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Reproductive Strategies in Sympatric Whiptail Lizards (*Cnemidophorus*): Two Parthenogenetic and Three Bisexual Species

JOSEPH J. SCHALL

Reproductive characteristics in five sympatric *Cnemidophorus* species were similar. All were multi-brooded with small clutches and low clutch weight/body weight ratios, an estimate of reproductive effort (RE). Interspecific differences in mean clutch sizes and egg weights are attributed partially to female body size differences. RE varies interspecifically perhaps as a result of differential habitat productivity. Intraspecifically, clutch size but not RE was positively correlated with body size. Intra-specific RE variation patterns differ among species. Egg weight-body weight correlation was not significant for the four larger species; however, egg weight was positively correlated with body weight in the smallest species. Smaller species also produced relatively larger eggs. A minimum egg size in *Cnemidophorus* is suggested. Whiptail RE's are difficult to measure because important costs such as courtship, mating, carrying eggs and locating suitable nest sites are not easily quantified.

The reproductive cycle is similar in all species. Males emerge from brumation with enlarged testes which decrease in volume throughout the summer. Females emerge with yolked follicles. Fat bodies are small in in both sexes early in the season, continue to drop during the summer, and rebuild after reproduction ceases. Males possess femoral "pegs" most commonly during the reproductive season.

No difference between bisexual and parthenogenetic species was observed. Unisexual species may simply resemble one of their bisexual parental species. *Cnemidophorus* reproductive characteristics depend on their body size and ecological position as fast moving, widely foraging species. Such factors could overshadow differential selection operating on the reproductive characteristics of "weedy" parthenogenetic and "non-weedy" bisexual species.

THE whiptail lizards (*Cnemidophorus*) are a taxonomically diversified group (about 40 species) which achieves highest species density in southwestern United States and northern Mexico. Maslin (1962) confirmed the existence of parthenogenetic populations within the genus. A high proportion (~30%) of *Cnemidophorus* species are known now only from females and are assumed parthenogenetic (Cole, 1975).

Wright and Lowe (1968) proposed a synthetic hypothesis to account for the evolution and distribution of parthenogenetic species in the United States. Their proposal, termed the "weed hypothesis," states that unisexual whiptails are adapted to disturbed, ecotonal, or unstable zones not optimal for sympatric bisexual species and are thus animal "weeds" analogous to plant weeds found primarily in such disturbed areas (Baker, 1974).

If unisexual species are animal weeds in the established meaning of the term, they should possess relatively *r*-selected (Pianka, 1970) reproductive traits compared to sympatric bisexual forms. For example, relative to the bisexual species their reproductive effort (RE, the fraction of assimilated resources devoted to reproduction) should be higher, clutch size larger, egg size and expenditure of RE per progeny lower. Also, unisexuals should reach sexual maturity faster than bisexual species. Characteristics of *r*-selected populations may not be expressed if other ecological or evolutionary factors intervene. Here I present data on reproductive characteristics of five whiptail species, including two parthenogenetic species. For a more generalized understanding of whiptail reproduction I include a brief summary of male reproductive patterns.

METHODS

In southwestern Texas six *Cnemidophorus* species are sympatric, with four occasionally ecologically sympatric (syntopic). I studied the ecology of five of these species: *C. exsanguis* and *C. tessellatus* (parthenogenetic) and *C. tigris*, *C. inornatus* and *C. gularis* (bisexual). The ecology and local distribution of these species has been discussed elsewhere (Schall, 1976, 1977). Some populations, at least, of *C. exsanguis* are thought to be descendants of *C. gularis* × *C. sp.* (perhaps *C. inornatus*) hybrids (Cole, 1975). *Cnemidophorus tessellatus* appears to have resulted from a cross or crosses between *C. tigris* and *C. septemvittatus* (Neaves, 1969). The latter species is the sixth form found in southwestern Texas and is confined in the United States to relictual highland populations.

Study areas were restricted to Brewster, Culberson, Jeff Davis, Pecos, Presidio and Reeves counties, Texas, within a range of about 2° longitude and 3° latitude, holding potential geographical variation in reproductive strategies to a minimum.

During May to August, 1973–1974 2,500 whiptails were observed and approximately 1,200 were collected and weighed at once with a Pesola spring scale to the nearest 0.1 gm. A slit was made in the venter and any oviducal eggs were removed, counted, measured, and the clutch weighed with a 0–5 gm Pesola scale to the nearest 0.1 gm.

In the laboratory preserved specimens were sexed and snout-vent lengths (SVL) measured to the nearest mm. Full stomachs were extracted and their volume determined by water displacement in a 10 cc graduated cylinder. Volume of testes was determined by water displacement in a 1 cc tuberculin syringe calibrated in 0.01 cc gradations. Testis size is assumed correlated with production of sperm. Maximum length and width of left postcoelomic fat body were measured with a vernier caliper and relative size estimated as the product of these two measurements divided by SVL. Presence or absence of waxy secretion (pegs) from femoral pores of males was recorded.

Number of yolked follicles over 3 mm in diameter and/or oviducal eggs in females was recorded. Clutch size estimates based on counts of yolked follicles over 3 mm in size were very similar to those determined from oviducal eggs. Preserved female specimens and their clutches were reweighed, allowing comparison between fresh material and specimens preserved for 12–18 months.

Definitions of reproductive effort vary and the determination of this reproductive characteristic is controversial. I determined an estimate of reproductive effort as the ratio of the weight of the oviducal clutch from a fresh specimen to that of the freshly caught female with her clutch. This is at best a crude estimate of RE (see “Discussion” below). A related measure, expenditure of effort per progeny, was estimated as mean weight of an egg in a clutch divided by body weight without the clutch.

RE can vary intraspecifically in several ways: egg and clutch size can vary within size classes or both could be constant for a range of body sizes. The relative importance of factors controlling variation in intraspecific RE was studied by simple correlations between RE and clutch size, egg size, and body weight as well as step-wise regression, with RE as the dependent variable, which ranked other variables in order of their contribution to reduction of residual sums of squares.

Live animals collected during 1974 and 1975 were housed in large seminatural indoor pens. Animals carrying oviducal eggs were isolated in small tanks where newly laid eggs could be weighted and measured.

RESULTS

Male reproduction.—Male whiptails appear to emerge from brumation (= winter inactivity in reptiles) with enlarged testes (Fig. 1). I began fieldwork each year 1–3 weeks after animals first appeared (communication from local residents). Testis size decreased throughout the summer (Kruskal-Wallis “*H*” test for differences between means for two-week periods: P 's < .001). Fat body size also varied over the season (*H* test, P 's < .001), first dropping, then increasing until late summer when fat tissue filled most of the posterior part of the body cavity.

Male fat bodies are assumed to be a source of energy during brumation (Gaffney and Fitzpatrick, 1973). Data presented in Fig. 1 show male *C. tigris* and *C. gularis* continue to lose fat volume when their testes are at peak size, suggesting that males use this extra energy source for sperm production and courtship activities. Male courtship behavior was observed only early in the season (May and early June).

Male *Cnemidophorus* commonly have femoral pegs and the frequency of their occurrence is highest during the period of largest testis size. For example, 100% of male *C. gularis* have femoral pegs in May; the frequency

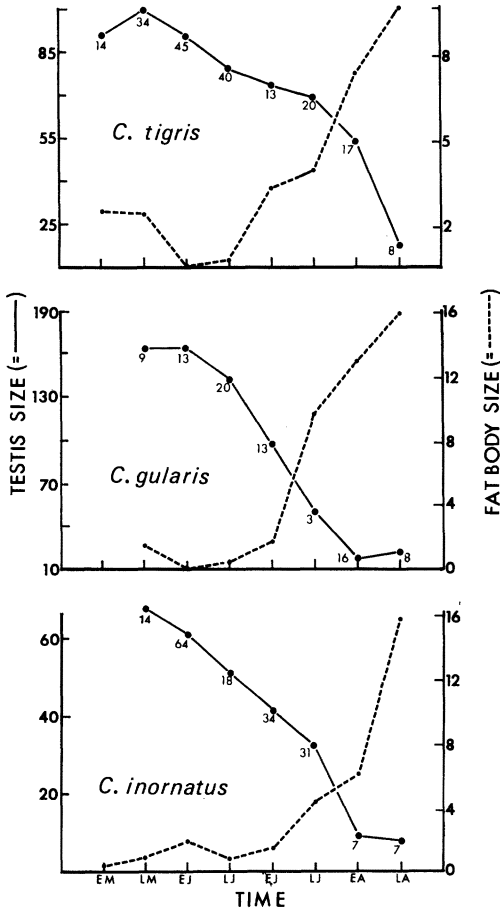


Fig. 1. Mean testis volume and mean fat body size by date for three whiptail species. Testis volume is the sum of both testes' volume divided by SVL. Numbers on left abscissa are $\times 10^{-5}$. Fat body size was determined as product of length and width divided by SVL. Numbers on right abscissa are $\times 10^{-1}$. Time scale ranges from early May (EM) to late August (LA) in half month periods. Numbers by data points are sample sizes for each time period for both testis and fat body sample.

drops continuously until only 17% have them in August. The purpose of these structures is obscure but probably they play a role in courtship and species recognition (Cole, 1966).

Female reproduction.—Adult females probably emerge from brumation with yolked follicles. Adult females collected in early May had yolked follicles and by mid May animals with oviducal eggs were common. Animals with yolked ova or eggs were found throughout the summer and, except for the first clutch, no synchrony of egg production was obvious. The

date when yolked follicles or eggs were no longer observed varied among species: *C. gularis* at 11 July, *C. exsanguis* and *C. tessellatus* at about 22 July, *C. inornatus* at 6 August and *C. tigris* at 10 August. Length of reproductive season among species thus varied about one month. Each species' reproduction ended at remarkably similar times during both summers.

Fat bodies are known to play an important role in female lizard reproduction (Hahn and Tinkle, 1964). Percent of adult females which were gravid and size of fat bodies are plotted by time of year in Fig. 2. Peak reproduction occurred early in the season (May-June) and fat bodies decreased in size during this period (*H* test for fat body size by time, *P*'s < .001). Fat bodies are consumed during brumation and first vitellogenesis and then continue to be consumed during early summer. Presumably females did not begin storing fat until after their last reproduction. Comparing data from bi-weekly periods, females begin rebuilding fat deposits later in the season than males but have equal sized fat bodies by season's end.

All five species are probably multiple-brooded. Some gravid females of all species except *C. gularis* were found with both yolked follicles and oviducal eggs, presumptive evidence that at least two clutches are laid.

Female whiptails with oviducal eggs apparently remained in relative seclusion since their occurrence in my collections is low. I collected only eight *C. gularis* with oviducal eggs in two seasons. The overall sex ratio of specimens by month was heavily weighted toward males during periods of peak female reproduction (73% in *C. tigris*, 67% in *C. gularis*, and 57% in *C. inornatus*).

Females also either do not feed or must take only small quantities of food at each feeding when yolked follicles are large or oviducal eggs present because the stomach is displaced and usually contains very little food. Relative stomach volume (= vol./SVL) is significantly smaller for animals with oviducal eggs than for nongravid animals (*H* tests, *P*'s < .05 - < .001).

Much water, though, is probably necessary for egg production as captive gravid animals not given water supplemental to that in insect food lost weight rapidly and soon became emaciated. Eggs laid by animals soon after being collected alive were very similar in size and weight to those extracted from dead specimens. Therefore, once egg shells are deposited, no large quantity of water is added while they are in the oviduct. After being laid eggs pick up environmental water; a pair of eggs laid

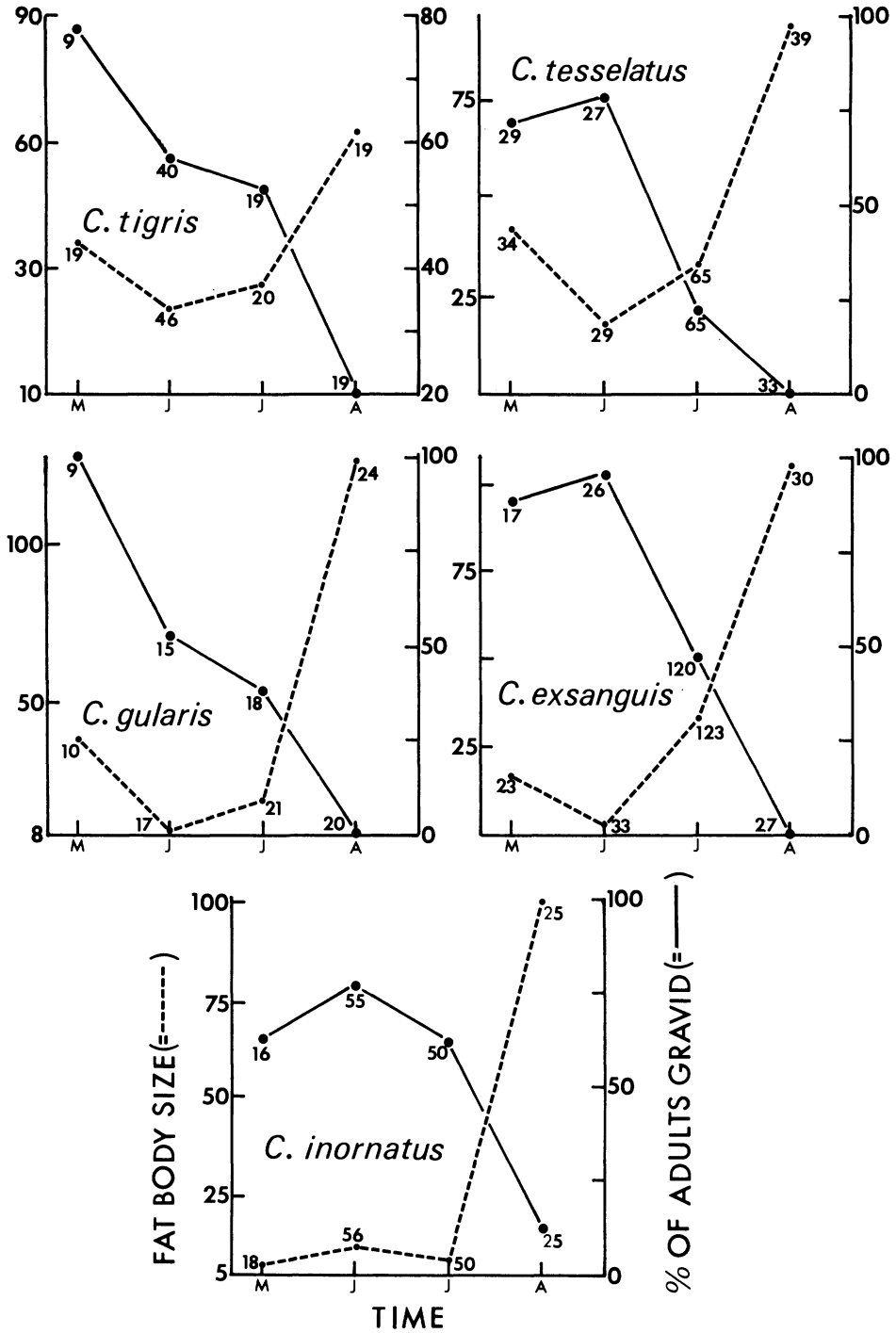


Fig. 2. Mean fat body size and percent of adult females sampled which were gravid by month for five whiptail species. Fat body size determined by method described for males. Numbers on left abscissa are $\times 10^{-2}$. Time scale is from May (M) to August (A). Fat body size was determined for all females collected while percent gravid from only adults. Therefore, sample sizes differ.

TABLE 1. SNOUT-VENT LENGTHS (MM) OF 5 *Cnemidophorus* SPECIES BASED ON COLLECTED SPECIMENS INCLUDING SOME JUVENILES, \bar{x} (S.D., N) RANGE. Reproductive females are those with enlarged yolked follicles or oviducal eggs. Only in *C. tigris* is the size difference between the sexes significant (H test; $P < .001$).

	Males	All Females	Reproductive Females
<i>C. tigris</i>	70.7 (9.7, 195) 46-94	66.6 (8.1, 104) 44-89	71.6 (6.5, 43) 60-89
<i>C. tessellatus</i>	—	78.3 (11.0, 167) 35-95	83.0 (6.1, 56) 66-93
<i>C. gularis</i>	70.8 (10.1, 84) 34-89	68.7 (11.6, 75) 34-89	73.1 (8.1, 24) 59-87
<i>C. exsanguis</i>	—	73.3 (8.3, 207) 36-92	75.0 (7.2, 94) 63-92
<i>C. inornatus</i>	55.1 (4.8, 126) 27-68	55.3 (5.4, 96) 43-68	56.9 (5.2, 87) 43-68

by one *C. exsanguis* in the laboratory increased their weight by 141% before hatching.

Table 1 presents snout-vent lengths of males, all females and reproductive females. Given the error in SVL measurements (about 1 mm), females of all species reach sexual maturity at about the same relative size (reproductive female minimum SVL/maximum female SVL = 63-69%). Raw data on date of collection, reproductive condition, and clutch sizes (where appropriate) for every female collected are presented by Schall (1976).

Clutch size.—Table 2 demonstrates *C. tigris* and *C. inornatus* have significantly smaller mean clutch sizes than the other three species (Newman-Keuls Test, P 's $< .05$) although ranges

overlap broadly. Intraspecifically, clutch size is positively correlated with SVL. All product-moment correlation coefficients are highly significant; larger animals have larger clutches (Table 3).

A similar pattern emerges from interspecific comparisons. *C. tessellatus*, the largest species (Table 1) has the largest mean clutch size whereas *C. inornatus*, the smallest species, has the second smallest clutch size. When the mean clutch size of each species is plotted against its mean SVL a positive correlation results (Spearman rank correlation, $r_s = .80$, $P > .05$). Thirty-nine percent of clutch size variation among species is accounted for by size ($R^2 = .39$), very similar to the figure of 41% obtained by Tinkle et al. (1970) for early maturing, small

TABLE 2. CLUTCH SIZE, INDIVIDUAL EGG WEIGHTS AND REPRODUCTIVE EFFORT (RE = CLUTCH WT/BODY WT) FOR FIVE *Cnemidophorus* SPECIES, \bar{x} (S.D., N) RANGE.

Species	Clutch Size	Egg Weights (gm)	RE
<i>C. tigris</i>	2.02 (.70, 43) 1-4	.594 (.12, 12) .30-.75	.105 (.04, 12) .072-.197
<i>C. tessellatus</i>	3.23 (1.1, 56) 1-6	.738 (.18, 11) .57-1.13	.126 (.04, 11) .065-.184
<i>C. gularis</i>	3.13 (1.4, 23) 1-5	.474 (.05, 8) .40-.53	.156 (.02, 8) .125-.186
<i>C. exsanguis</i>	2.96 (1.1, 91) 1-6	.549 (.12, 43) .28-1.10	.131 (.03, 43) .084-.224
<i>C. inornatus</i>	2.37 (.92, 87) 1-5	.296 (.07, 28) .15-.50	.147 (.04, 28) .046-.267
Grand Mean	2.72	.499	.134
Grand SD	1.11	.179	.037
N	300	102	102

TABLE 3. SVL-CLUTCH SIZE REGRESSIONS (SLOPES AND INTERCEPTS), CORRELATION COEFFICIENTS (r), AND SIGNIFICANCE LEVELS FOR r FOR 5 WHIPTAIL SPECIES. Clutch size = $a + b$ SVL.

	b	a	r	P
<i>C. tigris</i>	.06	-2.10	.52	<.001
<i>C. tessellatus</i>	.07	-2.79	.35	<.01
<i>C. gularis</i>	.12	-5.70	.75	<.001
<i>C. exsanguis</i>	.10	-4.57	.63	<.001
<i>C. inornatus</i>	.09	-2.77	.43	<.001

clutched species of lizards. Differences among species in clutch size could be a result of interspecific size differences; that is, data for all five species might lie on the same clutch size-SVL regression. To test this possibility, clutch size-SVL regressions for the five species were compared. Slopes of the five regression lines (Table 3) are very similar. Only *C. gularis* differed from *C. tigris* and *C. tessellatus* (t -tests for differences between slopes: $P < .05$ and $< .01$ respectively). Except for a *C. tigris*-*C. tessellatus* comparison, all pairs of regressions have significantly different elevations (F tests, P 's $< .05 - < .001$). The well known property of regression confidence bands flaring beyond the last datum point requires prudence in their interpretation. *C. inornatus*, though, may have the largest mean clutch size for its SVL.

A comparison of clutch size by date of reproduction reveals only *C. tessellatus* and *C. inornatus* show differences. Both have significantly larger clutches early in the reproductive season (H test, P 's $< .05$).

Egg weight.—Egg weights are given in Table 2. *C. inornatus* has the smallest and *C. tessellatus* has the largest eggs (N - K test, P 's $< .05$). Mean egg weight by species is strongly correlated with mean body weight ($r_s = .93$, $P < .05$). Within species, however, similar correlations are weak (r 's = .14-.48) and only that for *C. inornatus* is significant ($r = .48$, $P < .01$). Only *C. inornatus* has a regression slope significantly different from zero (t -test, $P < .05$). Expenditure per progeny for the two smaller species is about 0.05 whereas that for the larger three species is about 0.04 (H test for differences in means is significant, $P < .01$).

Egg or clutch weights do not significantly differ by time of year in any species.

Reproductive effort.—Statistics on estimated re-

TABLE 4. MATRIX OF "U" VALUES (UPPER NUMBERS) AND P 's (LOWER NUMBERS) FOR DIFFERENCE IN REPRODUCTIVE EFFORT IN FIVE SPECIES OF *Cnemidophorus*. ns = not significant.

	<i>C. tigris</i>	<i>C. tessellatus</i>	<i>C. gularis</i>	<i>C. exsanguis</i>
<i>C. tessellatus</i>	40 ns			
<i>C. gularis</i>	12 .003	24 ns		
<i>C. exsanguis</i>	114 .002	23 ns	66 .003	
<i>C. inornatus</i>	75 .003	104 ns	95 ns	400 .009

productive efforts (clutch weight/body weight) are given in Table 2. *C. tigris* has a lower mean RE and *C. gularis* has the highest (Mann-Whitney U tests in Table 4). RE is not correlated with SVL (Spearman correlations, P 's > 0.1) nor are there significant differences in RE by season in any species (H tests, P 's = .23 - $> .999$).

RE's computed from fresh clutch weight/body weights and from preserved specimens were very similar (17 *C. exsanguis*, 6 *C. gularis*, 9 *C. tessellatus*, 11 *C. inornatus*; U 's = 18-57; P 's $> .10$). Leakage of yolk or other damage to specimens would reduce potential sample sizes so future workers are advised to weigh fresh material.

Five *C. exsanguis*, 1 *C. tessellatus*, and 1 *C. gularis* maintained in captivity for at least one month and fed daily to satiation with insects produced exceptionally heavy clutches and their RE's were out of the observed range for field collected specimens (3 *C. exsanguis* RE = .23 - .26; *C. tessellatus* RE = .19; *C. gularis* RE = .22). The 5 *C. exsanguis* raised their RE by increasing both egg weights and clutch sizes, although keeping both within range of field collected data whereas the *C. gularis* raised only egg weights well beyond "normal" range and the *C. tessellatus* raised clutch size but not egg weight.

Factors controlling intraspecific RE variation (clutch size, egg weight and body weight) were examined by correlation analysis and step-wise regression. Table 5 presents the correlation coefficients and indicates variables in the order they were selected by regression analysis. The three variables together accounted for 83-98% of total variance.

TABLE 5. CORRELATION COEFFICIENTS (r) FOR REPRODUCTIVE EFFORT (RE) VS. THREE VARIABLES IMPORTANT IN DETERMINING RE, BODY WEIGHT, CLUTCH SIZE, AND EGG WEIGHT. Order in which these variables were added into a step-wise regression equation indicated by numbers in parentheses; the order reflects the relative importance of each variable in reducing RE variance.

Species	Body weight	Clutch size	Egg weight
<i>C. tigris</i>	.756 (1)	-.016 (3)	.158 (2)
<i>C. tessellatus</i>	.065 (3)	.574 (1)	.529 (2)
<i>C. gularis</i>	.587 (1)	.089 (2)	-.471 (3)
<i>C. exsanguis</i>	-.005 (3)	.228 (2)	.638 (1)
<i>C. inornatus</i>	-.242 (3)	.609 (1)	.535 (2)

DISCUSSION

The five species of *Cnemidophorus* studied here have similar reproductive strategies. All have multiple broods, small clutch sizes, and low RE's. They are also quite similar to other *Cnemidophorus* populations studied (Schall, 1976).

Differences among species' means for clutch size and egg weight can be partially attributed to interspecific differences in female body size. However, intraspecific variation patterns in whiptail reproductive characteristics also are useful in clarifying interspecific differences and the evolution of reproductive tactics. For example, mean egg size is positively correlated with mean body weight among the five species; however, within species egg size does not increase with increased body weight except in the smallest species, *C. inornatus*. *Cnemidophorus inornatus* also makes relatively larger eggs compared to body size (expenditure per progeny is highest for this species).

Thus, there appears to be a minimal egg size in *Cnemidophorus*. Smaller eggs may produce young unable to compete with juveniles of other *Cnemidophorus* species. Also, very small hatchlings of a widely foraging whiptail lizard would be subject to attack by small predators such as insects. Why larger species also do not increase egg size with body growth undoubtedly involves a trade-off between the number of eggs produced and their size. Once an optimum size is achieved, larger eggs may not increase juvenile survivorship. If an individual female locates a productive patch of the environment she might well increase egg size and RE. For example, eggs laid by laboratory maintained animals as well as eggs of a few

clutches removed from collected specimens were much larger than modal for that species.

An important feature in *Cnemidophorus* evolution has been changes in body size. Such changes necessitate shifts in reproductive tactics, as described above, and may play a role in thermoregulation in thermally different habitats (Asplund, 1974) and in resource partitioning among competing whiptail species (Schall, 1976).

Reproductive effort was estimated here as the clutch weight/body weight ratio. An alternative method uses calories in the carcass and eggs (Tinkle and Hadley, 1973). Ballinger and Clark (1973) demonstrated the energy content per gram of egg is constant in six lizard genera. Also, using calories per gram ignores water content of eggs. Water is a limiting resource in desert organisms and is vitally important in production of whiptail eggs.

The formal, and biologically most reasonable, definition of RE is the fraction of assimilated resources allocated to reproduction. Use of a weight ratio assumes this static measure is correlated with the dynamic resource allocation process. Any such possible correlation rests on the assumption, not often stated, that resources assimilated are proportional to body size. If the relationship between body size and assimilated resources available for reproduction is not linear, the use of body size as an index of energy assimilated would be unjustified.

Likewise, the use of egg weights as an index of energy allocated to reproduction is, at best, a crude estimate as numerous other factors are involved (Tinkle, 1969). In *Cnemidophorus* such high cost factors include 1) the cost of courtship and mating (testis size is maximum only early in the season and mating activity was seen only then suggesting reduced courtship and mating period), 2) carrying eggs (gravid females are secretive and have reduced stomach volumes), 3) selecting and digging nests (eggs must absorb environmental water during incubation). Obviously, better techniques are required to measure energy assimilated as well as the fraction expended on reproduction.

Despite these limitations some intriguing differences in clutch weight/body weight ratios among species emerge. *C. tigris* has a significantly lower RE than *C. gularis*. *C. tigris* lives in the most xeric habitat of the five species whereas *C. gularis* usually inhabits wetter areas more typical of the center of its range in central Texas (Schall, 1976). Figs. 1 and 2 show that among the five species, *C. gularis* stores the largest and *C. tigris* the smallest fat deposits

by summer's end. RE may be strongly influenced in lizards by environmental conditions (Pianka and Parker, 1975) and the difference in RE in these two whiptails could thus simply reflect differences in environmental quality.

The step-wise regression analysis also strongly suggests that factors varying RE intraspecifically differ among species. For example, examination of results for the unisexual species and their most similar (and probably parental) bisexual forms reveals body weight is most strongly correlated with RE in the bisexual species. That is, whereas clutch size \times egg weight increases to raise RE neither clutch size nor egg weight increase predictably. The two unisexual species, however, appear to consistently increase clutch size and/or egg weights to increase RE in a regular fashion. Thus, different species allocate resources differently toward an increase in RE. These scanty data hint that careful comparative study of these factors will be rewarding.

Each parthenogenetic individual produces only female progeny and potentially produces more F_2 offspring than an individual of a bisexual species. Whiptail clones have a higher intrinsic rate of increase than bisexual populations and parthenogenetic individuals may be viewed as being r -selected relative to a lizard of a bisexual species. However, consideration of three important reproductive variables [clutch size, egg size and reproductive effort (Tables 2, 4)] reveals the two unisexual species are not more similar to each other than they are to bisexual species. *C. exsanguis* and *C. gularis* are very similar; *C. exsanguis* is assumed to be of hybrid origin and may simply resemble one of its parental species, *C. gularis*. *C. tessellatus* has the largest clutch size and egg weight and may also resemble one of its parental species, the very large *C. septemvittatus*. Except for the higher intrinsic rate of increase for parthenogenetic lizards, any differences between unisexual and bisexual species' reproductive characteristics, if present, are subtle.

However, r - K strategy differences may be expressed in the dynamic aspects of reproduction such as age at first reproduction and clutches per season. My data suggest all species reach maturity at about the same relative size. Smith (1974) marked *C. gularis* and *C. exsanguis* near Alpine, Brewster county, Texas and concluded females of the bisexual species did not reach maturity until their second season whereas *C. exsanguis* matured in only 10 months. Good demographic data on these species are required.

Only a fraction of all whiptail species were studied here. Use of a larger number of species requires consideration of possible geographic variation, influence of body size, as well as possible resemblance of unisexuals to one of their parental species (Uzzell and Darevesky, 1975). One excellent natural study system exists, the parthenogenetic populations within the range of the normally bisexual *C. lemniscatus* in tropical Surinam (Hoogmoed, 1973). Neither geographic nor body size variation would be confounding factors in this system.

The small clutch-small RE *Cnemidophorus* reproductive strategy is probably related to the ecological position of these animals. They are rapidly moving, very active animals which forage widely, often in open areas and rely on speed to elude predators. Their behavior and long thin body form may preclude major alterations in clutch size or RE. Although gravid females remain secluded they probably emerge occasionally for food (especially later in the season as fat reserves are consumed) or are occasionally flushed by predators such as snakes. Any differential selective factors operating on weedy parthenogenetic and nonweedy bisexual whiptails' static reproductive characteristics (clutch size, egg size, clutch/body weight ratio) seem to be overshadowed by constraints imposed by body form, foraging technique and body size.

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