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COMPARISONS OF PHYSIOLOGICAL PERFORMANCE IN SEXUAL AND ASEXUAL WHIPTAIL LIZARDS (GENUS *CNEMIDOPHORUS*): IMPLICATIONS FOR THE ROLE OF HETEROZYGOSITY

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Abstract.—Many asexual animal species are of hybrid origin, with consequent high levels of heterozygosity. Data from some studies suggest that increased heterozygosity may be functionally correlated with superior performance in a variety of fitness-related traits. Thus, hybrid asexual species could be expected to exhibit some degree of heterosis. This spontaneous heterosis hypothesis is tested in a comparative study of asexual and sexual species of the lizard genus *Cnemidophorus.* Asexual species of the genus are parthenogenetically reproducing hybrids of the sexual species and as a result have high levels of heterozygosity that have persisted since their origins. Five whole-organism physiological traits (burst speed, endurance, maximal exertion, standard metabolic rate, and evaporative water loss rate) were examined in five asexual species and the sexual species that gave rise to them. Trait values for sexual and asexual species were compared using a nonphylogenetic approach and two phylogenetically controlled approaches capable of dealing with reticulate phylogenies. In contrast to the predictions of the heterosis hypothesis, performance for four of the traits in asexual *Cnemidophorus* was not statistically different than that in their sexual parental species, and asexuals had significantly worse endurance. On the whole, the overall trend appeared to be toward worse performance in asexuals. An obvious interpretation of these results is that heterozygosity and ''vigor'' need not be functionally related. However, other factors may be counterbalancing possible beneficial effects of heterozygosity, including detrimental epistatic effects resulting from the karyotypically mixed genome of these hybrids, and the accumulation of deleterious mutations in the asexual lineages via Muller's ratchet.

A notable feature of asexual animal species is that many of them have their origins in hybridization events involving related sexual species. This is especially true among vertebrates, for which all asexual species whose origins are known appear to be hybrids (Vrijenhoek et al. 1989). Many of these species show considerable ecological success, despite the numerous disadvantages hypothesized for asexual reproduction and the generally low incidence of asexuality in the animal kingdom (Bullini 1994). The possible reasons for the existence and persistence of such species have been the subject of considerable conjecture (e.g., Dawley and Bogart 1989).

The hybrid origin of these asexual groups has led a number of authors (e.g., White [1970]; Schultz [1971]; Cole [1975]; Mitton and Grant [1984]; and, more recently, Bullini [1994]) to suggest that at least part of the reason for their suc-

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cess may be that they exhibit some degree of hybrid ''vigor,'' or heterosis. Wetherington et al. (1987) have termed this proposal the spontaneous heterosis hypothesis. The idea is based mainly on the observation of two patterns, the first of which being that many asexual animals have high levels of heterozygosity (Dawley and Bogart 1989; Bullini 1994; and see below), often several-fold the levels seen in closely related sexual species. This extreme heterozygosity is attributed primarily to the nature of the formative hybridization events, since the parental individuals typically come from different species.

The second observation motivating the spontaneous heterosis hypothesis is that increased allozyme heterozygosity has been associated with improved trait values in studies on both wild and domestic species (reviewed in Mitton and Grant 1984; Mitton 1994). For example, life-history traits such as growth rate, viability, and fecundity have been correlated with heterozygosity in populations of mussels, oysters, butterflies, killifish, guppies, and salamanders (Mitton and Grant 1984; Mitton 1994; Zouros and Pogson 1994). Several studies have also found associations between heterozygosity and aspects of physiological performance, such as resting oxygen consumption rates (Koehn and Shumway 1982; Mitton et al. 1986; Danzmann et al. 1987; Hawkins et al. 1989), maximal oxygen consumption rates (Mitton et al. 1986), and feeding rates (Garton 1984). These sorts of findings have led several authors (Turelli and Ginzburg [1983]; Mitton and Grant [1984]; Zouros and Pogson [1994]; among others) to propose that the number of allozymes available to an organism should have a direct functional relationship with the overall vigor that the organism exhibits for a wide variety of traits related to fitness. The supposed mechanistic basis for this pattern of heterozygous advantage has not been well established, however. If the spontaneous heterosis hypothesis is true, then one of the main contributors to the success of many asexual lineages could be superior performance in a variety of traits, relative to related sexual species. In the study presented here, I test this hypothesis by examining a number of asexual species of the lizard genus *Cnemidophorus* (family Teiidae), all of which exhibit extremely high levels of heterozygosity (Dessauer and Cole 1989) and considerable ecological success.

ASEXUAL AND SEXUAL *CNEMIDOPHORUS*

Lizards of the genus *Cnemidophorus* (whiptails) are generally thermophilic, highly active foragers. They are found through much of the Americas' warmer regions but are particularly speciose in the deserts of the southwestern United States and Mexico. The group consists of both asexual and sexual species, with the former composed of ~30% of the 45+ members of the genus (Wright 1993). These asexual species are all-female and reproduce parthenogenetically, such that daughters are clonal copies of their mothers (the unfertilized egg undergoes a premeiotic endomitosis, and during meiosis identical rather than simply homologous chromosomes form tetrads, so crossing-over has no effect; Cuellar 1971). As a result, populations of asexual *Cnemidophorus* species tend to have extremely low levels of genetic diversity.

The origin of all asexual *Cnemidophorus* species is attributed to hybridization

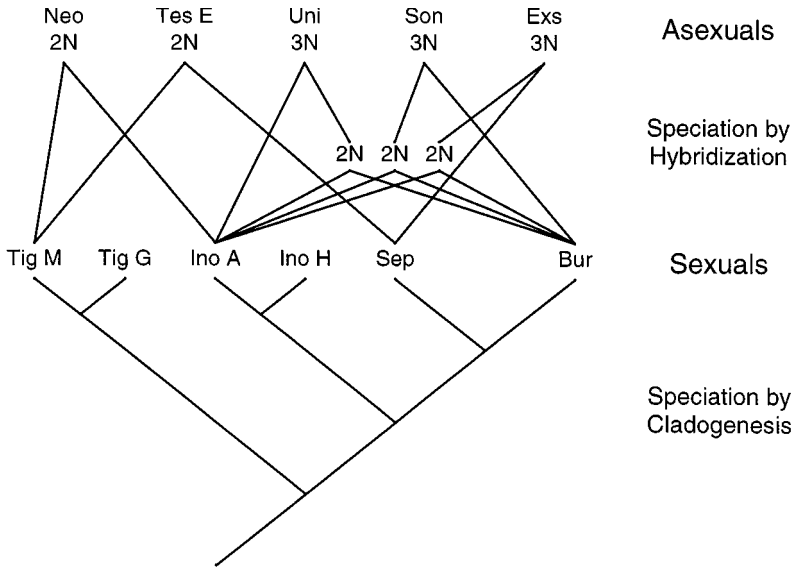

FIG. 1.—*Cnemidophorus* phylogeny. This hypothesized phylogeny of *Cnemidophorus* species examined in this study is intended only to show relationships among species, not the time of particular speciation events. The sexual group shows the typical bifurcating pattern of speciation via cladogenesis. The appearance of the asexual species exhibits the reticulate pattern of a hybridization event. Ploidy of asexual species is shown below their abbreviation. In triploid asexuals, intermediate diploid hybrids were believed to be involved in the two hybridization steps. Note that both sexual and asexual species have persisted independently since the hybridization events. Species abbreviations: *Neo, C. neomexicanus; Tes, C. tessellatus clone ''E''; Uni, C. uniparens; Son, C. sonorae; Exs, C. exsanguis; Tig M, C. tigris marmoratus; Tig G, C. tigris gracilis; Ino A, C. inornatus arizonae; Ino H, C. inornatus heptagrammus; Sep, C. septemvittatus; Gul, C. gularis;* and *Bur, C. burti stictogrammus.* Sexual species phylogeny based on Densmore et al. (1989*a*), Dessauer and Cole (1989), and Moritz et al. (1989). Asexual species phylogeny based on Good and Wright (1984) and Dessauer and Cole (1989).

between different sexual species in the genus (fig. 1). (Note: Because of their asexual nature, the term *species* as applied to parthenogenetic *Cnemidophorus* is clearly not meaningful in the traditional biological sense. Most systematists classify an asexual *Cnemidophorus* ''species'' as all the individuals resulting from a particular sex-specific combination of sexual species [Vrijenhoek et al. 1989]. Such species may represent one or more independent clonal lineages. I follow that convention here.) While such hybridization events probably were and are not uncommon, only a small fraction appear to have resulted in the formation of asexual lineages, presumably because the particular genetic conditions necessary for parthenogenesis typically do not occur in the hybrids. The formation of all known asexual lineages is thought to have occurred on the order of a few to perhaps 10,000 yr ago (Densmore et al. 1989*a,* 1989*b;* Moritz et al. 1989), with

no indication of recent hybridization events having contributed to current populations. While some asexual lineages may have died off, extant lineages have been very successful, particularly in the Sonoran and Chihuahuan Deserts. Populations of asexual *Cnemidophorus* can be quite dense in appropriate habitats (A. J. Cullum, personal observation), and range sizes of the asexual species are larger than those of some sexual species in the genus (Stebbins 1985).

The high levels of heterozygosity seen in asexual *Cnemidophorus* are the result of their hybrid origins and are maintained by the parthenogenetic reproduction of these species. While sexual *Cnemidophorus* have allozyme heterozygosity indexes of about 0.05 (i.e., 5% of loci are heterozygous) (Dessauer and Cole 1984), a level typical for sexual vertebrates (Dessauer and Cole 1989), the asexual species have heterozygosities of 0.24–0.44 (Dessauer and Cole 1989), among the highest values observed in vertebrates. Because most asexual species appear to consist of only a few independent clonal lineages, the variation in heterozygosity within species is very low. For the 40+ allozymes examined, clones within species typically vary at only one or two loci, and in many cases the loci show the same degree of heterozygosity (e.g., *abb* rather than *aab*) (Dessauer and Cole 1989).

If heterozygosity and superior performance are associated (i.e., if heterosis is exhibited), asexual *Cnemidophorus* should be better performers than their sexual congeners (Cole 1975). Because the parental species of most asexual *Cnemidophorus* species are known, and phylogenies of the sexual species have recently become available, historical (or phylogenetically based) approaches can now be used in comparative projects involving these species, allowing for more robust conclusions about the effects of heterozygosity than would otherwise be possible (Garland and Adolph 1994).

To assess the relative vigor of these species, I chose to examine a number of measures of whole-organism performance, each reflecting some aspect of overall physiological fitness. Three complementary locomotor performance characters were measured: burst speed, which reflects limits of muscular function and skeletal design; endurance, which is related to aerobic capacity; and maximal exertion, or distance running capacity, which reflects anaerobic capacity (Bennett 1989). Two additional traits, standard metabolic rate (SMR) and evaporative water loss rate (EWL), were also measured.

These sorts of traits are particularly appropriate for investigation for two reasons. First, they represent an integration of many levels of biological organization and functional domains (Bennett 1989). The heterozygous advantage hypothesis is based on the idea of a general increase in physiological (or biochemical) efficiency, and thus traits that are likely to reflect such efficiencies should be especially revealing (Koehn and Shumway 1982; Garton et al. 1984). Second, they are all traits that are likely to have important fitness consequences in these highly active desert species. Locomotor traits such as the ones measured here have demonstrated effects on survival in other reptile species (Miles 1989; Jayne and Bennett 1990) and are likely to be important in *Cnemidophorus* also (Garland 1993, 1994). For these sorts of traits, higher values are considered su-

perior because they indicate a greater capacity than could be accessed during periods of intense behavioral demands. For the remaining two traits, however, the opposite pattern holds true. With regard to SMR, proponents of the heterozygous advantage hypothesis have argued that lower standard (or resting) metabolic rates are beneficial, as energy that would ordinarily be used in metabolism can instead be used for growth (Koehn and Shumway 1982; Mitton et al. 1986; Hawkins et al. 1989), gamete production (Rodhouse et al. 1986), or normal development (Mitton 1993). As for EWL, the potential fitness advantage to lower water loss rates in the xeric environments *Cnemidophorus* typically inhabit is obvious.

Previous comparative studies on sexual and asexual *Cnemidophorus* have investigated areas such as morphology (e.g., body size, scale counts: Parker 1979), behavior (e.g., wariness: Price 1992; Paulissen 1995), social behavior (Leuck 1985), and fecundity (e.g., Congdon et al. 1978; Schall 1978). Many of these studies, however, have examined only a single asexual species and one or two of its parental species. In addition, those studies that have examined multiple species have not done so in a phylogenetic context. Perhaps for these reasons, no general pattern has emerged concerning the performance of asexual *Cnemidophorus* species relative to their sexual congeners. For example, Price (1992) found that the asexual *C. tesselatus* had inferior behavioral responses to an approaching predator than did its sexual parent *C. tigris marmoratus*, while Paulissen (1995) found no difference between the asexual *C. laredoensis* and its parent *C. gularis* in a similar study. For another class of traits, Congden et al. (1978) found significantly higher reproductive output in two asexual species than two sexual ones, while Schall (1978) found no difference between two asexual species and three sexual ones.

To make these sorts of comparative studies more powerful, greater numbers of species need to be examined, and comparisons among species should be considered in a phylogenetic context. In this study, I address the question of possible spontaneous heterosis in asexual *Cnemidophorus* species through comparison of five such species with the sexual species that gave rise to them, using both phylogenetically based and nonphylogenetic analyses. Specifically, I test the hypothesis that the higher levels of heterozygosity seen in the asexual species will result in superior physiological performance in comparison to their sexual ancestors.

MATERIAL AND METHODS

A total of six asexual species and six sexual species or subspecies were examined in this study. Figure 1 shows five of the asexual species and their phylogenetic relationship to the six sexual species. The sixth asexual species, *Cnemidophorus laredoensis* (clone A), was not used in one form of phylogenetically controlled analysis (see below), as no data on its parental species were obtained. The mean allozyme heterozygosity of these six asexual species is 0.33 ± 0.05 (SD) compared with 0.05 ± 0.01 for the sexual species (Parker and Selander 1976; Dessauer and Cole 1984; Dessauer and Cole 1989). Collection of all ani-

mals and measurement of their physiological performance were carried out during the summers of 1992–1994.

Collection

All animals used in this study were collected in the Chihuahuan and Sonoran Deserts of the United States by use of noose, drift fence, or pitfall traps under 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 localities are available from the author on request.

Animals were weighed and measured (snout-vent length, or SVL) within 1 d of capture. Animals were sexed by attempting to express hemipenes and examining femoral pores and head width. Any tail loss or gravidity was also noted when present. After capture, animals were kept individually in plastic shoe boxes until all five traits had been measured. Water was provided daily, but animals were not fed until standard metabolic and evaporative water loss rates had been measured.

Measurement of Performance Traits

All performance traits were measured using protocols that have become de facto standards among comparative physiologists (e.g., Bennett 1989; Garland 1993, 1994).

For each individual, the three locomotor traits were measured in a random order, and measurements were usually completed within 1 wk of capture. All traits were measured with animals at body temperatures at or near 40°C. Actual body temperatures were taken immediately after trials with a quick-reading cloacal thermometer.

Burst speed was measured on a 3-m-long electronic racetrack with a large funnel trap at the far end. Photocells placed at 25-cm intervals along the last 2 m of the track were connected to an IBM XT computer, and their triggering was timed with a custom program. The first meter of the track provided distance for acceleration. Each individual was chased down the track at full speed three times in rapid succession on two separate days. From these six trials, the fastest time over any 50-cm interval was used to calculate maximal burst speed in meters/second.

Endurance was measured as the number of seconds an animal could maintain speed on an electric treadmill moving at 1 km/h on a 20° incline. (With no incline, some individuals did not fatigue for >90 min.) Lizards were prodded to match tread speed by pinching the base of the tail. A trial ended when the animal failed to match the tread speed for more than 10 s despite repeated pinching or lost its righting response. Trials were timed by stopwatch. Each individual was measured once.

Maximal exertion was quantified as the distance an individual could run before exhaustion when being chased around a 5-m circumference circular raceway at full speed. Individuals were initially chased with the padded tip of a 1-m dowel; as animals slowed, they were kept moving by tail pinching, as above. An animal was considered exhausted when it either lost its righting response or

refused to move farther. Because individuals often changed direction during the trial, distance run could only be determined to the nearest 5 m. Individuals were measured once each.

Standard metabolic and evaporative water loss (EWL) rates were measured overnight after individuals had been fasted for at least 4 d. Standard metabolic rate (SMR) was determined via closed-chamber respirometry, using chambers constructed of various diameters of polyvinyl chloride (PVC) piping and end caps, with final volumes ranging from 425 to 1,540 mL. Stopcocks were fitted to each end of these chambers. I determined EWL gravimetrically, by passing dried air over the animals then through a series of columns containing Drierite. Mass changes in the Drierite columns were taken to the nearest 0.1 mg using Mettler balances.

Before measurements, individuals were placed in a PVC chamber roughly proportional to their size. These chambers were then placed in a temperature-controlled cabinet held at 40°C. The chambers were left undisturbed for 90 min, during which time preheated, dried air was passed through each chamber via the stopcocks.

I measured SMR using methods similar to those suggested by Vleck (1987). Measurements were started at a time between 2200 and 2330 hours by attaching a 60-mL syringe to a stopcock, flushing air in and out of the syringe a number of times to ensure mixing in the chamber, then drawing a 50-cc sample of air from each chamber and sealing both stopcocks. Chambers were then left undisturbed for between 60 and 100 min, after which time a second 50-mL sample of chamber air was taken in the same way. These samples were analyzed using an Applied Electrochemistry S-3A oxygen analyzer after removal of CO_2 and water vapor, then volumes were converted to standard temperature and pressure (STP), and oxygen consumption in milliliters/hour was calculated using the formula

$$\dot{V}_{O_2} = [(F_{O_2i} - F_{O_2f}) \times (V_C - V_L)]/t, \quad (1)$$

where $\dot{V}_{O_2}$ is milliliters of oxygen per hour; F_{O_2i} and F_{O_2f} are the fraction of oxygen in the initial and final air samples, respectively; V_C is the volume of the chamber in milliliters; V_L is the volume of the lizard (calculated as lizard mass in grams $\times$ 1.01 mL/g; Peterson 1990); and t is the time interval in hours. Partial pressure of oxygen (P_{O_2}) was kept above 120 torr at all times (F_{O_2} of 0.195 at 1,650-m altitude).

Evaporative water loss measurements took place subsequent to SMR measurements. Flow of dried, preheated air through each chamber was restarted at a rate of 125 mL/min. After 1 h, flow was diverted to pass through the tubes of preweighed Drierite. After 4 h, flow was rediverted, and the tubes were sealed then reweighed. One or more sets of tubes were attached to empty chambers in the temperature cabinet and served as controls. Evaporative water loss rate was calculated as

$$\dot{M}_{H_2O} = [(M_{Sf} - M_{Si}) - (M_{Cf} - M_{Ci})]/t, \quad (2)$$

where $\dot{M}_{H_2O}$ is milligrams of water per hour; M_{Sf} and M_{Si} are, respectively, the final and initial mass of the sample Drierite tubes in milligrams; M_{Cf} and M_{Ci}

are, respectively, the final and initial mass of the control Drierite tubes; and t is the time interval in hours.

Lizards were removed from their chambers in the morning and the chambers inspected. If a lizard had defecated during the trial, the data were not used for either SMR or EWL, and the lizard was retested the following night.

Final sample sizes for all traits are shown in table 1.

Basic Analyses

All statistical analyses were carried out using SYSTAT for Windows, version 5.04 (SYSTAT 1992). For all traits, only data on females were used to eliminate possible complications due to sexual dimorphism. To improve the overall normality of the data set, all traits were log-transformed before analyses.

Because all the traits measured in this study have the potential to be influenced by confounding factors such as body size, body temperature, number of days in captivity, and so forth, potential covariates were tested for significance within species by ANCOVA (with species as the factor) for each trait, after testing for significant species $\times$ covariate interaction terms. Any significant covariates were then used in a final ANCOVA for each trait, which generated an adjusted least-square mean (LSM) for each species. These adjusted LSMs were then used in all subsequent analyses, as described below. Significant intraspecific covariates are shown in table 1.

Since interspecific allometry may be different than intraspecific allometry and, in particular, may be significant despite a lack of detectable effect of body size within species, I considered this effect separately. An ANCOVA was performed with previously generated adjusted LSMs as the dependent variable, species' mean body sizes (log SVL or log mass; see table 1) as the covariate, and species type (sexual or asexual) as the factor. Using species type as the factor controlled for hypothesized differences between the types. The allometric slope was provided by SYSTAT's extended ANCOVA output.

Comparative Analyses

The hypothesized phylogeny of the *Cnemidophorus* species used in this study is shown in figure 1. The reticulate (i.e., branch joining) pattern of evolution resulting from hybridization means that commonly used approaches of historical analysis (e.g., Felsenstein's [1985] independent contrasts; related methods reviewed in Garland 1993) cannot be used without major modification, because these methods deal only with cladogenesis (i.e., diversification of phylogenetic branches).

I used two different approaches to this problem. The first approach (here termed *autocorrelation*) used Cheverud et al.'s (1985) phylogenetic autocorrelation method to make general comparisons between sexual and asexual species as a whole. This method corrects for genetic relatedness among species, rather than phylogeny per se, by using a genetic distance matrix for the species to partition the trait value for each species into a component that can be explained by the common genetic background and a component that is unique to that species. The phylogenetic component can then be removed from trait values, and the

TABLE 1

SAMPLE SIZES AND INTRASPECIFIC COVARIATES

	Species											Covariates	
Trait	*Bur*	*Exs*	*Ino-A*	*Ino-H*	*Lar*	*Neo*	*Sep*	*Son*	*Tes*	*Tig-G*	*Tig-M*	*Uni*	Intraspecific	Interspecific
Burst speed	14	25	23	19	11	25	14	3	2	19	10	29	Day (of year) of trial	Log SVL
Endurance	14	25	23	17	11	25	14	3	2	19	10	30	None	Log SVL
Maximal exertion	12	25	24	15	11	25	14	3	2	19	10	29	Body temperature	Log SVL
Standard metabolic rate	11	24	23	19	11	23	14	3	2	19	7	29	Log mass, position in temperature cabinet, days since capture	Log mass
Evaporative water loss	11	24	23	17	11	18	13	3	(1)	19	7	29	Log mass, mass relative to mass at capture	Log mass

NOTE.—For each log-transformed trait, the sample size for each species or subspecies is shown, along with the covariate(s) used (if any) in generating least-square means for each species via ANCOVA. Data on evaporative water loss in *Cnemidophorus tesselatus* were not used as $N = 1$. Species abbreviations are like those in figure 1, plus *Lar, Cnemidophorus laredoensis;* SVL is snout-vent length.

specific residuals analyzed as independent data. This procedure was applied to specific residuals of the interspecific allometry equations (see above) using the genetic distance matrix shown in appendix A and the computer program MRHO 3.5 (developed by Cheverud and Dow [1985]; modified by Miles and Dunham [1992]). The resulting specific values of the two species types were then compared via simple ANOVA.

The second approach (''species specific'') involves direct comparisons between each asexual species and the sexual species that gave rise to it. For each asexual species, a predicted value was generated for each trait and for body size by averaging the values of its parental species. (In triploids with only two parental species—e.g., *C. uniparens*—the value of the twice-represented parent was weighted twice as much as the value of the other parent.) Each predicted trait value was then adjusted for differences between predicted and observed body sizes, using allometric slopes derived as described previously. This predicted trait value was then compared with the observed value in the asexual species. Note that this approach assumes as its null hypothesis that genetic variation for traits is additive. If heterozygosity does in fact promote improved performance, the observed values for asexual species should be superior to the predicted values on average. The asexual *C. laredoensis* was not included in this analysis because data were lacking on one of its parental species.

In addition to these phylogenetically controlled analyses, a nonphylogenetic comparison of sexual and asexual species (''nonphylogenetic'') was made using ANCOVA on the original adjusted LSMs. Body size served as the covariate. This form of analysis is not revealing of evolutionary patterns but is more relevant to ecological issues such as interspecific competition.

Because sample sizes for two of the asexual species (*C. sonorae* and *C. tesselatus*) were quite small, all analyses were duplicated with these species excluded. In all cases, these results were highly similar to the results for the full data set and consequently are not reported.

RESULTS

The adjusted least-square means derived via ANCOVA for each species are shown for each trait in figure 2. The covariates used to calculate these LSMs are shown in table 1. Evaporative water loss rate was not analyzed for *C. tesselatus* as the sample size was one. Raw means of untransformed trait values are given in appendix B.

Figure 2 also shows the results of the nonphylogenetic comparison between the two species types. The significance values reported are for the main effect in each ANCOVA (i.e., the test for differences between species types). For none of the traits did asexuals show superior trait values. Endurance is actually inferior ($P = .003$) in the asexual species. Data on endurance previously published by Garland (1994) on some of the same species show a similar pattern.

Results of the autocorrelation analysis are shown in tables 2 and 3. Table 2 indicates the autocorrelation coefficient (ρ), its standard error (SE), and the proportion of the total variance in the traits explained by the relatedness among spe-

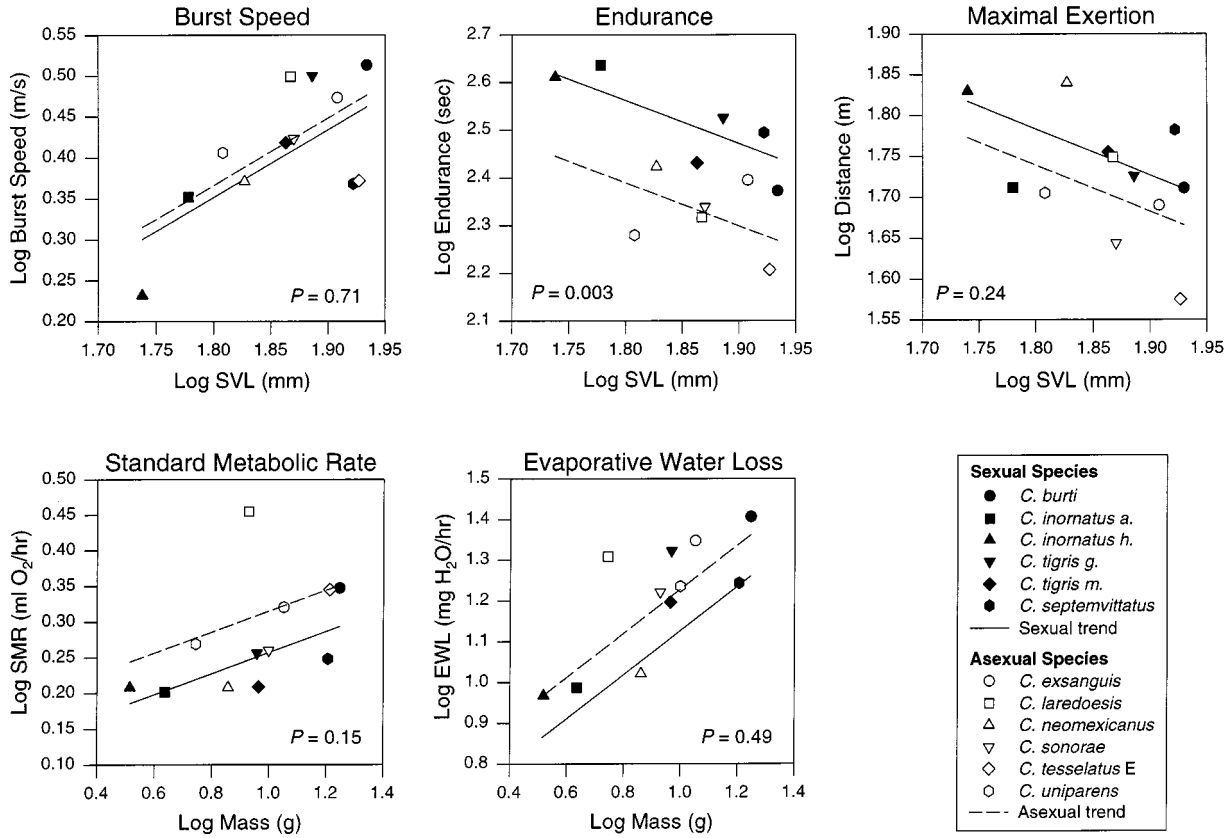

FIG. 2.—Asexual and sexual species means. Shown for each log-transformed trait are means versus log snout-vent length or log mass for the 12 *Cnemidophorus* species examined. Means are either simple means or adjusted least-square means (see the text). The allometric slopes shown were derived via ANCOVA of adjusted means, grouped by species type, with log body size as the covariate. Thus, the lines have the same (common) slope but different intercepts. For standard metabolic rate and evaporative water loss, intraspecific body-size effects were eliminated during the calculation of adjusted least-square means; thus, the slopes shown here represent the residual interspecific allometry.

TABLE 2

AUTOCORRELATION COEFFICIENTS FOR ALLOMETRICALLY SCALED TRAITS

Trait	ρ	SE	R^2	*P*
Burst speed	.03	1.00	.001	.49
Endurance	−.45	.59	.23	.22
Maximal exertion	−.25	.86	.07	.39
Standard metabolic rate	.13	.96	.02	.45
Evaporative water loss	.37	.68	.18	.29

NOTE.—The autocorrelation coefficients (ρ), associated standard errors (SE), proportion of total variance explained by phylogenies (R^2) were derived with the computer program MRHO 3.5 (developed by Cheverud and Dow [1985]; modified by Miles and Dunham [1992]). Significance values (calculated with a one-tailed *t*-test) refer to the autocorrelation coefficients. Coefficients were calculated from snout-vent length residuals of each trait (see text).

cies (R^2) (Cheverud et al. 1985). In no case is the autocorrelation coefficient significant, and thus the application of the phylogenetic autocorrelation method is unlikely to influence greatly the patterns seen in the ''uncorrected'' data. However, the conservative approach is to apply the method in any case. Not surprisingly, removal of the phylogenetic portion of the trait values and analysis of the specific remainders result in a pattern highly similar to the nonphylogenetic analysis, with the asexual species exhibiting significantly lower endurance ($P = .003$) and superior performance in none of the other traits (table 3).

The results of the species-specific approach are shown in table 4. This analysis included data only for asexual species in which all the sexual species involved in the hybridization have been measured, so *C. laredoensis* was not analyzed. Again, the patterns are similar to those of the previous analyses. Observed values for the asexual species are lower than predicted based on the parental species' values for endurance and no better than predicted for burst speed, maximal exertion, SMR, or EWL.

DISCUSSION

The idea that many hybrid asexual species owe their success at least in part to heterotic effects, or hybrid vigor, has been suggested by a number of authors (White [1970]; Schultz [1971]; Cole [1975]; Mitton and Grant [1984]; Bullini [1994]) and has been termed the spontaneous heterosis hypothesis (Wetherington et al. 1987). This hypothesis is based on the premise that high levels of heterozygosity should result in improved physiological efficiency (Turelli and Ginzburg 1983; Mitton and Grant 1984; Zouros and Pogson 1994). Mitton and Grant (1984) suggested that characters related to respiration rate (such as SMR and endurance; Garland 1993) and water use efficiency (such as EWL) should be superior in more heterozygous individuals. Thus, asexual species that exhibit high degrees of allozyme heterozygosity, such as parthenogenetic *Cnemidopho-*

TABLE 3

RESULTS OF ANOVAS BASED ON SPECIFIC AUTOCORRELATION RESIDUALS

SPECIES TYPE	BURST SPEED			ENDURANCE			MAXIMAL EXERTION			STANDARD METABOLIC RATE			EVAPORATIVE WATER LOSS		
	LS Mean	SE	*P*	LS Mean	SE	*P*	LS Mean	SE	*P*	LS Mean	SE	*P*	LS Mean	SE	*P*
Asexual	.117	.444	.72	−.759	.195	.003	−.393	.393	.19	.424	.400	.17	.099	.409	.77
Sexual	−.117	.444	...	.759	.195	...	.393	.393	...	−.424	.400	...	−.082	.409	...

NOTE.—Each ANOVA used as input values the specific component of the log snout-vent length or log mass (see table 1) residual trait value, as determined by MRHO 3.5. Least-square means (LS means) are of equal absolute value for the first four traits because of the balanced design of the analysis ($N_{asexual} = 6$, $N_{sexual} = 6$; except EWL $N_{asexual} = 5$; *Cnemidophorus tesselatus* excluded).

TABLE 4

SPECIES-SPECIFIC COMPARISONS OF OBSERVED VERSUS PREDICTED VALUES

	Burst Speed (log m/s)			Endurance (log s)			Maximal Exertion (log m)			Standard Metabolic Rate (log mL O_2/h)			Evaporative Water Loss (log mg H_2O/h)		
Species	Observed	Predicted	Difference	Observed	Predicted	Difference	Observed	Predicted	Difference	Observed	Predicted	Difference	Observed	Predicted	Difference
C. exsanguis	.473	.491	−.018	2.40	2.47	−.08	1.69	1.69	.00	.320	.284	.036	1.347	1.293	.054
C. neomexicanus	.371	.297	.074	2.42	2.56	−.13	1.84	1.81	.03	.208	.227	−.019	1.021	1.104	−.083
C. sonorae	.423	.449	−.026	2.34	2.47	−.13	1.64	1.72	−.07	.260	.292	−.032	1.221	1.242	−.021
C. tesselattus	.372	.454	−.082	2.21	2.49	−.28	1.58	1.74	−.17	.345	.271	.074	. . .	. . .	. . .
C. uniparens	.406	.387	.019	2.28	2.57	−.29	1.71	1.72	−.02	.269	.236	.033	1.235	1.075	.160
Mean			−.007			−.18			−.05			.018			.027
Upper CI			.065			−.06			.05			.072			.194
Lower CI			−.078			−.30			−.14			−.036			−.140
Paired *t*-test *P* value			.82			.01			.26			.40			.64

NOTE.—For each trait, the observed mean value and expected value (based on mean values of parental species and allometrically adjusted) for each asexual species is shown. The third column for each trait is the difference (observed − predicted); negative values thus indicate lower-than-expected trait values. Note that positive values are considered superior for burst speed, endurance, and maximal exertion, while negative values are considered superior for standard metabolic rate and evaporative water loss rate. The mean differences and the 95% confidence intervals (CIs) for the means are below each difference column. The paired *t*-test results are for two-tailed tests comparing observed and predicted values. Explanation for derivation of the expected values is given in the text.

rus, might be expected to have physiological performance superior to closely related sexual species with low heterozygosities. In contrast to the spontaneous heterosis hypothesis, however, I found no indication of extant superiority in asexual *Cnemidophorus* in comparison with sexual species using either of two phylogenetically controlled analyses or a more traditional form of analysis. Of the five integrative organismal traits examined, one (endurance) is clearly lower in asexual species, and there is little indication that any of the remaining traits might demonstrate heterosis. In fact, for three of the four or four of the four remaining traits (depending on the analysis), the directionality of the nonsignificant differences actually argues the opposite. Taken together, the results suggest that, if anything, the trend is for asexual species to have inferior physiological performance relative to sexual species.

One potential concern regarding this study's ability to refute the spontaneous heterosis hypothesis is the relatively small sample size of each species compared with those of many other studies on the effects of heterozygosity (e.g., studies cited in Mitton 1994). However, the conclusions reached may be considered reasonably robust for several reasons. First, most studies examine the effects of heterozygosity within a species, with the range of heterozygosities within a population being quite small. Here, I am comparing the mean values for a large number of species with very different levels of heterozygosity. Second, as noted earlier, the general trend in the traits examined is for asexual species to be inferior to sexual species. Thus it appears unlikely that the failure to find heterotic effects is simply a result of low statistical power. Third, this study examined only naturally existing asexual lineages and so may well have been biased toward hybrid superiority, since the lineages used represent the survivors of what was presumably once a larger set of clones. This bias should, if anything, have favored the corroboration of the heterosis hypothesis.

Given that the results of this study have not fulfilled the predictions of the spontaneous heterosis hypothesis (despite a possible favorable bias), it is worth examining possible reasons for this finding. The first and most obvious potential explanation is that the hypothesis is not generally true. Despite the patterns observed in a variety of studies on heterozygosity (see above), there may be no direct causal connection between an increased variety of allozymes and physiological efficiency or rates. Were there such a functional connection, one would expect a consistent relationship between heterozygosity and various aspects of fitness, such as growth rate and fecundity, in addition to physiological performance. However, a number of recent studies have failed to show any significant link between levels of heterozygosity and size or fecundity traits in Scot pines (Savolainen and Hedrick 1995), between heterozygosity and body size or fluctuating asymmetry in forked fungus beetles (Whitlock 1993), or between heterozygosity and growth rate in *Drosophila melanogaster* (Houle 1989). These results suggest that heterozygosity per se may contribute to fitness or performance only in limited circumstances, such as particularly stressful environments, and perhaps only in certain groups (notably mollusks; Houle 1989) and with certain allozymes.

At least two examinations of the spontaneous heterosis hypothesis itself have

been carried out using the highly heterozygous hemiclonal fish of the genus *Poeciliopsis,* which are all hybridogenetic (i.e., the genome from the maternal parental species is passed to the egg intact every generation, while that from the paternal parent is discarded and replaced when the hybrid mates with males of that same species; Leslie and Vrijenhoek 1978). Work by Bulger and Schultz (1979) showed that naturally occurring hybrids of *Poeciliopsis monacha* and *Poeciliopsis lucida* showed superior tolerance to both heat and cold than either parental species, but lab-produced hybrids did not show a clear trend. A different study (Wetherington et al. 1987), which focused exclusively on lab-produced hybrids, showed that while some hemiclones were as viable and fertile as their parental species, many were actually less fit than the parentals. The results of these studies suggest that heterotic effects are not a necessary result of the high heterozygosity seen in hybrid asexual species.

There may be reasons that extant populations of asexual *Cnemidophorus* (and other asexual species) might fail to display heterotic effects even if a pattern of heterozygote superiority were to be present within closely related sexual populations. In particular, three factors have the potential to cause reduced fitness (physiological or otherwise) in asexual *Cnemidophorus* species: outbreeding depression (i.e. epistatic effects), Muller's ratchet, and polyploidy.

Outbreeding Depression

The hybrid genomes of asexual *Cnemidophorus* consist of haploid chromosome sets from two or three different species, and these species are often not particularly closely related (see fig. 1). Thus, while within each haploid chromosome complement the genes (and their associated products) presumably represent coadapted complexes, the overall genome now consists of genes and gene complexes that have not previously coevolved. The interactions of these mixed genomes have the potential to produce strong epistatic effects; that is, individual alleles, or entire chromosome complements, are likely to interact with their counterparts in nonadditive ways (Dobzhansky and Spassky 1968; Lewontin 1974). For example, Dobzhansky and coworkers' studies on natural populations of *Drosophila pseudoobscura* revealed that, even within species, a particular chromosome can have highly variable effects on viability depending on the population from which the remainder of the genome comes (Dobzhansky and Spassky 1968; Anderson 1969). These epistatic effects tended to be negative when chromosomes were in a ''foreign'' background (Anderson 1969). If such negative effects are sufficiently common in mixed genomes, hybrids will exhibit outbreeding depression; that is, they will have lower fitness than offspring of more closely related individuals.

Unfortunately, the degree of genome differentiation required before hybrids begin to exhibit such negative epistatic effects is not well understood (Shields 1982; Lynch 1991). There is a relatively small body of work on the consequences of outbreeding in nondomesticated animals, and the number of studies on hybridization between subspecies or species is even more limited. One recent review of the literature (Arnold and Hodges 1995) included data on hybrids from 11 animal genera and found that those hybrid lineages more genetically

intermediate to their parental species tended to have inferior trait value relative to lineages more like one parental species or the other (e.g., backcrosses). Thus, the more mixed the genome was, the less fit was the hybrid. Similarly, a review of fitness in laboratory crosses of *Drosophila* species (Coyne and Orr 1989) revealed that inviability and infertility in hybrids increased with the genetic distance of their parents. These patterns suggest that, for at least some hybrids, any potentially beneficial effects of heterozygosity may be obscured by simultaneous deleterious interactions among genes from different specific ancestries.

Muller's Ratchet

Asexual populations are believed to have a tendency to slowly accumulate mildly deleterious mutations, due to the process known as Muller's ratchet (Muller 1964). Thus, even if asexual *Cnemidophorus* species initially exhibited hybrid superiority, this superiority may have decayed through time. With the accumulation of a sufficiently large number of independently small but unfavorable mutations, negative phenotypic consequences might become strongly pronounced in traits that reflect overall physiological performance and efficiency.

Although a number of models exist that attempt to predict the effects of Muller's ratchet (see Kondrashov 1988), their application is limited here by a lack of information on population sizes and the rate of appearance and typical effects of mutations in *Cnemidophorus.* Thus, it may be more useful to consider empirical data on other asexual or partially asexual vertebrate species. In *Poeciliopsis,* some hybridogenetic lineages appear to have accumulated a number of detrimental mutations in the part of their genome that is passed on asexually (Leslie and Vrijenhoek 1978, 1980), which suggests that Muller's ratchet is affecting these species. It should be noted, however, that in these species such mutations are generally sheltered from selection because the ''fresh'' (i.e., paternal species') portion of the genome in each individual provides a working copy of each allele. The effective deleterious mutation rate (i.e., assuming mutations are generally recessive, the rate at which all copies of an allele would have reduced function) is likely to be much lower in diploid than haploid lineages, and lower yet in polyploids. In the caudate genus *Ambystoma,* recent evidence from mitochondrial DNA suggests that some of the clonally reproducing triploid lineages have persisted for about 5 million yr independently of their sexual parental species (Spolsky et al. 1992*a,* 1992*b*). Thus, given the thousands-of-generations age of asexual *Cnemidophorus* species, the ratchet may have had only minor effects on their genomes. This possibility is supported by the fact that the great majority of the allozymes examined in asexual *Cnemidophorus* have exact electrophoretic matches with the allozymes of their parental species (Dessauer and Cole 1989).

Polyploidy

Another characteristic that might have physiological consequences for at least some asexual vertebrate species is polyploidy. Three of the six asexual species examined here are triploid, and it is possible that an increase of 50% or more in the amount of DNA per cell has effects in and of itself on physiological traits. Polyploidy generally results in an increase in average cell size (Szarski 1970,

but see Morris 1984), with a resulting decrease in surface-to-volume ratio. Such changes might well have metabolic consequences for processes that are limited by influxes and effluxes of materials through membranes, and Szarski (1983) has suggested that animals with larger cells should have lower maintenance energy requirements and hence lower standard metabolic rates. Presumably upper limits on metabolic rates might also be limited. However, in the few studies that compare the physiology of sexual polyploid species with that of closely related diploid species, such effects appear to be either extremely minor or nonexistent. The tetraploid frog *Hyla versicolor,* for example, is similar to its diploid ancestor *Hyla chrysoscelis* in standard and active metabolic rates (Kamal et al. 1985), lactic acid levels after forced locomotion (Kamal et al. 1985), and locomotor muscle contractile properties (McLister et al. 1995). These results suggest that a simple increase in the amount of DNA or chromosomes per cell is not likely by itself to result in physiological differences between species.

Conclusion

In summary, there is no evidence for improved physiological performance due to heterozygosity in extant asexual species of *Cnemidophorus;* if anything, these species show performance inferior to that of their sexual progenitors. It is difficult to say, however, whether heterosis may have been present when these species first arose and subsequently lost because of the effects of processes such as Muller's ratchet or it whether it never existed, either because of the counterbalancing effects of outbreeding depression or because heterozygosity does not generally improve physiological efficiency or performance.

The immediate ecological potential of asexual *Cnemidophorus* species does not depend on their evolutionary past, of course, but rather on their current status. If organismal performance really is compromised in these species, they might well have average survival rates lower than those of their sexual counterparts. Other classes of traits could similarly affect survival and fecundity. But asexual species have a twofold reproductive advantage over sexual species, since populations are all female and hence should produce twice as many offspring per capita (Maynard Smith 1978). Such an advantage could outweigh the selective disadvantages of mildly inferior trait values and thus could be the reason that asexual *Cnemidophorus* species have been able to expand their ranges relatively quickly. This reproductive advantage may not be able to sustain these species indefinitely, though, if survival and fecundity decline over evolutionary timescales, as might be expected in asexual populations (Williams 1975; Maynard Smith 1978). Our understanding of the long-term fitness consequences of asexual reproduction is simply too rudimentary, however, to know how realistic these expectations are or to make meaningful predictions about the future prospects of these species.

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APPENDIX A

TABLE A1

GENETIC DISTANCE MATRIX OF *CNEMIDOPHORUS* SPECIES

	Bur	*Exs*	*Ino-A*	*Ino-H*	*Lar*	*Neo*	*Sep*	*Son*	*Tes*	*Tig-G*	*Tig-M*	*Uni*
Bur	.000											
Exs	.242	.000										
Ino-A	1.076	.266	.000									
Ino-H	1.076	.266	.095	.000								
Lar	.393	.14	.394	.394	.000							
Neo	.755	.315	.256	.256	.461	.000						
Sep	.224	.207	.868	.868	.317	.765	.000					
Son	.272	.087	.258	.258	.241	.372	.299	.000				
Tes	.341	.308	.669	.669	.483	.324	.263	.394	.000			
Tig-G	1.019	.972	.874	.874	1.367	.358	1.519	.85	.449	.000		
Tig-M	.772	.706	.899	.899	.936	.254	1.015	.759	.275	.161	.000	
Uni	.223	.064	.198	.198	.238	.273	.303	.093	.295	.769	.668	.000

NOTE.—This matrix was used in the phylogenetic autocorrelation analysis discussed in the text. Values are derived from data in Dessauer and Cole (1989) and Densmore et al. (1989*a*). See legend to figure 1 for the key to abbreviations.

APPENDIX B

TABLE B1

SIMPLE MEANS OF UNTRANSFORMED TRAIT VALUES

TRAIT	SPECIES											
	Bur	*Exs*	*Ino-A*	*Ino-H*	*Lar*	*Neo*	*Sep*	*Son*	*Tes*	*Tig-G*	*Tig-M*	*Uni*
Burst speed (m/s)	3.06	3.01	2.22	1.86	2.86	2.49	2.84	2.74	2.49	2.77	2.58	2.60
Endurance (s)	246	266	528	476	216	279	366	220	162	279	323	198
Maximal exertion (m)	54	51	55	69	57	67	54	42	35	59	58	54
Standard metabolic rate (mL O_2/h)	4.42	2.99	1.15	1.00	2.21	1.64	2.13	2.37	4.00	1.94	3.19	1.57
Evaporative water loss (mg H_2O/h)	36.2	25.6	8.8	7.6	21.3	11.1	26.1	18.0	...	16.8	23.4	16.2
Mass (g)	19.7	12.0	4.4	3.3	8.5	7.3	9.3	10.3	16.4	9.4	16.4	5.6

NOTE.—For each species examined, the means of the raw trait measurements and body mass are given. The trait values used for all analyses in this study were first log-transformed and then adjusted for significant covariates (see Material and Methods). Sample sizes are given in table 1, and abbreviations are as in figure 1.

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