

An Alimentary Specialization for Herbivory in the Tropical Whiptail Lizard

*Cnemidophorus murinus*

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To fully understand the diversity of results in the current literature as well as our own study will require multigenerational skeletochronological studies of a variety of anurans from the same as well as disjunct populations. However, suboptimal conditions during larval development probably carry over into postmetamorphic and adult life as suggested by Halliday and Verrell (1988). Ryser (1988), for example, found a positive correlation between adult body size in *R. temporaria* and size at the end of the first year, supporting the suggestion that factors which influence juvenile size do carry over into adulthood. The fact that all of our specimens were collected in the same spring suggests two possibilities: (1) that individual variation in body size in relation to age is common (perhaps for genetic reasons relating to growth rate) and would be seen repeatedly if samples were taken from these same localities over a longer interval; or (2) that animals representing three-year olds in our samples were affected by environmental influences and experienced a "bad year" caused by suboptimal conditions for growth during year one but not year two. Because anurans grow throughout life, and we sampled more than one locale, and because the largest males in our samples were age two in each of three cases, the second alternative seems more likely. It should also be pointed out that two of the three populations in this paper (2 and 3) represented all of the calling males at those sites, so that although sample sizes are small from a statistical perspective, they are biologically meaningful in that they represent all that the females had to choose from.

The present study has shown that freeze-sectioned skeletochronological techniques can be successfully applied to chorus frog femurs but not to phalangeal sections, and that males in our breeding choruses from the Great Plains are commonly either two or three years of age and occasionally reach age four. Our results show a slight negative and non-significant correlation between age and body size among calling males, further suggesting that the assumption, often made in the past, that bigger means older is not necessarily true in chorus frogs. If older males were also usually larger, then Trivers's (1972) suggestion that females might prefer older males if age is correlated with genetic quality, would be supported. Dominant frequency is inversely correlated with body size in chorus frogs ( $r = -0.62$ ,  $N = 158$ ; JEP, unpubl. obs.) as is generally the case in anurans. However, our data argue against the likelihood that female chorus frogs would be able to use dominant frequency in this manner. The implications of our original observations toward an understanding of reproductive behavior in chorus frogs in the Great Plains suggests that male size rather than age may be more important in determining which males call and which operate as satellites. The fact that no one-year old males were among those calling suggests that individuals of this age did not participate in the choruses we examined and may in fact be satellite males.

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### An Alimentary Specialization for Herbivory in the Tropical Whiptail Lizard *Cnemidophorus murinus*

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Although lizards occupy an enormous range of habitat types, their foods are relatively monotonous. The vast majority of the over 3000 extant lizard species consume small arthropods; only approximately 2% are

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TABLE 1. Mean relative capacities of full alimentary tract organs (organ mass/[body mass – organ mass] × 100) of a large specialized herbivorous lizard, *Iguana iguana* (from Troyer, 1984), a small herbivorous lizard, *C. murinus*, and an insectivorous whiptail, *C. tigris*. Standard deviations are in parentheses after the mean. Sample size and variation were not reported in the literature for *I. iguana*.

	Total tract	Stomach and small intestine	Colon and large intestine
<i>I. iguana</i>	18.5	8.7	11.8
<i>C. murinus</i> N = 20	16.9 (4.9)	7.4 (3.0)	9.5 (2.3)
<i>C. tigris</i> N = 10	9.0 (2.3)	6.6 (2.4)	2.5 (0.8)

known to be herbivorous (Pough, 1973). Pough (1973) concluded that herbivorous lizards are usually large animals (>100 g) compared to most lizards, and that metabolic constraints both require and allow larger lizards to utilize plant materials. In addition to large body size, herbivorous lizards possess a suite of alimentary adaptations that facilitate digestion of plant material (McBee, 1971). The green iguana, *Iguana iguana*, for example, has an enlarged colon with a series of valves that presumably allow efficient processing of plant foods (Iverson, 1980). Moreover, all herbivorous lizards are believed to have a compartmentalized colon (Iverson, 1982). The anatomical adaptations, diets, and digestive capabilities of several species of large herbivorous lizards have been investigated (Nagy, 1977; Johnson and Lillywhite, 1979; Iverson, 1980; McBee and McBee, 1982; Christian et al., 1984; Troyer, 1984). Almost all of these studies, and the generalizations about herbivorous lizards that follow from them, have not considered the feeding ecology of smaller herbivorous lizards like *Cnemidophorus* or *Amieva* (but see Mautz and Nagy, 1987). Most of these small herbivorous lizards have insectivorous congeners (Janzen, 1973; Schall and Ressel, 1991). What, if any, specializations they possess allowing for utilization of plant foods is unknown.

On several Caribbean islands endemic whiptail lizards (*Cnemidophorus*; family Teiidae) occur in very dense populations (Bennett and Gorman, 1979; Schall, 1983). The insular whiptail lizards do not possess any obvious specialized gut organs, such as an enlarged colon (Lonnberg, 1902), and are also much smaller (20–50 g) than the size requirement for herbivorous lizards as described by Pough (1973). Here I examine the morphology of the digestive tract of a small herbivorous lizard, *Cnemidophorus murinus*, from the island of Bonaire in the Netherlands Antilles. The capacities and lengths of the gut and individual organs were compared with similar measurements made on the congeners *C. tigris*, *C. sexlineatus*, and *C. inornatus*, and also with data from the literature on herbivorous lizards. My goal was a preliminary understanding of the structural characteristics of the alimentary tract that may permit small lizards to exploit a herbivorous diet.

To assess the gut capacity in units comparable to those in the literature, I followed the protocol of Parra (1978) as used by Troyer (1984). Free-ranging *C. murinus* were shot with a .22 caliber airgun during their peak activity period as part of a study on diet selection (Dearing, 1988; Dearing and Schall, 1992). Only apparently full digestive tracts from these wild lizards were measured. Gut measurements for *C. tigris* were similarly performed on preserved specimens at the University of Utah. The stomach, small intestine, and large intestine were each removed and weighed. Capacity was calculated as the wet mass of the organ and its contents/body mass minus the digestive organs × 100. Length was measured to the nearest mm for each organ after its contents had been removed. To provide consistency in measurements, each organ was stretched to its maximum length possible without obviously disturbing the integrity of the tissue. Proportions of the total alimentary tract length as well as that of each organ were calculated by dividing the tract or organ length by the animal's snout-vent length (SVL). Comparisons of these measurements were made with the data from Troyer (1984) on *Iguana iguana*, and Lonnberg (1902) on 36 species of lizards of various diet modes. Alimentary tract measurements were made on one fresh individual each of *C. inornatus* and *C. sexlineatus* by C. Townsend (pers. comm.).

The capacities of the digestive tract and individual alimentary organs of *C. murinus*, *C. tigris*, and *Iguana iguana* appear in Table 1. The relative gut capacity of *C. murinus* is comparable to that of a large herbivorous lizard, *I. iguana*, and possesses a significantly larger entire gut due to greater large intestine capacity than its congener *C. tigris* (Wilcoxon rank test for *C. murinus* and *C. tigris* on entire gut:  $z = 4.07$ ,  $P = 0.0003$ ,  $N = 30$ ; stomach and small intestine:  $z = 1.03$ ,  $P = 0.31$ ,  $N = 30$ ; large intestine:  $z = 4.38$ ,  $P = 0.0001$ ,  $N = 30$ ). Statistical comparisons with gut capacity of *I. iguana* were not possible due to lack of information in Troyer (1984).

Table 2 lists the relative lengths of the small and large intestines, combined and individually, of lizards with different dietary habits. *Cnemidophorus murinus* is more similar to other herbivorous lizards than to the congeneric insectivorous lizards. *C. murinus* had significantly longer small and large intestines than its insectivorous congener, *C. tigris* (Wilcoxon rank test, small intestine:  $z = 4.8$ ,  $P = 0.0001$ ,  $N = 49$ ; large intestine:  $z = 4.71$ ,  $P = 0.0001$ ,  $N = 49$ ; large and small intestine:  $z = 4.84$ ,  $P = 0.0001$ ,  $N = 49$ ). It is worth noting that even though the *C. tigris* were preserved, their relative gut lengths were not smaller (as might be expected due to shrinkage during preservation) than the other insectivorous species measured fresh.

No elaborate valve system or compartmentalization was seen in dissection of the large intestine of *C. murinus*. Large populations of unidentified nematodes were present in the large intestine of all animals. The odor of the contents of the large intestine was pungent, more characteristic of fermenting herbivores than that of an insectivorous whiptail (Schall, pers. comm.).

Approximately 74–78% of the annual diet of the Bonaire whiptail lizard consists of leaves, fruit, flowers, seeds, and nectar. Insects comprise 12–16% of the diet (Dearing and Schall, 1992). Although a number of insular species of *Cnemidophorus* are herbivorous,

TABLE 2. Intestine length relative to SVL of herbivorous lizards (mean of 6 species), insectivorous lizards (mean of 27 species), and omnivorous lizards (mean of 3 species). Also given are measurements from at least one species of teiid lizard from each group. Means of species and data for *Tupinambus teguixin* are from Lonnerberg (1902); no measures of variation or sample size were available for these data. Standard deviations are in parentheses.

	Entire intestine	Small intestine	Large intestine
Herbivorous	2.93	1.95	0.97
<i>C. murinus</i> (N = 39)	2.79 (0.34)	2.10 (0.29)	0.76 (0.13)
Omnivorous	1.84	1.29	0.55
<i>T. teguixin</i>	1.71	0.95	0.76
Insectivorous	1.31	0.87	0.34
<i>C. tigris</i> (N = 10)	1.36 (0.21)	0.93 (0.17)	0.44 (0.09)
<i>C. sexlineatus</i> (N = 1)	1.14	0.78	0.36
<i>C. inornatus</i> (N = 1)	1.22	0.87	0.35

the majority of whiptails primarily consume small arthropods (Schall, 1976). In captivity *C. murinus* prefers animal foods over any plant material offered (pers. obs.), and therefore appears to be an opportunistic feeder. My goal was to determine if *C. murinus* has any structural characteristics of its alimentary tract that facilitate herbivory. The results indicate this animal has at least one morphological trait, an elongated and more massive gut relative to insectivorous congeners.

Plant foods contain less energy per volume than do animal food items (Southwood, 1973). Moreover, much of the energy can be bound up in fiber which is difficult for vertebrates to digest. To accommodate the increase in the volume of plant foods most herbivorous vertebrates have longer, bulkier digestive tracts compared to their carnivorous or insectivorous relatives (Schieck and Millar, 1985).

Herbivorous *C. murinus* appears to be no exception. Its gut capacity is nearly twice as large and its alimentary tract length more than twice as long as in insectivorous *Cnemidophorus* species. Its relative gut capacity and length is much more similar to that of the distantly related but herbivorous *Iguana iguana* than to its insectivorous congeners. Because of this similarity to other herbivorous lizards and because digestive tract organs are metabolically expensive to maintain (Webster, 1981), I suggest that the relatively large alimentary tract of *C. murinus* is an adaptation for a herbivorous lifestyle. In addition, the acrid odor of the large intestine and the presence of nematodes suggests that *C. murinus* may possess other specializations for herbivory.

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### Common Snapping Turtles Associated with Ant Mounds

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One of the most unusual associations between invertebrates and vertebrates is the anting phenomenon. Anting is the utilization of ants by vertebrates to control epibionts. As described for birds, anting involves placing or rubbing ants into feathers. Coating the feathers with formic acid to deter ectoparasites (e.g., mites) and ant auxins to inhibit bacterial and fungal growth have been suggested as advantages of this behavior (Groskin, 1950; Ehrlich et al., 1986). In addition to birds, at least one primate (*Cebus capucinus*) is known to exhibit anting behavior (Longino, 1984).

Riley et al. (1985) reviewed published accounts of squamates associated with ant and termite mounds. They reported that 33 species used mounds as nesting sites, but it was not indicated whether the mounds were occupied by ants or not. Possible benefits of such nesting behavior include constant temperature and moisture regimes, and protection from predation. We are unaware of any published accounts that suggest chelonians engage in anting behavior or nest in ant mounds.

During research conducted on the University of Michigan's E. S. George Reserve in southeastern Michigan over the past 15 years (Congdon et al., 1987), common snapping turtles (*Chelydra serpentina*) were observed nesting in active ant mounds on three occasions (Fig. 1). These nests represent approximately 1% of the total number of snapping turtle nests observed (340). Each of the three turtles successfully deposited and covered the eggs, but all three nests were subsequently destroyed by predators. In addition to the three completed nests, snapping turtles were occasionally observed digging in ant mounds prior to ovipositing elsewhere (J. Congdon, pers. obs.).

A recent observation prompted us to further examine the relationship between snapping turtles and ant mounds. On 26 May 1991, during a morning search to locate turtle nests, a disturbed ant mound in a known snapping turtle nesting area was found; the normally peaked dome of the approximately 1 m diameter mound was flattened. While we examined the area around the mound for evidence of the cause of the disturbance, the entire mound quaked. Upon careful excavation of the mound, a snapping turtle was located approximately 10 cm below the surface, roughly in the center of the mound.

The turtle was a 20-year old gravid female with a record of 17 captures since she was first marked on the George Reserve at the age of eight in 1979. Her straight-line carapace length was 234 mm and she weighed 3.17 kg. An X-radiograph indicated her clutch size was 27. The turtle was covered with carpenter ants (*Formica obscuriventris*). She appeared to have normal locomotory abilities, became aggressive when handled, and began walking when released. Superficial examination of the shell and skin revealed no damage. The most unusual feature of the turtle was the absence of leeches. Leeches are common ectoparasites of snapping turtles (Brooks et al., 1990) and all other gravid female snapping turtles examined during the 1991 nesting season (N = 39) had several to dozens of leeches attached, generally at the posterior end.

Vogt (1979) observed a common grackle (*Quiscalus quiscula*) removing leeches from basking map turtles (*Graptemys* spp.). The map turtles apparently offered no resistance as the grackle detached and consumed the leeches. Although the turtle we observed probably had its leeches removed by the ants (via consumption), it is not possible for us to determine if the turtle's behavior was directed for that result (i.e., if the turtle was exhibiting anting behavior).

The fact that snapping turtles are rarely seen in ant mounds may result from (1) infrequent use of ant mounds by turtles or, (2) the difficulty of observing the event. Three months after our observation the flattened top of the ant mound caused by the turtle's intrusion remained apparent. We hypothesized, therefore, that flat-topped ant mounds should occur