

In addition, an African softshell turtle, *Trionyx triunguis*, was seen in the canal next to Calistepe in 1993, and another in Fethiye harbor. Thus, the existence of this species which occurs further west at Dalaman (Atatürk, 1979) (Fig. 1) was recorded for the first time in this area.

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Stomach Contents of Commercially Harvested Adult Alligator Snapping Turtles, *Macrolemys temminckii*

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Studies of diet can provide insight into the behavior and habitat selection of a species. Individual growth rates, health, movement patterns, habitat preferences, and longevity are some factors that are strongly influenced by diet. For rare or declining species, diet data may be important for developing effective management strategies and identifying changes in natural systems.

The alligator snapping turtle, *Macrolemys temminckii*, is the largest freshwater turtle in North America (Ernst et al., 1994) and is confined to drainage systems along the Gulf Coast of the United States (Pritchard, 1989). It ranges west to the San Antonio River in Texas, east to the Suwannee River in Florida, and north in the Mississippi River system to central Illinois (Lovich, 1993). *Macrolemys* has historically been an important part of the culture and cuisine of the southeastern United States and is a common inhabitant of its wetlands. Exploitation of the meat of *Macrolemys* has caused a steep population decline in recent times (Pritchard, 1989; Ernst et al., 1994; Sloan and Lovich, 1995) and the species is currently a candidate for protection under the US Federal Endangered Species Act.

Habitats occupied by *Macrolemys* are usually highly productive, rich in organic matter, and possess a great diversity of potential food items. Habitats occupied by adults include freshwater lakes, rivers, canals, bayous, swamps with permanent water, and brackish coastal areas (Jackson and Ross, 1971; George, 1987; Sloan and Taylor, 1987; Dundee and Rossman, 1989).

A wide variety of food items have been identified from the stomachs of *Macrolemys*. Faunal components of the diet include many species of fish, salamanders (including *Siren* and *Amphiuma*), snakes, turtles, small alligators, crayfish, freshwater mussels, snails, ducks, and mammals. Vegetable matter includes spider lily seeds, acorns, tupelo fruit, palmetto berries, wild grapes, pawpaws, Spanish moss, and briar roots (Allen and Neill, 1950; Redmond, 1979; George,

1987; Shipman et al., 1991; Ernst et al., 1994; B. Harrel, pers. comm.).

Since most of the available diet data on alligator snapping turtles is based on only a few individuals, an analysis based on a large sample is needed to provide additional insight into their trophic ecology and to help design conservation and management plans. In this paper we present a quantification of the diet of adult *M. temminckii* harvested from the wild.

Methods. — Data were collected from alligator snapping turtles sold by commercial turtle trappers to a Louisiana processing operation that requested anonymity. Stomach contents were examined from 65 adult *Macrolemys temminckii* (53 females, 11 males, and 1 sex undetermined) collected from 27 March to 26 October 1986. Most of the turtles were harvested in Louisiana but a few were collected in Arkansas and Mississippi. All individuals examined were sexed based on the appearance of the reproductive organs as described in Dobie (1971). Males were captured only during March and April, whereas females were collected from March through October. Viscera and carapaces were removed, bagged, labeled, and frozen for later analysis. Data collected from each specimen included sex, total live weight, and carapace length. Age was estimated by removing the second right pleural scute, soaking it in water, backlighting it and counting annuli (Zangerl, 1969; Dobie, 1971). Means for various data, when presented, are followed by the standard deviation of the sample.

After thawing, stomach contents were removed and identified to genus and, whenever possible, to species. The following measurements were recorded regarding items consumed: weight (g), percent weight of the entire stomach sample, volume displaced (ml), and percent total stomach volume displaced. We also determined the frequency of occurrence for each item consumed (Bowen, 1983).

Table 1. Abundance of items (ranked by percent weight) found in the stomachs of 65 *Macrolemys* collected between March and October 1986.

Item	Number of Stomachs	Frequency Percent	Percent Weight	Percent Volume
Acorn	28	43.1	54.78	56.20
Mammal	10	15.4	11.73	10.46
Bird	3	4.6	6.69	6.86
Fish	37	56.9	5.95	6.61
Persimmon	5	7.7	5.84	5.71
Plant tuber	6	9.2	4.01	4.44
Cardboard	2	3.1	3.79	4.13
Wood	23	35.4	2.20	1.46
Turtle	9	13.8	1.77	1.78
Crayfish	17	26.2	1.47	1.30
Mollusk	7	10.8	0.68	0.46
Wild grape	9	13.8	0.30	0.29
Rock	1	1.5	0.25	0.09
Hickory nut	3	4.6	0.18	0.18
Unid. seeds	5	7.7	0.16	0.15
Pecan nut	3	4.6	0.06	0.09
Snail	1	1.5	0.05	0.03
Fish bait	1	1.5	0.03	0.03
Leeches	1	1.5	<0.01	<0.01
Fish hook	1	1.5	<0.01	<0.01

Results. — Mean carapace length for males ($\bar{x} = 49.46 \pm 7.04$ cm, $n = 11$, range = 36.0–57.1 cm) was significantly different from that of females ($\bar{x} = 43.08 \pm 4.32$ cm, $n = 53$, range = 35.0–50.9 cm) as shown by a two-tailed t-test for unequal variances ($t = 2.89$, $df = 11.6$, $P < 0.05$). Growth annuli were counted for 9 males ($\bar{x} = 25.24 \pm 11.37$, range = 11–45) and 27 females ($\bar{x} = 22.23 \pm 5.93$, range = 15–37) and provide minimum age estimates for the overall sample.

Many animal and plant taxa were represented in the 65 stomachs sampled as were some non-food items (Table 1). Mammal taxa included raccoon (*Procyon lotor*), muskrat (*Ondatra zibethica*), and rabbit (*Sylvilagus* sp.). Birds included wood duck (*Aix sponsa*) and unidentified passerines. Turtles included the slider turtle (*Trachemys scripta elegans*), carapace fragments of immature *M. temminckii* found in the stomachs of two males, and unidentified turtle carapace fragments. One stomach containing fragments of *M. temminckii* lacked any other contents and was the only stomach with a single prey taxon. Fish included chain pickerel (*Esox niger*), gar (*Lepisosteus* sp.), and European carp (*Cyprinus carpio*). Crustaceans included crayfish (*Procambarus* sp.) and mollusks included snails (*Helix* sp.) and freshwater unionid mussels. Leeches were found in one animal, and bait (fish heads of *Cyprinus* and *Ictalurus* cut with a knife and having monofilament attached) in another.

Plant material included unidentified plant tubers and stalks, persimmons (*Diospyrus virginiana*), wild grapes (*Vitis* sp.), acorns from water oak (*Quercus nigra*), overcup oak (*Q. lyrata*), and willow oak (*Q. phellos*), as well as pecans (*Carya illinoensis*), water hickories (*Carya aquatica*), and locust (*Robinia* sp.). In addition, several non-food items were identified, including rocks, fish hooks, wood, and cardboard.

Acorns (*Quercus* sp.) were consumed by 28 turtles (Table 1) and represented the most abundant food item by weight ($\bar{x} = 129.7$ g, range = 1–643 g) and by volume ($\bar{x} = 120.1$ ml, range = 1–685 ml). The next most abundant items by both weight and volume were mammal, bird, fish, and persimmon, respectively (Table 1). Fish were consumed by 37 turtles and represented the most commonly consumed item by frequency percentage (Table 1).

Since all males were captured in March and April, we compared their diets with those of females that were captured during the same time period (Table 2). We found no significant differences in the overall types of food items consumed, but frequency of occurrence calculations indicate that males and females were consuming these items in somewhat different abundances, though fish were the most commonly consumed item in both sexes. In descending order of frequency, the four most commonly consumed food items of males were fish, wood, turtle, and unidentified seeds, whereas females consumed primarily fish, wood, acorns, and crayfish.

Discussion. — Our study of the diet of alligator snapping turtles portrays an opportunistic omnivore and generalist and is consistent with the reports of other authors regarding its trophic ecology (Redmond, 1979; Pritchard, 1989),

Table 2. Sexual differentiation in abundance of items (ranked by frequency of occurrence in males) found in the stomachs of 11 male and 23 female *Macrolemys* collected between March and April 1986.

Item	Males		Females	
	Number of Stomachs	Frequency Percent	Number of Stomachs	Frequency Percent
Fish	8	72.7	17	74.0
Wood	6	54.5	15	65.2
Turtle	4	36.4	2	8.7
Unid. seeds	3	27.3	5	21.7
Mammal	2	18.2	5	21.7
Persimmon	2	18.2	4	17.4
Bird	2	18.2	3	13.0
Acorn	2	18.2	12	52.2
Plant tubers	1	9.1	3	13.0
Wild grape	1	9.1	8	34.8
Crayfish	1	9.1	10	43.5
Cardboard	1	9.1	1	4.3
Rock	1	9.1	0	—
Mollusk	1	9.1	4	17.4
Fish bait	0	—	1	4.3
Leeches	0	—	1	4.3

particularly in regard to the importance of fish in its diet. Based on the ability of *Macrolemys* to lure fish (Allen and Neill, 1950; Drummond and Gordon, 1979), we might surmise that fish are commonly caught by this method. However, at least some of the fish identified, such as gar and carp, are unlikely to have been lured by a worm imitation and were most likely scavenged or captured while foraging. The extent to which scavenging and predation are used in the acquisition of food can only be determined by detailed observations of *Macrolemys* feeding in the wild.

Spindel et al. (1987) suggested that luring to catch fish may become less important with increasing age and size. However, Sloan and Taylor (1987) found that although adult turtles do occasionally travel long distances, up to 6.8 km in six days, they were largely sedentary, suggesting that foraging is less important than luring by adults to obtain food. Consequently, if mobility decreases with age and size, then luring should not decrease, but might increase. Active foraging may be more important for *Macrolemys* in habitats that do not support fish stocks in adequate numbers.

The propensity for *Macrolemys* to eat other turtles, as shown by our data, is well known. Allen and Neill (1950) reported that *Macrolemys* consumed *Deirochelys*, *Kinosternon*, *Sternotherus*, and *Pseudemys*, and Pritchard (1989) added *Sternotherus minor* and *Chelydra serpentina* (also see Shipman et al., 1994) to the list of chelonian prey species. Selection to evade predatory *Macrolemys* is very strong in some turtle species. Jackson (1990) demonstrated that *Sternotherus minor* can detect and actively avoid the unseen presence of *Macrolemys* using chemical cues. Documentation of cannibalism in *Macrolemys* in the literature is scarce but our observations confirm the data summarized by Pritchard (1989).

Bivalve mollusks were not found in the diet in large numbers as might have been expected based on previous accounts (Redmond, 1979; Pritchard, 1989). In fact, Pritchard (1989) noted that alligator snapping turtles possess excep-

tionally heavy crushing jaws, presumably adapted for mollusk feeding, and Redmond (quoted in Pritchard, 1989) observed that large, heavy-shelled mussels comprise a large portion of the diet of *Macrolemys* in the Flint River of Georgia. The lack of mollusks observed in our study has several potential explanations. First, the disparity may represent geographic variation in the diet of *Macrolemys*. Second, the paucity of mollusks may be reflective of widespread declines in mollusk populations attributed to pollution, siltation, and riverine habitat destruction that are currently threatening 213 of 297 United States mollusk species with extinction (Williams et al., 1993). Third, *Macrolemys* in our study area may occupy habitats that do not favor mollusks. More detailed studies will be required to identify the causes of dietary differences.

Interpretation of diet by gut content analysis has several shortcomings that should be recognized. First, because of variation in digestive rates of different food items, the actual weights and volumes of food items may be misleading. For example, acorns were often found whole, whereas crayfish were represented by a single claw or fish by several scales. The calculation of simple frequency of occurrence is useful for determining how commonly food item types are being ingested, but does not necessarily represent their importance in the diet. Therefore, it is important to look at both calculations when evaluating the contributions of different food types.

The abundance of acorns and other nuts in the diet of alligator snapping turtles was surprising. Although acorns have been reported previously (A. Redmond, *pers. comm.* as cited in George, 1987; R. Vogt, *pers. comm.* as cited in Pritchard, 1989), the phenomenon has received little recognition and raises an interesting question. Although many animals are known to ingest and disperse seeds, are acorns being dispersed by alligator snapping turtles? If some are not digested, then alligator snapping turtles may play an important role as seed dispersers and germination enhancers in riparian ecosystems as whole seeds pass through the digestive tract intact and are deposited with the feces. Moll and Jansen (1995) discussed the role of two aquatic turtle species in the establishment of certain riparian plant species. They concluded that the distinctive flora of some microhabitats was attributable to the foraging activity of turtles.

Seasonally fluctuating water levels certainly bring *Macrolemys* into shallow floodplains that dry out later in the summer. The seeds of certain species of bottomland hardwoods possibly deposited in ephemeral shallows by *Macrolemys* may germinate when the water recedes. Of the nuts consumed by *Macrolemys*, pecans are native to floodplain soils of the Mississippi Valley from Louisiana to Illinois. Water hickories and the three oak species found in our samples occur primarily in river bottoms and are often in association with overcup oak (Elias, 1980). Although downstream dispersal of nuts of these species is passive, potential agents of seed dispersal such as alligator snapping turtles may be important for upstream and lateral distribution. Substantial upstream movements of *Macrolemys* have been documented by Wickham (1922) and Shipman et al. (1991).

Although it is widely recognized that alligator snapping turtle populations are heavily exploited (Sloan and Lovich, 1995) and likely declining (Pritchard, 1989; Ernst et al., 1994), little attention has been focused on the overall role of the species as a scavenger, predator, and possible plant disperser. Our data suggest that *Macrolemys* has an important function in the trophic structure and dispersal mechanisms of riparian systems. Effective management strategies for rivers and wetlands in the southern United States should include efforts to protect turtles such as *Macrolemys*.

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Distribution of Nesting Sites of Sea Turtles in Okinawajima and Adjacent Islands of the Central Ryukyus, Japan

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The Ryukyu Archipelago is located in the subtropical region of East Asia and extends from Taiwan to Kyushu in Japan (123°E, 24°N – 131°E, 31°N, Fig. 1). Three sea turtle species, the loggerhead (*Caretta caretta*), green turtle (*Chelonia mydas*), and hawksbill (*Eretmochelys imbricata*), are known to nest on islands of this archipelago (e.g., Kamezaki, 1989, 1991). Nesting data have largely been collected from the southern and the northern Ryukyus (Kamezaki, 1991). Very little information is available regarding sea turtle nesting in the Okinawa Islands of the central Ryukyus (Uchida et al., 1984), even though islands in this region have many sandy beaches that are apparently suitable for sea turtle nesting. Considering that quite a few