Phenotypic variability of physiological traits in populations of sexual and asexual whiptail lizards (genus *Cnemidophorus*)

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ABSTRACT

One of the major potential disadvantages to asexual reproduction is believed to be a reduction in phenotypic variability. This study represents an empirical test for such a reduction in the variance of physiological traits in parthenogenetic species of the lizard genus *Cnemidophorus*. Five performance traits (burst speed, endurance, maximal exertion, standard metabolic rate and evaporative water loss rate) were examined in four asexual species and the sexual species that hybridized to produce them. A phylogenetically controlled analysis revealed less trait variance in asexual species for the first three traits, but no detectable differences between asexual and sexual species for the other two traits. A second analysis examining the average shape of trait distributions in the two types of species suggests that sexual populations produce distributions with more elongate tails than do asexual populations. Thus, part of the reason for increased variance in sexual populations may be a greater tendency for these populations to produce extreme phenotypes.

Keywords: asexuality, *Cnemidophorus*, genetic variability, locomotion, metabolic rate, phenotypic variability.

INTRODUCTION

The possibility that asexual groups will have lower phenotypic variability than otherwise similar sexual groups is viewed as a major potential disadvantage of asexual reproduction, largely because greater variation in populations may be useful in environments that vary in space or time (Ghiselin, 1974; Williams, 1975; Maynard Smith, 1978; Bell, 1982). For example, if different microhabitats or resources are available to the offspring of an individual, increased phenotypic diversity should allow them to utilize these differences more effectively. This will increase the overall fitness of the progeny and, by extension, the population as a whole. Similar arguments apply if the environment varies in time, especially if this

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variation is unpredictable, since individuals with phenotypically variable offspring are more likely to leave at least some survivors every generation (Williams, 1975). An extreme example of this stochastic environment model involves relatively rare environmental events that result in very strong selection for exceptional phenotypes (Grant and Grant, 1989; see also Williams, 1975, and references therein).

These arguments require, of course, that asexual species actually exhibit reduced phenotypic variation. Asexual (i.e. apomictic) populations do typically possess less genetic variability than do sexual populations. Among vertebrates, for example, some asexual species of the lizard genus *Cnemidophorus* show little or no detectable genetic variation within populations and, in at least one case, an entire species appears to consist of a single clonal lineage (Parker and Selander, 1984; Cole *et al.*, 1988; Dessauer and Cole, 1989). Although available evidence on heritabilities (a measure of the genetic contribution to trait values) from sexual populations (Mousseau and Roff, 1987) suggests that reduced genetic variation should decrease phenotypic diversity for many traits, relatively few studies have examined the patterns of variability in closely related sexual and asexual animals. Those that have focused almost exclusively on size and meristic characters (e.g. Atchley, 1977; Vrijenhoek, 1984).

The aim of this study is to investigate the issue of phenotypic variability for a group of closely related vertebrates, the parthenogenetic and related sexual species of the lizard genus *Cnemidophorus*, using a previously unexamined class of traits. Specifically, I examine the variability of five physiological performance traits in these species. These analyses extend an examination of the fitness implications of reproduction mode in these species presented in Cullum (1997). That study, which focused on the specific means of these performance traits, provided evidence that asexual *Cnemidophorus* species on average show inferior physiological performance relative to their sexual relatives. While those findings provide one argument that these asexual populations will show lower average fitness than their sexual counterparts, the work presented here uses the same data to examine a second possible fitness consequence of asexual reproduction in these species, namely that phenotypic variability will be reduced.

Study system

A brief description of the species and traits examined in this study is provided here. Additional details are presented in Cullum (1997).

The lizard genus *Cnemidophorus* (family Teiidae) consists of both sexual and asexual species, with the origin of the asexuals attributed to hybridization between different sexual species in the genus (Dessauer and Cole, 1989; Fig. 1). Both diploid and triploid asexual species occur, the latter resulting from secondary hybridizations. The asexual species are all-female and reproduce via parthenogenesis (for references, see Vrijenhoek *et al.*, 1989), so all offspring are females genetically identical to their mothers (except for *de novo* mutations). As a result, populations of these species tend to have extremely low genetic diversity.

Four asexual species (*C. exsanguis*, *C. neomexicanus*, *C. uniparens* and *C. laredoensis*) and six sexual species or sub-species of *Cnemidophorus* were examined in this study. The six sexual taxa included all the parental species of the first three asexual species. These nine species (i.e. all but *C. laredoensis*), and the phylogenetic relationships among them, are shown in Fig. 1. The low genetic diversity of the four asexual species studied, relative to
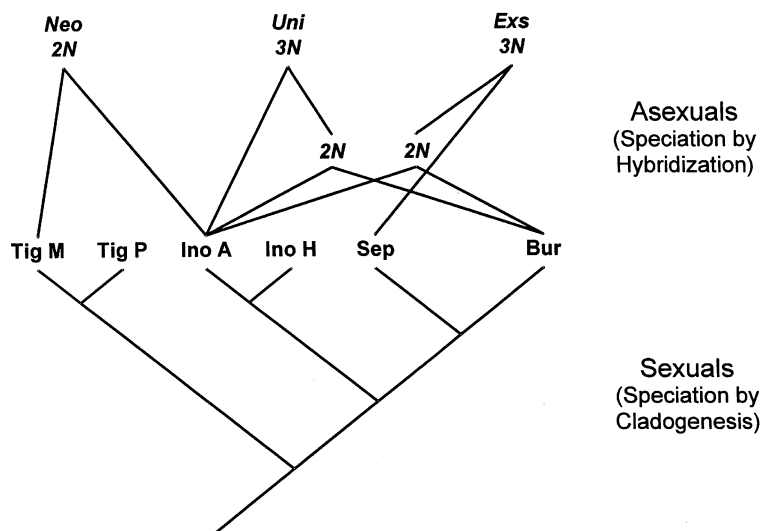
Fig. 1. *Cnemidophorus* phylogeny. The hypothesized phylogeny of *Cnemidophorus* species examined in this study (the asexual *C. laredoensis*, for which the parental species were not examined, is not shown). Asexual species are shown in italics. The tree is intended only to show relationships among species, not the time of particular speciation events; all named species are still extant. While the sexual group shows a typical bifurcating pattern resulting from speciation via cladogenesis, the appearance of the asexual species exhibits a reticulate pattern, as these species arose from hybridization between sexual species. 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 are as follows: Neo = *C. neomexicanus*; Tes = *C. tesselatus* Clone E; Uni = *C. uniparens*; Son = *C. sonorae*; Exs = *C. exsanguis*; Tig M = *C. tigris marmoratus*; Tig P = *C. tigris puntilinealis* (previously *C. tigris gracilis*; see Taylor and Walker, 1996); Ino A = *C. inornatus arizonae*; Ino H = *C. inornatus heptagrammus*; Sep = *C. septemvittatus*; Gul = *C. gularis*; Bur = *C. burti stictogrammus*. Sexual species phylogeny based on Moritz *et al.* (1989b), Densmore *et al.* (1989) and Dessauer and Cole (1989). Asexual species phylogeny based on Dessauer and Cole (1989) and Good and Wright (1984).

their sexual counterparts, has previously been demonstrated by three types of evidence: allozyme diversity (Parker and Selander, 1984; Cole *et al.*, 1988; Dessauer and Cole, 1989), mitochondrial DNA (mtDNA) diversity (Moritz *et al.*, 1989a, 1992) and histocompatibility studies involving reciprocal skin grafts (Cuellar, 1976, 1977).

I examined five whole-organism performance traits that are probably important in the interactions of these lizards with their biotic and abiotic environments (Huey and Stevenson, 1979; Bennett, 1989). The first three are complementary locomotor performance characters: burst speed, endurance and maximal exertion. This combination of traits is useful for study in that each is thought to represent different physiological limitations on performance (Bennett, 1989). The other two traits examined are standard metabolic rate and evaporative water loss, both of which are likely to have fitness consequences in the energy- and water-limited habitats *Cnemidophorus* typically inhabit. Although the heritability of none of these traits is known for any teiids, moderate heritability (and hence genetic variability) has been observed for similar traits in other sexual squamates

(Van Berkum and Tsuji, 1987; Garland, 1988; Tsuji *et al.*, 1989; Sorci *et al.*, 1995). Populations of asexual *Cnemidophorus*, exhibiting minimal genetic variation, should be expected to show markedly less phenotypic variation than their sexual relations.

METHODS AND MATERIALS

Collection and measurement of animals

Detailed descriptions of animal capture and husbandry, and of measurement of the five traits studied, are provided in Cullum (1997). Briefly, all population samples in this study were collected in very localized areas of the Chihuahuan and Sonoran deserts during the summers of 1992–94 (see Appendix for details). I measured performance using established methods (e.g. Bennett, 1989; Tsuji *et al.*, 1989; Garland, 1993, 1994), and followed a set protocol to minimize extraneous variation. Locomotor traits were measured one per day within the first 5 days after capture, and standard metabolic rate and evaporative water loss were measured subsequently on fasting animals between 22.00 and 04.00 h. The numbers of individuals of each species measured for each trait are shown in Table 1.

Analyses

Only female animals were considered in this study. All traits except burst speed were log-transformed to improve the normality of the population samples. Statistical analyses were carried out using SYSTAT for Windows 5.04 (SYSTAT Inc., Evanston, IL) or statistical functions in Microsoft Excel 97 (Microsoft Corp., Redmond, WA) and the associated Analysis ToolPak (GreyMatter International, Inc., Cambridge, MA).

The major test of patterns of relative variability examines the overall variance (i.e. s^2) of each population. In addition, I examined the possibility that sample distributions show different shapes in sexual and asexual populations. These analyses are detailed below. Since the active hypothesis predicts that asexual species will show less trait variation than sexual species, I decided *a priori* to use one-tailed tests of significance when possible in my analyses.

Phylogenetic comparisons of overall variation

The hypothesized phylogeny of the *Cnemidophorus* species used in this study is shown in Fig. 1. The reticulate (i.e. branch joining) pattern of speciation cannot be accommodated by most commonly used methods of phylogenetically corrected analysis (Felsenstein, 1985; others reviewed in Garland *et al.*, 1993), since these methods deal only with cladogenesis (i.e. diversification of phylogenetic branches). I therefore developed an approach that involves direct comparisons between each asexual species and the sexual species that hybridized to form it (Cullum, 1997). For each trait of each asexual species, a predicted variance was generated by averaging the values of the appropriate parental species. If the reduced genetic variation in the asexual species does tend to reduce phenotypic variance, then the asexuals should on average exhibit lower trait variances than predicted; I tested for such a difference by comparing observed and predicted variances using a one-tailed *t*-test for each trait (a paired *t*-test providing relatively little power with d.f. = 2). The asexual *C. laredoensis* was not included in this analysis, since data were lacking for its parental species.

Table 1. Sample size and intraspecific covariates

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

Note: For each trait, the sample size for each species or sub-species is shown, together with the covariate(s) used, if any, in generating corrected trait values before computation of variances.
* Abbreviations are as in Fig. 1, plus Lar = *C. laredoensis*.

The rationale for using a simple average of the parental variances to generate predicted variances for the asexual populations is as follows. The phenotypic variability of a population, V_P, may be influenced by genotypes both through the explicit genetic component of population variance, V_G (Falconer, 1989), and by the fact that different genotypes may differentially respond to environmental variation, and hence may influence the environmentally induced variance, V_E (Scheiner, 1993; Via *et al.*, 1995). Unfortunately, relatively little is known about the exact genetic basis of V_P or V_E for any traits (Barton and Turelli, 1989; Scheiner, 1993; Via *et al.*, 1995). It is likely, however, that a fairly large number of loci affect both V_G and V_E for all the traits studied here, so a reasonable first approximation for the expected results of crossing different genomes is that the effects of each genome will be additive (Barton and Turelli, 1989). I therefore use an additive model to estimate the predicted (i.e. null model) V_P from crossing sexual species. Because each parental species contributes equally (one haploid genome) to the diploid or triploid genome of an asexual species, the predicted variance is the arithmetic mean of the variance of the appropriate parental species.

Two other types of analyses were also used to compare population variances in sexual and asexual species. The first of these was another phylogenetically based approach, the phylogenetic autocorrelation method of Cheverud *et al.* (1985). Details of this method as applied here are provided in Cullum (1997). The second additional form of analysis used to address the issue of relative variance was a simple comparison of all sexual and asexual species that ignored phylogeny. Both the phylogenetic autocorrelation and phylogenetically uncontrolled comparisons were made on a trait-by-trait basis using one-tailed *t*-tests.

Patterns of trait distributions in sexual and asexual populations

The variance of a population can be strongly affected by one or more extreme data points. Relatively high variances might, therefore, reflect one or two exceptional values in a population rather than a general pattern of increased variability. Sexual populations, through the occasional appearance of individuals with unlikely gene combinations, may be more likely to produce such extreme phenotypes. If so, their trait distributions should show different shapes, and more specifically relatively elongate tails, in comparison to asexual populations.

As one approach to examining the relative shape of sexual and asexual sample distributions, I used a standard measure of this shape, kurtosis (Sokal and Rohlf, 1981). Populations with an excess of extreme values will tend to show sample distributions with positive values for kurtosis (leptokurtosis). To test for the presence of a relatively greater number of exceptional phenotypes in sexual populations, the kurtosis values for all 50 sample distributions used in this study were calculated according to the equations in Sokal and Rohlf (1981) and the average kurtosis values of sexual and asexual populations (all traits combined) were compared using a one-tailed *t*-test.

The more specific hypothesis, that any differences in distribution shape are driven by the most extreme phenotypes, was tested using the ranges of the samples. If a distribution has relatively long tails, its range will be greater than expected, given its standard deviation; the opposite is also true. To test this, I calculated a 'range deviate' for each sample distribution as the standardized observed range minus the expected range for a normal sample of the same size (Rohlf and Sokal, 1981, table 26). A range deviate greater than zero indicates that

the tips of the distribution tails are more elongate than expected. Hypothesis testing using these values was then carried out as above.

Analyses of covariates and correlated factors

Because the variance of a population may potentially be influenced by a number of extraneous factors, several preliminary analyses were undertaken before the main analyses outlined above. First, because traits measured in this study might be influenced by factors such as body size, number of days in captivity, and so on, I tested potential covariates for significant effects within species using analysis of covariance as detailed in Cullum (1997). The effects of any significant covariate were then corrected for by calculating population variances from residual trait values.

Second, I considered the possibility that populations with higher mean values for a particular trait would have higher variances as well; in other words, variances may be positively correlated with means. If this is the case, two calculations for reducing the correlation might be used: either coefficients of variation (CV = [standard deviation × 100]/mean) or empirically derived residual variances. In the latter case, variances are regressed on means with a binary independent variable included to control for hypothesized differences in variances between species types (sexual or asexual). The relative utility of each method depends on the particular pattern of the correlation; this point will be addressed in the Results section.

Analysis of correlations among traits. If traits are strongly correlated, then any pattern observed for one trait cannot be considered independent of that observed for another. To test the possibility that any such correlations caused variances to covary across traits, I generated a residual variance (or CV in the case of log endurance) for each species and trait. These residual values were generated by subtracting the mean sexual or asexual variance (as appropriate) from each species variance; this method controlled for any influence of species type on variance. Pearson correlation coefficients were then calculated using these variance residuals.

RESULTS

Means and variances of raw data values for each species and trait are shown in Table 2.

Analyses of covariates and correlated factors

Intraspecific covariates. All traits except endurance were significantly influenced by at least one confounding variable at the intraspecific level (Table 1). Consequently, analyses of the data sets used values corrected for the effects of these covariates.

Mean–variance correlations. Regressing variances of species on covariate-adjusted means (while controlling for species type) revealed a significant dependence of variances on means only for log endurance (Table 2). The remaining four traits show no indication of any relationship between means and variances (but note that log transformations can eliminate such a relationship in many cases; Sokal and Rohlf, 1981).

The correlation seen for endurance suggests the need in this case to adjust each species' variance for its mean value. Although regression might normally be considered to describe

Table 2. Trait means and variances for each species

Species	Burst speed (m · s⁻¹) Mean	Variance	Log endurance (s) Mean	Variance	Log max. exertion (m) Mean	Variance	Log SMR (ml O₂ · h⁻¹) Mean	Variance	Log EWL (mg H₂O · h⁻¹) Mean	Variance
Asexual										
C. exsanguis	3.006	0.185	2.395	0.0297	1.690	0.0098	0.320	0.00297	1.347	0.0160
C. laredoensis	3.105	0.027	2.317	0.0169	1.749	0.0016	0.455	0.00140	1.308	0.0136
C. neomexicanus	2.370	0.135	2.423	0.0206	1.840	0.0087	0.208	0.00285	1.021	0.0151
C. uniparens	2.570	0.082	2.280	0.0153	1.705	0.0103	0.269	0.00269	1.235	0.0187
Sexual										
C. burti	3.258	0.332	2.372	0.0180	1.711	0.0057	0.347	0.00376	1.406	0.0169
C. i. arizonae	2.305	0.150	2.636	0.0853	1.712	0.0175	0.202	0.00245	0.987	0.0342
C. i. heptagrammus	1.712	0.171	2.611	0.0599	1.830	0.0105	0.208	0.00479	0.968	0.0099
C. septemvittatus	3.127	0.173	2.525	0.0328	1.726	0.0099	0.256	0.00227	1.322	0.0134
C. t. marmoratus	2.378	0.193	2.494	0.0163	1.782	0.0137	0.248	0.00160	1.243	0.0157
C. t. punctilinealis	2.647	0.084	2.431	0.0141	1.755	0.0075	0.209	0.00164	1.196	0.0084
Mean–variance regression P-value*	0.44		0.005		0.86		0.63		0.51	
Ratio of mean variances (Asexual : Sexual)	0.58		0.84		0.70		0.90		0.97	

Note: Means and variances are based on covariate-adjusted trait values. SMR = standard metabolic rate, EWL = evaporative water loss.
* The value shown for each trait is the significance of the regression of variance on mean, with possible differences in sexual and asexual species included in the model.

Table 3. Correlations between variances of traits

Trait	Log endurance (CV)	Log max. exertion	Log SMR	Log EWL
Burst speed	−0.030	0.002	0.546	0.107
Log endurance (CV)		0.558	0.418	0.600
Log max. exertion			0.042	0.666*
Log SMR				−0.063

Note: The values shown are Pearson correlation coefficients calculated using variance residuals for each species (see Methods and Materials).
Significant values are marked with an asterisk. SMR = standard metabolic rate, EWL = evaporative water loss.

most accurately the relationship between these two values, this was not the case here. The derived slope and intercepts are unrealistic, predicting that a sexual species with a mean endurance as low as that of some asexual species should have a negative variance. I therefore used coefficients of variation as a compromise between ignoring mean–variance scaling and using the biologically impossible scaling derived from the observed values.

Correlations among traits. The correlation coefficients among trait variances are shown in Table 3. Only one of the 10 correlation coefficients is significant, and the two traits (log maximal exertion and log evaporative water loss) are unlikely to be functionally (i.e. physiologically) related; in addition, the patterns of observed versus predicted variances for the three asexual species do not appear similar for the two traits (Table 4). Thus, this significant correlation is unlikely to have biased the overall pattern of results observed.

Comparative analyses

Comparisons of overall variation

The observed and predicted (see Methods and Materials) values of variance for each trait and asexual species are presented in Table 4. The three locomotor traits showed a strong trend towards lower variance in the asexual species, relative to their parental species. Endurance and maximal exertion showed significant differences between observed and predicted values, and burst speed nearly so. (Note that, for burst speed, there is a large confidence interval on the overall asexual variance due to an especially low value for *C. uniparens*.) On average, these traits had variances 26% lower than predicted. This value is in accord with expectations based on observed heritabilities of similar traits (Van Berkum and Tsuji, 1987; Garland, 1988; Tsuji *et al*., 1989; Sorci *et al*., 1995). Standard metabolic rate and evaporative water loss also averaged lower observed than predicted values, but these differences were not significant, with the ratio of observed to predicted variances for these two traits averaging 0.91. In total, 13 of 15 comparisons between predicted and observed values revealed lower than expected variances in the asexual species.

The other two methods of analysis, phenotypic autocorrelation and phylogenetically uncontrolled, gave results qualitatively similar to those above. In the autocorrelation analysis, differences in phylogenetically corrected variances (i.e. the specific residuals) between sexual and asexual species showed borderline significance for burst speed ($P = 0.052$) and endurance ($P = 0.085$), while the difference for maximal exertion was

Table 4. Comparisons of observed versus predicted variances for three species of asexual *Cnemidophorus**

Species	Burst speed (raw variances)			Log endurance (coefficients of variation)			Log max. exertion (raw variances)			Log SMR (raw variances)			Log EWL (raw variances)		
	Obs.	Pred.	Ratio	Obs.	Pred.	Ratio	Obs.	Pred.	Ratio	Obs.	Pred.	Ratio	Obs.	Pred.	Ratio
C. exsanguis	0.185	0.218	0.85	7.20	7.97	0.90	0.0098	0.0110	0.88	0.00297	0.00283	1.05	0.0160	0.0215	0.74
C. neomexicanus	0.135	0.182	0.74	5.93	7.25	0.82	0.0087	0.0121	0.71	0.00285	0.00320	0.89	0.0151	0.0128	1.18
C. uniparens	0.082	0.211	0.39	5.43	9.27	0.59	0.0103	0.0136	0.76	0.00269	0.00289	0.93	0.0187	0.0284	0.66
Mean	0.204	0.134	0.66	6.19	8.16	0.77	0.0096	0.0122	0.79	0.00284	0.00297	0.96	0.0166	0.0209	0.86
t-test P-value (one-tailed)*	0.058			0.034			0.019			0.20			0.22		

Note: For each trait, the observed variance and predicted variance (calculated as the average variance of the parental species) is shown for the three asexual species with complete parental data. The third column under each trait is the ratio of observed to predicted; values less than 1.0 indicate lower than expected variances.
* Results are for one-tailed *t*-tests comparing observed to predicted values, with the hypothesis that observed values are less than predicted values.

non-significant $(P = 0.13)$. For standard metabolic rate and evaporative water loss, phylogenetically corrected variances were very similar for sexual and asexual species. The non-phylogenetic analysis showed the same trends as the autocorrelation analysis, but only burst speed showed borderline significance $(P = 0.08)$. Ratios of average asexual to sexual variance for the non-phylogenetic analysis are shown in Table 2.

Patterns of trait distributions in sexual and asexual populations

The analysis of kurtosis provided support for the hypothesis that sexual and asexual species differ in the average shape of their trait distributions. Sexual species showed a mean kurtosis value of 0.55 (slightly leptokurtic), compared with –0.13 (slightly platykurtic) for the asexual species (one-tailed heteroscedastic *t*-test of all sample distributions: $t_{48} = 1.74$, $P = 0.044$). Note that unadjusted variances, rather than coefficients of variation, were used for log endurance in this analysis.

The comparison of standardized ranges between sexual and asexual species supported the more specific hypothesis that the tails of sexual species' distributions are more elongate than those of asexual species. Standardized range deviates were significantly greater in sexual than asexual populations when averaged across all traits (sexual mean = 0.19, asexual mean = –0.09; one-tailed *t*-test: $t_{48} = 2.31$, $P = 0.013$).

DISCUSSION

The hypothesis that the highly reduced genetic variability of asexual *Cnemidophorus*, relative to sexual species, would result in decreased phenotypic variability was supported for the five physiological performance traits examined here. All traits showed lower than expected variance, on average, in the three asexual species examined using phylogenetically controlled methods. These differences were significant (or nearly so) for the three loco-motor traits. A separate analysis suggests that differences in variability between sexual and asexual populations are due, at least in part, to the presence of more extreme phenotypes in the former.

Only two previous studies have addressed explicitly the question of relative variability in asexual versus sexual *Cnemidophorus*. Parker (1979) examined a number of scale and tooth counts and several metric characters in the asexual *C. tesselatus* and one of its parental species, *C. tigris*. He found that the meristic traits were less variable in the asexuals, while variability in size traits did not differ between the two species. Case (1990) examined diets in *C. tigris* and the asexual *C. sonorae* (which is not a descendant of *C. tigris*) and found less variation among individuals in the latter, but was uncertain as to the generality of his findings. Taken in combination, however, the results of Parker (1979), Case (1990) and the present study provide strong evidence that a broad variety of traits show reduced variability in asexual *Cnemidophorus* species. Thus if the long-term viability of populations is partly dependent on the amount of variability in these populations, or on the presence of extreme phenotypes during severe environmental conditions, sexual species of *Cnemidophorus* should fare better than asexual ones.

A potentially interesting finding of the present study is that the average ratio of observed to predicted variances is much higher for the physiological efficiency traits – standard metabolic rate and evaporative water loss – than for the locomotor traits (ratios of 0.91 and 0.74, respectively). There are three general reasons why sexual and asexual species might

show similar phenotypic variation for some traits. The first of these is that intra-individual variation simply may be higher in some traits than others, to the degree that the relative contribution of inter-individual variation (the variable of interest here) to total sample variation becomes relatively unimportant.

The second reason why phenotypic variation might be similar in sexual and asexual populations is that the latter may have an increased environmentally induced component to variation. Several authors have proposed that clonal populations might be phenotypically plastic (see Lynch, 1984, and references therein), with a population's genotype expressing different, adaptive phenotypes under different conditions. Alternatively, strong environmental contributions to the variability of asexual populations might reflect lower developmental stability in these species. The latter possibility might be tested in *Cnemidophorus* by assaying fluctuating asymmetry in asexual versus sexual species of the genus.

Finally, both types of species might exhibit similar phenotypic variation in some traits if sexual populations have relatively low genetic variation. This could occur if sexual populations were inbred (Falconer, 1989), or in the case of traits that are closely related to fitness (Mousseau and Roff, 1987; Falconer, 1989). Arguing against the former possibility in the case of *Cnemidophorus* are the moderate levels of heterozygosity in these species (about 5% of loci are heterozygous; Dessauer and Cole, 1989) and the large, continuous habitats of the populations studied here. The latter possibility is somewhat more compelling, however. In his study of *C. tesselatus* and *C. tigris*, Parker (1979) found that meristic characters, most of which are probably not strongly related to fitness, generally showed lower phenotypic variability in the asexual species, while metric traits, which are more likely to affect fitness, were equally variable in the two species. Parker (1979) reasoned that size traits were likely to be less genetically variable in the sexual species due to their greater impact on fitness. Perhaps the similarity in phenotypic variation between sexual and asexual *Cnemidophorus* populations in the case of standard metabolic rate and evaporative water loss reflects stronger selection on these traits than on the locomotor traits.

In conclusion, the results of the present analysis and those of Cullum (1997), Parker (1979) and Case (1990) suggest that asexual species of *Cnemidophorus* suffer a dual disadvantage compared with their sexual relations: on average, their physiological performance is inferior to that of sexual species (Cullum, 1997) and many traits also exhibit reduced phenotypic variability. In combination, these trends suggest that asexual *Cnemidophorus* may have lower average fitness than members of sexual species. The persistence of these species thus may depend on the two-fold reproductive advantage all-female populations possess relative to their bisexual counterparts (Maynard Smith, 1978; Paulissen *et al*., 1992).

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APPENDIX: COLLECTION DATES AND LOCALITIES FOR *CNEMIDOPHORUS* TAXA

Taxon	Collection dates	Collection locality	Type
C. burti	12 July–11 August 1993, 14 June–31 July 1994	Guadalupe Canyon, Hidalgo Co., NM (collected by B. Tomberlin)	Sexual
C. exsanguis	9 July–4 August 1993	Southwestern Research Station, 8 km southwest of Portal, Cochise Co., AZ	Asexual
C. inornatus arizonae	17–27 July 1993	Near Arizona 186, 6.2 km from junction with Business I-10 (Willcox). Willcox Playa, Cochise Co., AZ	Sexual
C. inornatus heptagrammus	2–13 August 1992	Junction of frontage road east of I-25 (NM 157) and College Ranch Road, 5.8 km north of I-25's Radium Springs exit. College Ranch, Doña Ana Co., NM	Sexual
C. laredoensis	12–15 June 1994	10 km north of La Joya, Hidalgo Co., TX (collected by M. Paulissen)	Asexual
C. neomexicanus	2–13 August 1992	Junction of frontage road east of I-25 (NM 157) and College Ranch Road, 5.8 km north of I-25's Radium Springs exit. College Ranch, Doña Ana, Co., NM	Asexual
C. septemvittatus	30 June–4 July 1994	Near Terlingua Ranch office, on Terlingua Ranch Road, 29 km east of Texas 118, Brewster Co., TX	Sexual
C. tigris punctilinealis	25 July–9 August 1993	0.8 km west of NM 80 on dirt road 2.6 km north of Cienega Ranch. Hidalgo Co., NM	Sexual
C. tigris marmoratus	2–12 August 1992	Along frontage road east of I-25 (NM 157), 2.0 km north of I-25's Radium Springs exit. College Ranch, Doña Ana Co., NM	Sexual
C. uniparens	20 July–4 August 1993	0.5 km west of NM 80 on Portal Road (NM 533). Hidalgo Co., NM	Asexual