

INTRASPECIFIC COMPARISONS OF DIET
OF *CNEMIDOPHORUS GULARIS*
(SAURIA:TEIIDAE) IN CENTRAL TEXAS

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ABSTRACT.—Aspects of the diet of *Cnemidophorus gularis* were examined in two dominant habitats (mesquite and juniper woodlands) of central Texas. One hundred thirty-two lizards were categorized into groups based upon age and sex. Morphometric data of individual *C. gularis* were collected to characterize the relationship between body size and food size for age-sex groups within each habitat. Diet composition was determined from stomach contents, which were quantified by number and volume of each prey taxon present for each lizard. The distribution of prey categories within age-sex groups then were compared via a log-linear model of three-way contingency tables within each habitat. Isoptera (termites) were the numerically dominant prey category for all groups of lizards, whereas Orthoptera were dominant based on volumetric contribution to the diet. No differences in the proportional contribution of prey taxa to the diet of different age-sex groups were detected in the juniper habitat. A significant three-way interaction among prey taxa and age and sex of lizards was detected in the mesquite habitats, but the observed difference is probably an artifact of small sample size of juveniles. Consistent secondary sexual dimorphism was found regardless of age or habitat. Similarly, significant differences in size of prey between lizard age groups were detected regardless of sex or habitat. Nonetheless, variation in diet among individuals could not be ascribed to differences in age, sex, habitat, or their interactions, when number, volume, or proportional volume of prey were considered as dependent variables using multivariate analyses of variance. Dietary differences in prey size regardless of taxon were detected for maximum prey size (but not minimum or mean prey size) using analysis of covariance. However, only the covariate (lizard size) was significant and the magnitude of variation accounted for was small. *Key words:* ecology; niche; whiptail lizard; *Cnemidophorus*.

Body size is an important attribute of an organism from both ecological and evolutionary perspectives. Differences in body size appear to be a major mechanism by which various species avoid competition for resources (Wilson, 1975; Brown et al., 1979; Werner and Gilliam, 1984), and in some situations, it is an important reflection of community structure (Schoener, 1977). Nonetheless, the range of individual body sizes within a species, particularly in those taxa with indeterminate growth, commonly spans one or more orders of magnitude, and ontogenetic changes in body size often transcend size differences among strongly competing species (Werner and Gilliam, 1984). Given such circumstances, differences in resource utilization among size classes of a single species might be greater than those among different competing species. This assumes predator size constrains prey choice either directly

through trophic limitations or indirectly through other factors (for example, habitat selection) that may impinge upon prey selection. In addition to dietary differences associated with age due to size; modifications in foraging strategy associated with habitat selection, or the physiological requirements associated with reproductive status, reproductive potential, or sexual maturity, could produce diet shifts between age classes. Thus, intraspecific differences in size or physiology could produce considerable dietary variation within a population.

Ontogenetic niche shifts are defined as changes in the pattern of resource utilization by an organism as it increases in size with age. Ontogenetic diet shifts have been well documented for many invertebrates (Wilson, 1973; Maly, 1976; Sebens, 1981; Hines, 1982) and vertebrates, including fish (Ross, 1978; Grossman, 1980), amphibians (Townsend, 1985; Southerland, 1986), and reptiles (Schoener and Gorman, 1968; Pough, 1973; Ballinger et al., 1977; Schoener, 1977; Mushinsky et al., 1982). Size differences among age groups or between sexes may separately or in combination reduce intraspecific competition for resources (see Selander, 1966, 1972), regardless of the selective forces responsible for the size differences.

Food habits of a variety of species of whiptail lizards (*Cnemidophorus*) have been studied in several areas of the southwestern United States (Pack, 1923; Milstead, 1957a; 1957b; 1958; 1965; Johnson, 1966; Milstead and Tinkle, 1966, 1969; Pianka, 1970; Bickham and MacMahon, 1972; Scudday and Dixon, 1973; Mitchell, 1979; Best and Polechla, 1983; Best and Gennaro, 1985). The overall diet composition of *Cnemidophorus* in similar habitats has been reported by several authors. Milstead and Tinkle (1969) found Orthoptera, Coleoptera, and Isoptera to be the major foods of *C. tigris* in southwestern Texas. The diet of *C. tigris* in an oak-mesquite habitat of southeastern New Mexico consisted mainly of Orthoptera, Isoptera, Coleoptera, and Araneae, whereas *C. gularis* from New Mexico consumed Orthoptera, Isoptera, and Araneae (Best and Gennaro, 1985).

Milstead (1958) examined the diet of four species of *Cnemidophorus*. He found that although variation occurred between species, termites formed the largest portion of the diet, with orthopterans, coleopterans, and lepidopterans ranking second, third, and fourth, respectively. Smith (1989) found the consumption of termites by *C. gularis* and *C. exsanguis* in western Texas to vary with rainfall and suggested that the use of termites as food is associated with dry or drought conditions. These studies documented that whiptails are opportunistic feeders and that different species eat similar foods. Although intraspecific dietary differences between the sexes have been documented in several studies of *C. tigris* (Johnson, 1966; Pianka, 1970; Karasov and Anderson, 1984; Best and Gennaro, 1985), no dietary differences associated with age have

been demonstrated. Paulissen (1987) has stated that juvenile *C. sexlineatus* eat smaller prey items than do adults, but adults and juveniles of this species show a pronounced separation in their seasons of activity. They are, therefore, not competing for the same prey resources. In contrast, Anderson and Karasov (1988) found no evidence for dietary differences between sexes of *C. tigris* in California. Similarly, Best and Polechla (1985) found no differences in diet between sexes of *C. gularis* in New Mexico, but their study was conducted in habitats where other closely related and possibly competing lizard species were present. In speciose assemblages, interspecific competition may result in intraspecific niche compression, thereby making differences in diet between the sexes less pronounced than in situations where a species niche is not affected by closely related competitors.

We investigated intraspecific resource partitioning among age-sex classes of *Cnemidophorus gularis*, a large, common, teiid lizard that ranges widely from the prairies, grasslands, and rocky hillsides of Texas and northern México, into southern Oklahoma and the eastern edge of New Mexico. These whiptails are slow-moving, methodical foragers that turn small rocks and sticks in search of food; they actively stalk moving objects as well (Scudday and Dixon, 1973). Most feeding occurs on lower branches of shrubs or under ground litter, whereby a variety of burrowing and surface prey may be discovered.

MATERIALS AND METHODS

We selected sites at The Junction Center of Texas Tech University, 1 mi. S Junction, Kimble County, Texas (30°30'N, 99°45'W), to study whiptail ecology because this area provided both diverse habitats and an abundant whiptail population. Moreover, *C. gularis* represents an appreciable portion of the herpetofauna and is virtually free of other lizard competitors in this area. Only two other lizard species (*Sceloporus undulatus* and *Phrynosoma cornutum*) were observed in the area, and each was present in extremely low numbers in both habitats.

Lizards were collected over an 18-day period in late June and early July of 1986 in each of two distinct habitats. The first, dominated by mesquite and prickly pear, was flat and sandy, with sparse shrub and ground cover (approximately 20 percent) occurring in small patches. The second habitat comprised mostly juniper with some mesquite. The terrain was rocky and broken; both shrub and ground cover were dense and pervasive (approximately 40 percent).

Individual lizards were characterized as to sex, age (reproductively mature adult or juvenile), and habitat affinity (mesquite or juniper sites), and body measurements including snout-vent length, head length, and head width were taken to the nearest 0.1 millimeter using ruler and digital caliper. Weight was recorded to the nearest 0.01 gram using a Pesola balance. Specimens were dissected and stomach contents were removed immediately after collection, placed in vials, and preserved in 70 percent ethanol. They were identified to the ordinal or familial level and quantified as to the total number of individuals of each taxon, the volume (by displacement) of each individual prey item, and the total volume (to the nearest 0.1 milliliter) of each taxon. Data were analyzed by multivariate analysis of variance (MANOVA), analysis of covariance (ANCOVA), and regression procedures (SPSS-X Inc., 1988).

The diet of an organism can be characterized in a variety of ways, each elucidating particular aspects of foraging ecology. One approach is to categorize prey into discrete taxa and evaluate if different main treatment factors (age, sex, and habitat, for example) affect diet composition based on results from MANOVA. With this approach, the dependent variable can be quantified according to the number of individual items within each prey category or according to volume (either total volume of each prey category within a stomach or the proportional volume of each prey category within a stomach). A second approach, especially useful for opportunistic or eurytopic consumers, is to categorize prey items by size without regard to their taxonomic identity. Two-way ANCOVA (age versus sex) then can be used to evaluate the degree to which age- or sex-associated differences in diet (that is, minimum, maximum, or mean prey size) are a product of the size of the lizards within age-sex groups or are emergent properties related to physiological and behavioral correlates of sex and age.

Pooling counts of prey taxa from all individuals within age-sex group produces a prey taxon frequency distribution. Log-linear model approaches to contingency tables then can be evaluated by G-tests (Sokal and Rohlf, 1981) in order to ascertain if the proportional distribution of prey categories is affected by the age or sex of the consumer (analyses were conducted separately for mesquite and juniper habitats).

RESULTS AND DISCUSSION

A total of 140 lizards was collected, of which eight had empty stomachs and were excluded from analyses. Approximately twice as many males as females, and four to five times as many adults as juveniles were collected. Sample sizes categorized by age, sex and habitat are: 73 adult males (34 mesquite, 39 juniper); 37 adult females (16 mesquite, 21 juniper); 12 juvenile males (two mesquite, 10 juniper); 10 juvenile females (one mesquite, nine juniper). Body measurements were analyzed by three-way MANOVA with habitat, sex, and age as treatment factors (Table 1). Significant differences in body size were detected between age groups and sex groups, but not between habitats. The absence of significant two- or three-way interactions indicated that each of the significant main factors had consistent effects, regardless of the levels of the other factors. Subsequent univariate analyses demonstrated that *C. gularis* exhibited consistent significant size variation between age and between sex groups for snout-vent length, as well as head length and width (feeding parts). Adults were 10 to 35 percent larger than juveniles, whereas males were eight to 14 percent larger than females, depending on the morphometric variable.

Stomach contents were classified into eight orders (Table 2). Orthoptera (grasshoppers), Isoptera (termites), and Araneida (spiders) were the only three categories that occurred in sufficient frequency (at least one percent based upon the numbers of individual items) to be considered common. The remaining five categories, Scorpionida (scorpions), Lepidoptera larvae (butterflies), Coleoptera (beetles), Dictyoptera (roaches), and Isopoda (isopods) were considered rare and were pooled into a single prey category for subsequent analyses.

TABLE 1. Three-way MANOVA (age \times sex \times habitat) results for *Cnemidophorus gularis* using snout-vent length, head length, and head width as variables. Pillias', Hotellings', and Wilks' criteria yielded identical F-values and significance.

Source	DF	Pillias'	F	Significance
Age (A)	3	0.924	4.347	0.01
Sex (S)	3	0.087	4.042	0.01
Habitat (H)	3	0.484	2.171	0.10
H \times A	3	0.165	0.716	0.54
H \times S	3	0.040	1.791	0.15
A \times S	3	0.028	1.241	0.30
H \times A \times S	3	0.013	0.545	0.65
Error	128			

Because significant size differences existed between lizard sex groups as well as between age groups, we examined diets for both intersexual resource partitioning and ontogenetic niche shifts. Because dietary differences could be manifested in a variety of ways, we analyzed data using a number of approaches. We first evaluated dietary differences associated with age, sex, or habitat using three-way MANOVA on numbers of each prey category. However, because prey items from one category to the next can vary greatly in size (grasshoppers are larger than termites, for example), we additionally used both total volume and proportional volume of prey categories as dependent variables in subsequent three-way MANOVA analyses. Regardless of the analysis, no significant differences were detected for any main treatment or their interactions for Pillias', Hotellings', or Wilks' criteria (Table 1). This indicates indistinguishable diets, regardless of age, sex, or habitat. High within-group variability makes differences between groups difficult to detect with this parametric test. Therefore, we pooled data on stomach contents from individuals to make a composite diet for each age-sex group within each habitat. Four prey categories, each of the three common prey taxa and a category comprising all rare prey, were used to define diets (rare taxa had to be pooled into a single category in order to meet the requirements of the Goodness of Fit Test). These prey categories were evaluated via G-tests to examine whether proportional dietary composition was independent within each habitat for each age-sex group. In the juniper habitat, significance was not detected for any main effect or interaction, whereas a significant three-way interaction was detected in the mesquite habitat ($G = 26.974$, $df = 3$, $P < 0.001$). Significance was attributable to juvenile females, which consumed a higher proportion of Orthoptera, by numbers, than any other age-sex group. All other groups exhibited virtually identical diets dominated by Isoptera (for numbers) and Orthoptera (for volume). Although these results may reveal an actual group preference, it is more likely to be an artifact. The number of

TABLE 2. Number of prey items, followed by total volume (milliliters) consumed (in parentheses) by age and sex groups of *Cnemidophorus gularis* in mesquite and juniper habitats (A, adults; J, juveniles; sample size in parentheses).

Taxa	Mesquite				Juniper			
	Males		Females		Males		Females	
	A(34)	J(2)	A(16)	J(1)	A(39)	J(10)	A(21)	J(9)
Orthoptera								
Acrididae	32(57.1)	3(7.0)	9(18.6)	4(6.0)	40(75.1)	12(16.1)	17(20.8)	10(9.6)
Isoptera								
Kalotermdae	1300(26.4)	191(3.0)	869(27.0)	7(0.1)	1395(31.4)	514(9.7)	886(21.9)	27(6.2)
Araneida								
Araneae	11(11.3)	1(0.1)	6(6.1)	0	16(7.4)	7(0.5)	16(8.5)	5(1.7)
Scorpionida								
Scorpionidae	2(5.0)	0	0	0	1(0.1)	0	1(1.0)	0
Lepidoptera								
Larvae	1(2.0)	0	0	0	0	2(2.5)	2(1.1)	0
Dictyoptera								
Blattidae	0	0	2(0.5)	0	5(2.1)	0	3(2.0)	0
Isopoda	0	0	0	0	2(0.2)	0	0	0
Coleoptera								
Carabidae	4(3.5)	0	2(1.0)	0	1(1.1)	2(2.0)	0	1(0.5)

juveniles in our sample was small in each habitat; moreover, the diet for juvenile females in mesquite was determined from only one individual. Thus, the difference between adults and juveniles may represent individual differences rather than group differences.

Additionally, we examined diet by prey size regardless of taxonomic identity. Maximum, minimum, and mean size prey size (volume) in each stomach were used to evaluate differences between groups (Table 3). We used ANCOVA to examine whether differences in predator size obscured dietary differences related to age and sex. Using lizard size (head width) as a covariate, no significant differences in maximum, minimum, or mean prey size could be attributed to age or sex. Head width was chosen as the covariate measurement because differences in mouth size, as indicated by head width, would more likely reflect differences in the size of prey consumed. A significant relationship existed between predator size and maximum size of prey ($P < 0.005$); in contrast, no significant relationship existed between predator size and either minimum or mean prey size (Fig. 1). Nonetheless, consumption of larger prey must be infrequent as mean prey size does not increase significantly with body size. Ontogenetic diet shifts in prey size do occur to some extent in *C. gularis* (Table 3). Diet differences are attributable only to lizard size (the covariate in the ANCOVA) and not to other physiological or behavioral differences between adults and juveniles, which per se are uncorrelated with size. Even so, only a small percentage of the variation in maximum prey size was accounted for by lizard size (four percent). This suggests that larger lizards, although able to consume large prey, either do not specialize on

TABLE 3. Maximum and minimum prey sizes for each age-sex group of *Cnemidophorus gularis*. Only individuals with stomachs containing two or more prey items are included. Range is followed by mean and standard deviation (in parentheses).

Age and sex	N	Head width	Maximum prey	Minimum prey
Adult males	(45)	7.8-13.2 (9.53, 1.17)	0.1-14.0 (2.18, 2.48)	0.1-13.2 (1.04, 2.36)
Adult females	(22)	7.0-10.3 (8.69, 0.53)	0.1- 8.0 (1.93, 2.01)	0.1- 4.0 (0.29, 0.72)
Juvenile males	(9)	7.7- 8.8 (8.31, 0.33)	0.5- 4.0 (1.82, 1.01)	0.1- 3.0 (0.53, 0.99)
Juveniles females	(7)	7.5- 8.8 (8.05, 0.40)	0.5- 4.0 (1.36, 1.07)	0.1- 3.8 (0.92, 1.27)

larger taxa or encounter them too infrequently to have an appreciable impact on the diet.

C. gularis appeared to be an ideal candidate for exhibiting ontogenetic diet shifts. Although we found significant intraspecific differences in body size between age and sex classes, no intraspecific differences in diet composition were detected. As other lizard competitors were absent from these habitats, we expected to see intraspecific differences maximized. *C. gularis* is an active and methodical predator. It thus has the potential to encounter a greater number and variety of prey items from which it can be selective than would a sit-and-wait predator (Anderson and Karasov, 1988). However, prey that are sedentary and distributed in a patchy fashion (for example, termites) are more likely to be discovered and eaten by active foragers (Eckhardt, 1979; Krebs, 1978). Other studies of lizards with foraging modes similar to those of *C. gularis* (Pianka, 1966; Wilson and Clark, 1977; Huey and Pianka, 1981; Anderson and Karasov, 1988) have demonstrated that these predators have substantial numbers of termites in their diets. In both of our study sites, termites were abundant and individuals were distributed in a clumped fashion. It may be more energetically economical to wait for larger prey than to consume a single termite; however, their clumped distribution may result in a more attractive packaging with a total energetic payoff equal to or greater than that of larger prey items.

Our study on the feeding ecology of *C. gularis* has shown that although morphological variation exists between groups, diets of these groups are indistinguishable. Sex and age differences, at least at the levels we investigated, do not act to reduce intraspecific competition for food. It is possible that dietary differences exist but are obscured by other factors. Because of the abundance of small prey in the diet of *C. gularis*, it is difficult to detect an effect by occasional large items. Also, prey seldom could be identified below the familial level; categorization at such taxonomic levels may obscure differences that would otherwise be detectable at lower levels (Krzysic, 1979). For example, groups may consume different species of Orthoptera, and preferences detectable at the generic or specific level may not be detected at the ordinal level.

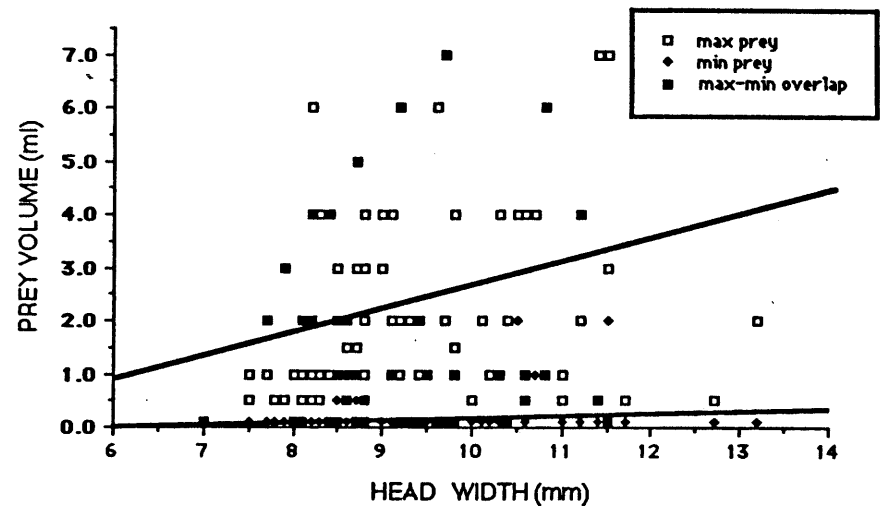


FIGURE 1. Relationship between predator size (head width) and diet (prey volume) for maximum and minimum prey from lizards that had consumed two or more prey items. The regression equations, plotted as solid lines, are: minimum prey and head width, $Y = -0.227 + 0.041X$, $r^2 = 0.04$; maximum prey and head width, $Y = -1.091 + 0.303X$, $r^2 = 0.02$.

Moreover, our size categories were discrete, corresponding to adult and juvenile. In actuality, lizards are characterized by indeterminate growth and continue to grow larger as they get older. There is a continuum of body sizes present throughout the population. Analysis using only two body sizes (effectively large and small), though related to sexual maturity, may serve to mask diet shifts that occur.

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