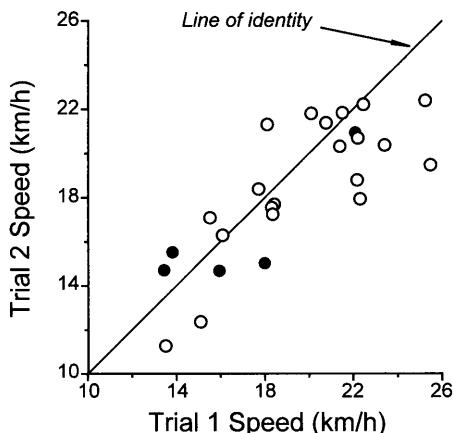


Fig. 1. Scatter plot of sprint running speeds of 25 *Cnemidophorus tigris* lizards measured on two different days with a high speed treadmill ($r = 0.88, P < 0.001$). Line of identity is also shown for reference. Performance of five individuals that were missing part or most of their tails (●) relative to individuals with intact tails (○) is also displayed [two individuals (not shown) lost tails following the first trial and were not measured again].

0.001; sex: $F_{1,39} = 21.60, P < 0.001$; body mass: $F_{1,39} = 99.15, P < 0.001$; Fig. 4C–D).

Relationships with body mass.—Pooling data from all 40 individuals, males and females differed significantly for maximal sprint running speeds, and sprint speed was positively related to body mass (see Fig. 2):

$$\text{speed} = 14.987 + 0.239(\text{mass}) + 2.074(\text{sex}), \quad (1)$$

with units of km/h for speed, g for mass. Sex was coded as a dummy variable (0 for females, 1 for males). The coefficient of determination (R^2) for equation (1) was 0.19 ($F_{2,37} = 7.18, P = 0.002$; SE and partial F -statistics were: intercept $\pm 1.5804, F_{1,37} = 89.94, P < 0.001$; mass $\pm 0.1114, F_{1,37} = 4.60, P = 0.039$; sex $\pm 1.000, F_{1,37} = 4.30, P = 0.045$).

Inspection of plots of the residuals versus body mass suggested that the relationship may not be linear (see also Fig. 2). Therefore, we fit a polynomial regression to the data:

$$\begin{aligned} \text{speed} = & 2.944 + 2.085(\text{mass}) \\ & - 0.064(\text{mass})^2 + 2.075(\text{sex}). \quad (2) \end{aligned}$$

The polynomial equation fit the data significantly better than did the simple linear regression ($R^2 = 0.40, F_{3,36} = 7.95, P < 0.001$; SE of intercept was $\pm 4.747, F_{1,36} = 0.38, P = 0.539$; slopes: mass $\pm 0.700, F_{1,36} = 8.87, P = 0.005$;

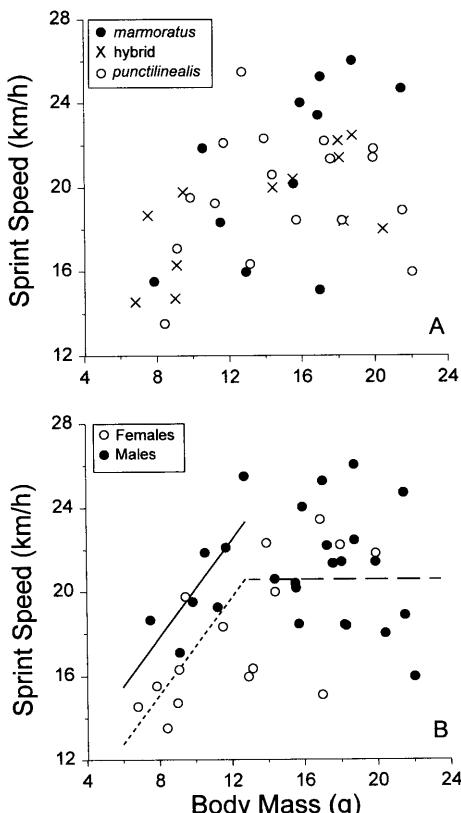


Fig. 2. Maximal sprint running speeds versus body mass of 40 *Cnemidophorus tigris*. ANCOVA indicated no statistically significant differences among populations (A), but a statistically significant relationship between both speed and sex (B) and speed and body mass. Both polynomial [see eq. (2) in text] and two-phase regression [(B), see eq. (3) in text] fit the data better than did a simple linear regression [see eq. (1) in text]. Results from the two-phase regression indicated that body mass was significantly associated with sprint speed for individuals smaller than the change point body mass of 12.85 g (B), solid line = males; dotted line = females). For larger individuals, however, sprint speed was independent of both body mass and sex (B), dashed line = plot of mean sprint speed = 20.585 km/h.

mass $^2 \pm 0.024, F_{1,36} = 7.11, P = 0.011$; and sex $\pm 0.9262, F_{1,36} = 5.02, P = 0.031$.

Although the fit of the polynomial to the data was significantly better than the fit of a simple linear regression equation, a plot of residuals from the polynomial versus body mass revealed a pattern in which the fit was relatively poor for lizards of average mass (greater variance) but better (lower variance) in the data regions for smaller and larger individuals. We, therefore, also applied change-point regression methods (Chappell, 1989) to this dataset (Fig. 2B). A

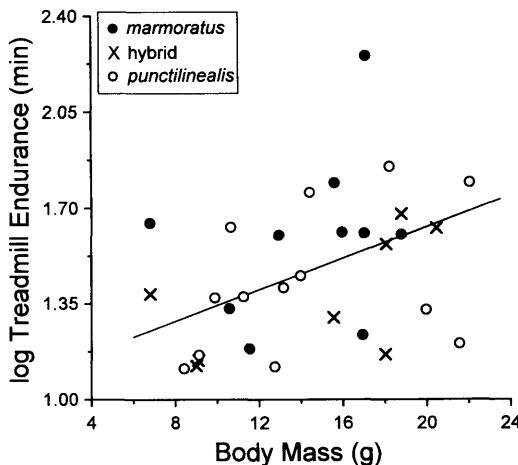


Fig. 3. Semi-log scatter plot of treadmill endurance at 1.0 km/h of 31 *Cnemidophorus tigris* ($r = 0.38$, $P = 0.017$). Regression line was drawn for the two pure populations only, demonstrating that performance of hybrids was not different from the parental forms.

transition body mass of 12.85 g was identified by use of the algorithm described in Yeager and Ultsch (1989). For smaller individuals (seven females, seven males), sprint speed increased linearly with body mass [eq. (3), $R^2 = 0.76$, $F_{2,11} = 17.61$, $P < 0.001$].

$$\text{speed} = 5.842 + 1.153(\text{mass}) + 2.715(\text{sex}); \\ \text{body mass range} = 6.81\text{--}12.76 \text{ g} \quad (3)$$

[SE and F -statistics for eq. (3) were intercept ± 2.906 , $F_{1,11} = 4.04$, $P = 0.070$; mass ± 0.318 , $F_{1,11} = 13.16$, $P = 0.004$; sex ± 1.067 , $F_{1,11} = 6.47$, $P = 0.027$]. For larger individuals (8 females, 18 males, body mass range = 12.94–22.06), sprint speed was independent of body mass and sex (mean = 20.585 km/h, $R^2 = 0.02$, $F_{1,24} = 0.50$, $P = 0.486$).

Pooling data from all individuals, log-stamina was positively related to body mass (Fig. 3; $n = 31$, $P = 0.008$; slope \pm SE = 0.023 ± 0.0105 ; intercept = 1.130 ± 0.1578 , $R^2 = 0.15$, $F_{1,29} = 4.95$, $P = 0.034$). Residual plots did not suggest deviations from linearity; therefore, we did not calculate curvilinear or change-point models.

Allometric equations for the suborganismal traits (log₁₀-transformed) are listed in Table 3. We report pooled within group slopes for liver and kidney mass for allometric equations because the regression slopes were not statistically different among populations. Hematocrit levels were weakly, positively correlated with body mass. Heart (not shown), liver, and kidney masses were all significantly correlated with body mass (Fig. 4). Scaling coefficients for heart and

liver mass were not statistically significantly different from isometry (slope = 1). Kidney mass scaled with a slope significantly greater than one; therefore, larger lizards had proportionately larger kidneys (Fig. 4C–D).

DISCUSSION

Population comparisons.—The principal objective of this study was to determine whether we could detect differences among populations of *C. tigris* across a narrow contact zone in southwestern New Mexico and adjacent Arizona for two measures of locomotor performance, standard metabolic rate (SMR), or for a series of suborganismal traits that support locomotor activity. By measuring multiple components of activity metabolism, we sought to test whether hybrids were less physically fit than their parent populations. If hybrids had lower values for the measures of activity metabolism, then it would be reasonable to conclude that they might be at a selective disadvantage. The hybrids did not differ uniformly from the parental populations, however, consistent with findings from other studies of this kind (e.g., Harrison and Hall, 1993; reviews in Grant and Grant, 1992; Arnold and Hedges, 1995).

We conducted eight separate analyses using ANCOVA to test for population differences in components of activity metabolism. With the exception of correlations with body mass, correlations among locomotor performance, SMR, and suborganismal traits were small in magnitude and only one (between residual SMR and sprint running speed, see below) approached statistical significance at the 5% level. Therefore, we combined the probabilities from the seven virtually independent comparisons ($-2 \Sigma \ln P = 27.72$; P -values from the eight full ANCOVAs, excluding body mass) to obtain an overall test (overall χ^2) of the null hypothesis (Sokal and Rohlf, 1981:779–782). With 14 df, this quantity corresponds to a $P < 0.025$ (Rohlf and Sokal, 1981:table 14, p. 98). Therefore, we conclude that population differences were present but that trait values for the hybrids were not consistently different from the pure populations. Furthermore, differences among the populations were attributed to organ masses rather than SMR or locomotor performance (see below).

Cnemidophorus tigris punctilinealis, *C. t. marmoratus*, and their hybrids did not differ significantly for speed, endurance, or SMR at 40°C (3 comparisons, overall $\chi^2 = 6.79$, $df = 6$, $P > 0.1$). Our sample sizes were relatively small (i.e., we are practicing limited collecting in the hybrid

TABLE 2. DESCRIPTIVE STATISTICS FOR SUBORGANISMAL TRAITS MEASURED ON *Cnemidophorus tigris punctilinealis*, *C. t. marmoratus*, AND TWO HYBRID POPULATIONS FROM 1993.

		n	Mean	SD	Minimum	Maximum
Body mass (g)						
<i>C. t. punctilinealis</i>	males	8	16.6	3.71	12.1	22.1
	females	2	9.6	0.50	9.9	19.1
Hybrid, same area as 1992	males	5	18.7	1.65	16.9	20.9
	females	5	12.9	2.37	10.6	16.4
Hybrid, North Animas Valley	males	4	22.1	6.21	14.6	28.2
	females	6	10.9	1.64	8.0	12.5
<i>C. t. marmoratus</i>	males	5	16.5	2.20	13.4	18.8
	females	5	9.6	2.88	7.3	14.6
Snout-vent length (mm)						
<i>C. t. punctilinealis</i>	males	8	84.6	4.69	77.0	92.0
	females	2	75.5	0.71	75.0	76.0
Hybrid, same area as 1992	males	5	87.4	3.36	84.0	93.0
	females	5	80.0	4.95	74.0	86.0
Hybrid, North Animas Valley	males	4	91.5	6.61	83.0	99.0
	females	6	76.3	3.98	69.0	80.0
<i>C. t. marmoratus</i>	males	5	83.6	3.29	80.0	87.0
	females	5	73.2	5.76	68.0	83.0
Heart mass (mg)						
<i>C. t. punctilinealis</i>		10	21.6	6.36	13	33
Hybrid, same area as 1992		10	23.5	7.43	11	38
Hybrid, North Animas Valley		10	22.9	11.91	8	43
<i>C. t. marmoratus</i>		10	17.2	5.01	11	26
Liver mass (mg)						
<i>C. t. punctilinealis</i>		10	226.4	63.27	162	345
Hybrid, same area as 1992		10	302.5	82.42	183	425
Hybrid, North Animas Valley		10	270.1	101.34	168	457
<i>C. t. marmoratus</i>		10	207.3	72.05	111	306
Kidney mass (mg)						
<i>C. t. punctilinealis</i>		10	100.9	39.97	40	160
Hybrid, same area as 1992		10	92.3	31.93	52	143
Hybrid, North Animas Valley		10	93.8	49.04	44	172
<i>C. t. marmoratus</i>		10	66.0	28.96	33	107
Hematocrit (%)						
<i>C. t. punctilinealis</i>		9	32.8	3.35	28.0	40.0
Hybrid, same area as 1992		10	32.1	4.87	21.0	38.0
Hybrid, North Animas Valley		10	29.3	4.52	22.0	35.0
<i>C. t. marmoratus</i>		10	31.5	5.38	20.0	39.0

zone) and probably yielded low statistical power. However, much larger sample sizes would be required to demonstrate significance ($P \leq 0.05$) for population differences of the small magnitude we observed for measures of locomotor performance. For the sprint speed comparison, for example, a posteriori power analysis (Sokal and Rohlf, 1981:166–168) indicated that a sample size of at least 80 individuals would be required to show that hybrids were significantly slower than were lizards from the pure populations (see above and Table 1). Similarly, for sta-

mina (see Table 1), a minimum of 30 additional individuals would be needed to demonstrate a statistically significant effect at $P \leq 0.05$. Nevertheless, our results suggest that if, in fact, hybrids do differ from the two parental populations in locomotor performance, then the differences are small in magnitude.

We found statistically significant differences among populations for two of the four suborganismal traits measured in this study (five comparisons, overall $\chi^2 = 20.93$, df = 8, $P < 0.01$). Hybrid individuals tended to have larger livers

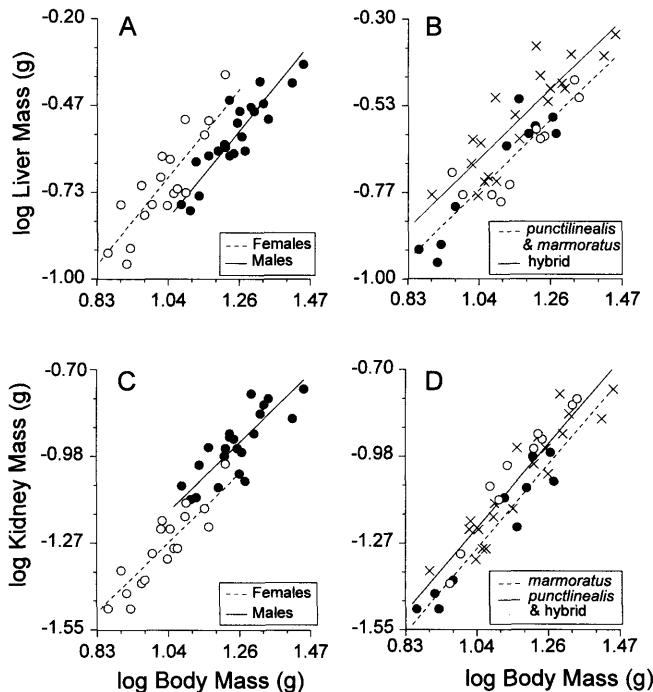


Fig. 4. Log-log scatterplots of liver (A, B) and kidney (C, D) mass versus body mass of 40 *Cnemidophorus tigris*. Regression lines in plots (A) and (C) represent ANCOVA lines and show sex differences (male = ● and solid line, female = ○ and dotted line) in organ mass. For plots (B) and (D), closed circles represent *C. t. marmoratus*, open circles represent *C. t. punctilinealis*, and crosses represent hybrids. Regression lines in plots (B) and (D) represent the pooled within-groups slope from an ANCOVA comparing [plot (B): liver mass] pooled *C. t. punctilinealis* and *C. t. marmoratus* (dotted line) versus hybrids (solid line) and [plot (D): kidney mass] pooled *C. t. punctilinealis* and hybrids (solid line) versus *C. t. marmoratus* (dotted line).

than did individuals from either parental population. We also detected a significant difference in kidney mass between the hybrids plus *C. t. punctilinealis* versus *C. t. marmoratus*. Hybrids and *C. t. punctilinealis* had similar kidney masses, whereas both had significantly heavier kidneys than did *C. t. marmoratus*. Possible ex-

planations for these results include “hybrid vigor” for liver mass [i.e., superior phenotype relative to that of parental populations attributed to increased heterozygosity resulting from crosses between differentiated populations (Falconer, 1989)], “directional dominance” for kidney mass [i.e., dominance of genes associated with

TABLE 3. ALLOMETRIC EQUATIONS FOR SUBORGANISMAL TRAITS MEASURED IN *Cnemidophorus tigris*, 1993.

	Allometric equations, all individuals ^a			
	$a \pm 95\% \text{ CI}^b$	$b \pm 95\% \text{ CI}^c$	$R^e, \%^d$	SEE ^d
Heart mass (mg)	$0.001392 \div \times 1.6631$	1.0042 ± 0.1907	75.0	0.0843
Liver mass (mg)	$0.020581 \div \times 1.5944$	0.9236 ± 0.1749	75.1	0.0773
Kidney mass (mg)	$0.002354 \div \times 1.5334$	1.3307 ± 0.1603	88.2	0.0708
Hematocrit (%)	$24.418332 \div \times 1.5351$	0.0900 ± 0.1601	3.4	0.0690

^a Allometric equations (least-squared linear regressions of log-transformed data) are reported in the form $a(\text{body mass})^b$, where a is the Y-intercept and b is the slope. Mean ($\pm \text{SD}$, n) body mass (g): *C. t. punctilinealis* males 16.6 (3.71, 8), females 9.6 (0.50, 2); *C. t. marmoratus* males 16.5 (2.20, 5), females 9.6 (2.88, 5); hybrids, same area as 1992, males 18.7 (1.65, 5), females 12.9 (2.37, 5); hybrids, northern Animas Valley, males 22.1 (6.21, 4), females 10.9 (1.64, 6). For all traits, sample sizes were $n = 40$ (10 individuals measured from each population), except for hematocrit, *C. t. punctilinealis* $n = 9$. Data were pooled from all populations because slope heterogeneity was not detected. For liver and kidney mass, we corrected the data to a common mean prior to calculating allometric equations because the means differed significantly among the populations.

^b a , Antilog of y -intercept estimate (i.e., value at body mass equal to 1 g) from log-log regression equations. Confidence intervals of the intercept are asymmetrical about the mean on the arithmetic scale (e.g., hematocrit: $20.05 \div 1.224$ to 20.05×1.224 represents a 95% CI of 16.4 to 24.5).

^c Slopes for heart, liver, and kidney mass, but not hematocrit, were significantly different from zero. Slopes from regressions of heart and liver mass with body mass were not statistically different from one, whereas kidney mass and hematocrit slopes were statistically different from one.

^d R^2 , coefficient of determination; SEE, standard errors of estimate of regressions in \log_{10} units.

the phenotype are primarily in one direction (Falconer, 1989)], or reproductive state. Seasonal variation in kidney (Fox, 1958) and liver mass (Dessauer, 1955) have been documented previously in other species. The functional, and therefore selective, consequences of population differences in kidney and liver mass are not known. Differences in kidney mass may be associated with differences in water flux and osmoregulation capacities. Variation in liver mass may be related to detoxification abilities or storage of carbohydrate and other metabolic fuels.

Individual variation, sexual dimorphism, and effects of tail loss on locomotor performance.—The proximate causes of individual or interspecific variation in locomotor performance is an outstanding issue in the fields of ecological physiology and morphology (Garland and Losos, 1994). Consistent with previous studies with reptiles (e.g., Garland, 1984; Bulova, 1994; reviewed by Garland and Losos, 1994), we found substantial individual variation for locomotor performance in these populations of *C. tigris*. Although we found sex differences for sprint running speed, this was probably related to sexual dimorphism in body mass. The sexes did not differ in treadmill endurance or SMR. Individual variation for mass-independent sprint speed (using change-point regression equation residuals) was not related to treadmill endurance after removing the effects of body mass ($r = 0.11$, two-tailed $P = 0.616$, $n = 24$). Similarly, individual differences in residual SMR were not correlated with treadmill endurance ($r = -0.25$, $P = 0.215$, $n = 26$). SMR and sprint speed performance were, however, marginally negatively associated ($r = -0.42$, $P = 0.053$, $n = 22$). After accounting for the common effects of body mass on organ size, we found no significant correlation between suborganismal traits.

A long, intact tail probably helps a running lizard to maintain balance (Ballinger et al., 1979; Arnold, 1988). Thus, its loss may significantly affect running performance, especially in species like *Cnemidophorus*, which are capable of bipedal locomotion. In our study, individuals missing half or more of their tail were, on average, 2 km/h slower while sprinting (Fig. 1) but ran for 10 min longer at 1.0 km/h compared with individuals with intact tails. These performance differences were not statistically different, however. Our study was not designed to test for an effect of autotomy on locomotor performance. Because of low statistical power (i.e., only eight tailless individuals), it is premature to claim that tail loss has no effect on sprint running in *C. tigris*. Reduced sprint speed

performance as a consequence of tail loss has been noted for *Cnemidophorus* and other lizard species (Ballinger et al., 1979; Daniels, 1983; additional references in Arnold, 1988).

Allometry of locomotor performance and suborganismal traits.—Sprint running speed was positively associated with body mass, but a simple linear model did not fit the data as well as polynomial and change-point regression models (Fig. 2B). We found that estimated maximal running speeds for the smallest and largest individuals (Table 1) from the polynomial [eq. (2): 14.8 and 19.6 km/h] and change-point [eq. (3): 14.0 and 21.0 km/h] regressions were similar and these estimates agreed reasonably well with the observed data (Fig. 2B). From the polynomial model, a maximal speed of 21.4 km/h was predicted at the optimal body mass [16.9 g, following differentiation of eq. (2)], whereas the change-point models predicted a comparable value of 21.5 km/h for a 12.85 g individual [i.e., transitional body mass, eq. (3)]. Thus, both polynomial and change-point regression analyses indicated that the largest individuals were not the fastest (Fig. 2). Previous intraspecific studies with reptiles have generally found that sprint speed increases monotonically with body size (e.g., lizards, Garland, 1985; Sinervo, 1990; Sinervo and Huey, 1990; snakes, Arnold and Bennett, 1988; additional references in Garland and Losos, 1994), although nonlinear relationships have also been documented (e.g., *Thamnophis sirtalis*, Jayne and Bennett, 1990). For interspecific studies with reptiles, no general pattern has emerged (reviewed by Garland and Losos, 1994); across all mammals, maximal running speeds are nonlinearly related to body size (Garland, 1983; Garland et al., 1988; Chappell, 1989).

Endurance was positively associated with body mass, consistent with previous studies (reviewed by Garland, 1993; Garland and Losos, 1994). Within other populations of lizards, for example, stamina also tends to increase with body size (Garland, 1984, 1994; Garland and Else, 1987). Individual treadmill performance values at 1.0 km/h were log-normally distributed, a common observation for such data in lizards (Garland, 1994).

SMR at 40°C also scaled allometrically with body size as in numerous previous reports (see reviews in Andrews and Pough, 1985; Garland, 1993; Beck and Lowe, 1994). Scaling coefficients for heart and liver mass were not significantly different from one (Table 2); similar values have been reported for adult *Sceloporus* (John-Alder, 1990; John-Alder and Joos, 1991),

whereas other reports using a broader range of body masses and including juveniles, clearly indicate that these organs scale allometrically (e.g., Garland, 1984; Garland and Else, 1987). The mass exponent for kidney mass in *C. tigris* was significantly greater than one; other reports have found that the scaling exponent is not significantly different from isometry in adult lizards (e.g., Beuchat and Braun, 1988; John-Alder, 1990; John-Alder and Joos, 1991). Male *C. tigris* in our study also had heavier livers and kidneys than did females (after accounting for mass differences), but scaling coefficients were not statistically different.

Comparison of locomotor performance and SMR with previous *C. tigris* studies.—Garland (1993) reported that adult *C. t. tigris* from California maintained a speed of 1.0 km/h on a treadmill “for one or two hours or more” (1993:174), as compared with an average stamina for *C. tigris* in this study of less than one hour at this treadmill speed (Table 1). Potential explanations for the higher stamina of Californian populations include larger body size (Garland, 1993; see also Anderson and Karasov, 1988) or capacities of some functional correlates at lower levels of organization. However, hematocrit levels reported by Garland (1993) were virtually identical to those reported in this study (Table 2). Similarly, liver mass accounted for 1.98% of body mass in the Californian *C. tigris* compared with 1.6% for the populations studied here. Differences in heart mass as a proportion of body mass [0.24%, Garland (1993) vs 0.14%, this study], are probably spurious because different individuals blotted the hearts in the two studies. Therefore, these populations probably differed for stamina as a result of the positive correlation between stamina and body mass (Garland and Else, 1987; Sinervo and Huey, 1990; Garland, 1994).

SMR values were similar to published values for *C. tigris* (Anderson and Karasov, 1988; Garland, 1993). However, our mass-specific values were about 11% lower than those reported by Garland (1993, also measured at 40°C). At least two explanations may account for the differences. First, we fasted our lizards for longer periods than did Garland (1993; lizards were fasted for only two days). Periods of moderate fasting/starvation generally do not depress mass-specific SMR in lizards but lead, instead, to proportionately reduced whole-animal metabolic rates (Roberts, 1968; Bennett and Dawson, 1976). Second, genetically based differences between populations are possible, but, again, testing this would require a “common garden” ap-

proach (Garland and Adolph, 1991; Garland and Carter, 1994).

Conclusions.—Our SMR and locomotor performance results, together with the findings of previous morphological and genetic studies on this hybrid zone (Dessauer et al., 1962; Zweifel, 1962; Dessauer and Cole, 1991), suggest that the hybrids are not less fit than either of the parental *C. tigris* populations. Our results from analyses of suborganismal traits were inconclusive because of the potential sampling biases noted above (e.g., effects of season or reproductive status). Thus, we found no data to suggest that the hybrid zone was maintained by selection against the hybrid class. The most likely explanations for the existence of the narrow hybrid zone between *C. t. punctilinealis* and *C. t. marmoratus* continue to be its recent origin and that contact between the two subspecies occurs near a population density sink (Dessauer and Cole, 1991; but see discussion in Barton and Hewitt, 1985).

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