

Food Habits of the Chinese Stripe-necked Turtle, *Ocadia sinensis*, in the Keelung River, Northern Taiwan

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ABSTRACT.—Stomach contents from 186 *Ocadia sinensis* collected from the Keelung River, northern Taiwan, between July 1995 and April 1997 were examined. Diet composition varied by sex. Females shifted from an omnivorous to a herbivorous diet as they grew, and they consumed more plant material compared to males. Volumetrically, plant matter represented 87.7% of the total stomach contents in females, whereas it only constituted 39.5% in males. Seasonal differences in diets were also found. Animal matter contributed more to cool season diets. Females, especially, tended to take plants in much greater proportion in the warm season (94.8% in volume) compared to the cool season (50.9%). In males, animal matter occupied 54.4% and 71.1% of the total volume of stomach contents both in the warm and cool season, respectively. The percentage of empty stomachs was greater in the cool season (41.2%) than in the warm season (13.3%).

The Chinese stripe-necked turtle (*Ocadia sinensis*) is reported to be largely herbivorous, feeding mainly on plant material both in nature and in captivity (Smith, 1923; Horikawa, 1934; Ernst and Barbour, 1989). Although *O. sinensis* is abundant and widespread in rivers, ponds, and lakes of Taiwan (Pope, 1935; Mao, 1971), its life history is poorly known. Until recently, little has been published dealing with its taxonomy and ecology (McCord and Iverson, 1992; 1994; Chen and Lue, 1998).

Knowledge of the food habits of a given species may provide insights into the links between animals and their environments. Many studies on turtles have described resource partitioning in terms of food, space, time, or their interaction (see Toft [1985] for review). Morphometrics and growth rates often are associated with feeding niches (Berry, 1975), and dietary shifts with body size have been documented for several turtles (Clark and Gibbons, 1969; Moll, 1976; Georges, 1982; Hart, 1983). As ectothermic organisms, the foraging behavior and diet composition of turtles may also be affected by seasonal changes of ambient temperature and food availability (Parmenter and Avery, 1990; Lagueux et al., 1995).

In this study, we provide data on the dietary habits of *O. sinensis*, and examine intersexual, ontogenetic, and seasonal variation in the composition of the food consumed.

MATERIALS AND METHODS

Study Area.—We collected turtles from a 3.5-km stretch of the midstream of the Keelung River

(121°41'E, 25°06'N), at 4–6 m elevation. The river in the study area is narrow, meandering, and sluggish, with a width of about 25 m and depth of approximately 1.5 m (Fig. 1). The river bottom mainly consists of silt and sand. The water is usually turbid. Both banks of the river are covered mostly with cultivated bamboo shrubs. Riparian vegetation consists primarily of exotic perennial grasses (including *Brachiaria mutica* and *Pennisetum purpureum*). Some non-grass herbaceous plants, including *Murdannia keisak* (Commelinaceae), *Ludwigia octovalvis* (Onagraceae), *Seigesbeckia orientalis*, *Elipta prostrata* (Compositae), and some species of Polygonaceae, occasionally grow on both banks. Few typically aquatic plants exist in this area. Only some filamentous algae and *Lemna aequinoctialis* (Lemnaceae) appear in early summer.

The average monthly temperature in the warm season (May–November) was 25.4 °C (range: 20.5–28.5 °C) and 17.1 °C (15.2–20.6 °C) in the cool season (December–April). According to data collected by the Environmental Protection Administration, average water temperature also changes seasonally, from 20.0–31.4 °C in the warm months to 14.5–18.9 °C in the cool months. Precipitation is distinctly seasonal, with an average of 218 mm of rain per month during April–August, although typhoons may bring heavy rain in the course of a few days. A total of 320 mm of rain falls per month during the rest of the year (Fig. 2). Discharge in this area was highly variable, with 7.71–20.16 m³/sec during April–August and 25.34–46.76 m³/sec during September–March. In the cool season, changes in water level often result in the inundation of bank vegetation. The water quality in the midstream of the Keelung River was graded

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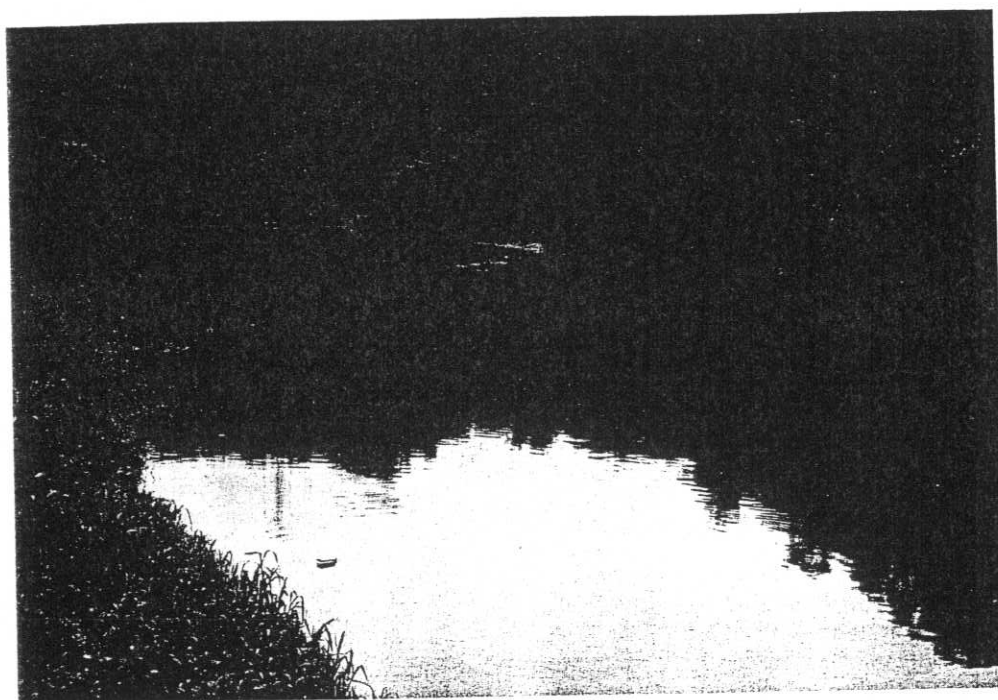


FIG. 1. Representative view of the study site of *Ocadia sinensis* in the Keelung River, northern Taiwan.

as medium-polluted by organic sewage discharged from the nearby area.

Methods—Our study was conducted during both the warm and cool seasons, July–December 1995, February–May 1996, and March–April 1997. Turtles were collected with funnel traps baited with canned cat food, with a long-handled dipnet, or by hand while patrolling along the banks. The bait was enclosed in a wire cage

to prevent it from being ingested by turtles. Maximum carapace length (CL) of each turtle captured was taken with dial calipers to the nearest 0.1 mm. Turtles were considered as males if the position of cloacal opening was located beyond the rear carapacial margins (Ernst and Barbour, 1989; McCord and Iverson, 1992).

Stomach contents were obtained by gently flushing the stomach (Legler, 1977; Parmenter, 1980) and were preserved in 70% ethanol for later identification and quantification. Turtles were flushed as soon as possible, usually within one hour after capture. We released turtles at the site of capture within one day thereafter. Food items were identified to the lowest taxon possible. Several items, apparently plant roots and shoots, were not clearly identified and thus were simply classified as “shoots and roots.” Some fragile items of apparent terrestrial insect origin (e.g., wings, appendages, carapaces) were grouped as “unidentified terrestrial insects.” Fragments of litter (sands, dry leaves, and stems) were assumed to have been ingested accidentally and were treated as a separate category.

Percent frequency of occurrence, percentage of total volume, and index of relative importance were determined for each item. The volume was estimated by removing excess moisture and measuring by water displacement in a graduated cylinder (Hart, 1983). Frequency of occurrence of a given item was defined as the

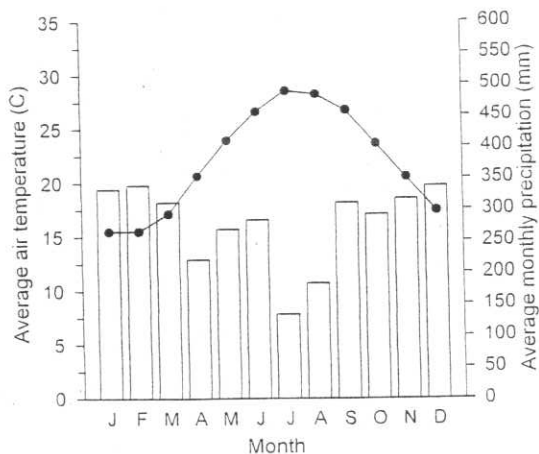


FIG. 2. Climatological data for Keelung (5 km E of the study site), taken from Central Weather Bureau, R.O.C. Shaded bars represent monthly precipitation; filled circles show mean monthly air temperature. All values represent average from 1901–1995.

number of samples containing an item expressed as a percentage to the total number of samples. The index of relative importance (IRI) was calculated for each food item using the method of Bjørndal et al. (1997):

$$\text{IRI} = 100(F_i V_i) / \sum (F_i V_i)$$

where F is the percent frequency of occurrence, V is the percentage of total volume, and n is the number of food items.

To test for seasonal variation in diet composition, we divided samples into two periods, December–April, the cool season, and May–November, the warm season. To investigate variation in dietary habits with body size, we classified turtles arbitrarily into five size classes on the basis of CL (I: ≤ 99.9 mm, II: 100.0–124.9 mm, III: 125.0–149.9 mm, IV: 150.0–174.9 mm, and V: ≥ 175.0 mm). Because *O. sinensis* is sexually dimorphic in size, size-class V consisted entirely of females. Because of small sample sizes, we did not estimate the volume percentage of the food items for juveniles.

Items found in $<1\%$ of the samples were considered of insignificant dietary importance and were omitted from these analyses. Major food items, $>20\%$ by percent occurrence, $>10\%$ by volume, and >10.0 by IRI, were compared between the sexes and seasons. As has been pointed out (Hyslop, 1980; Bjørndal, 1997), analysis of one dietary parameter alone may yield misleading results of the relative importance of specific food items. Dietary diversity, breadth, and overlap were estimated using the index of relative importance. We calculated Shannon-Wiener's index to estimate dietary diversity (Krebs, 1989). The diversity index increases with an increase in the number of dietary resources, so low values represent dietary specialists and high values represent generalists. Dietary breadth was calculated using the standardized Levins' measure to determine uniformity of food resource used (Levins, 1968; Hurlbert, 1978). This measure is expressed on a scale from 0.0 to 1.0 and usually used to compare specialist tendencies among groups. Dietary overlap between groups was assessed using Horn's measure (Horn, 1966). The measure ranges from 0.0 to 1.0; the fewer the commonly used resources are, the lower the measure of overlap becomes.

RESULTS

A total of 186 stomachs were flushed, yielding 136 samples. Of these, 64 were from males (100.6–180.4 mm CL), 58 from females (100.0–250.0 mm CL), and 14 from unsexed juveniles (62.8–99.3 mm CL). Two males were flushed twice at an interval of about 50 d. Cumulative volume of stomach contents was 49.5 ml ($N =$

64) in males, and 117.1 ml ($N = 58$) in females. Table 1 summarizes the percent occurrence and volume percentage of each food item. The diet composition varied with sex, season, and body size.

Variation in diet between the sexes and body size classes.—Females tended to feed predominately on plant matter, despite ingesting a wide range of animal food items. Plant items (mainly terrestrial *Murdannia keisak* leaves) occurred in 75.9% of the stomachs and occupied 87.7% of the samples by volume (Table 1). Diet composition of males was a fairly balanced mix of plant and animal foods. Although animal matter was present in 82.8% of the stomach samples, it only comprised 60.5% of the total volume.

By percent occurrence, males mainly fed on exotic aquatic snails (*Physa acuta*) (37.5%), dipteran larvae and pupae (mainly blackflies, Simuliidae) (35.9%), oligochaeta (including earthworms and sewage worms) (28.1%), *M. keisak* leaves (26.6%), and terrestrial insect fragments (20.3%). Females ate *M. keisak* leaves (55.2%), dipteran larvae and pupae (34.5%), snails (31.0%), and terrestrial insect fragments (29.3%). By volume, males fed on dipteran larvae and pupae (28.7%), *M. keisak* leaves (22.5%), and oligochaeta (13.6%), whereas females predominately ate *M. keisak* leaves (74.4%). In the major food items, there were significant intersexual differences in relative frequency ($G = 25.87$, $P < 0.01$), volume ($G = 64.76$, $P < 0.01$), and IRI ($G = 111.09$, $P < 0.01$). Dietary overlap between the sexes was 0.53.

Analyses for dietary diversity and breadth using IRI indicated that females had a narrower dietary range than males (Table 2). Females had higher selectivity for *M. keisak* leaves within the broad spectrum of food items, whereas males ingested a greater variety of food items.

Diet changed dramatically with body size in females. By percent occurrence, females showed a gradual increase in percent occurrence of plant matter and a decrease in animal items with an increase in body size (Fig. 3). The most pronounced shift occurred in the size classes from the 125.0–149.9 to 150.0–174.9 mm CL (size class III to IV). Larger females were primarily herbivorous, ingesting *M. keisak* leaves more frequently, and much less animal matter than did smaller females (Table 3). However, there was no obvious dietary variation with body size increase in males.

Turtles <100.0 mm CL fed on a limited number of food types. They tended to be carnivorous with animal matter present in 85.7% of the stomach samples.

Seasonal variation in diet.—Because diet composition differed greatly between the sexes, we

TABLE 1. Stomach contents (percentage occurrence and percentage of total volume) of *Ocadia sinensis* captured in the Keelung River, northern Taiwan.

Food items	Juveniles (N = 14) % Freq.	Males (N = 64)		Females (N = 58)	
		% Freq.	% Vol.	% Freq.	% Vol.
PLANT MATERIAL	50.0	54.7	39.5	75.9	87.7
Filamentous algae	—	—	—	1.7	<0.1
Grasses	7.1	3.1	0.2	17.2	3.9
<i>Murdannia keisak</i> (leaves)	—	26.6	22.5	55.2	74.4
<i>Polygonum</i> sp. (seeds)	7.1	12.5	1.5	15.5	0.4
<i>Eclipta prostrata</i> (leaves and fruits)	7.1	12.5	9.8	5.2	0.8
<i>Lemna aquinoctialis</i>	—	—	—	3.4	6.8
<i>Ageratum conyzoides</i> (leaves)	—	—	—	5.2	1.0
Plant roots and shoots	35.7	18.8	5.5	3.4	0.3
ANIMAL MATERIAL	85.7	82.8	60.5	62.1	12.3
Gastropoda	—	37.5	9.2	31.0	4.7
Insecta	57.1	53.1	33.7	43.1	6.2
Ephemeroidea larvae	—	1.6	0.4	—	—
Coleoptera	—	3.1	<0.1	1.7	<0.1
Diptera larvae and pupae	57.1	35.9	28.7	34.5	3.5
Lepidoptera larvae	—	7.8	1.2	5.2	0.3
Plecoptera larvae	—	1.6	0.2	5.2	2.1
Odonata larvae	—	3.1	<0.1	3.4	<0.1
Unidentifiable terrestrial insects	14.3	20.3	3.0	29.3	0.3
Decapoda	—	—	—	1.7	<0.1
Amphipoda	—	6.3	<0.1	1.7	<0.1
Oligochaeta	14.3	20.3	13.6	3.4	1.0
Hirundinea	14.3	12.5	2.8	5.2	<0.1
Pisces	7.1	14.1	1.1	6.9	0.3

analyzed the seasonal variation of diet in males and females separately. There were seasonal differences in major diet composition in both sexes: by percent occurrence (males: $G = 121.94$, $P < 0.01$; females: $G = 51.08$, $P < 0.01$), by overall volume percentage (males: $G = 123.44$, $P < 0.01$; females: $G = 73.82$, $P < 0.01$), and by IRI (males: $G = 187.53$, $P < 0.01$; females: $G = 49.94$, $P < 0.01$).

Females tended to feed predominantly on plant matter in the warm season, when plants composed 94.8% of the total volume (Fig. 4). However, females consumed mixed diets of various food items in the cool season, with plant matter only contributing 50.9% of the total volume. Males were more generalized in the warm season, with animal food occupying only 54.4% of the overall volume, although they ate more animals in the cool season (71.1%). By percent occurrence, the consumption of plant matter decreased in the cool season. In males, plant matter was present in 66.7% of the warm-season samples and 41.9% of the cool-season sample; in females, plant matter contributed 81.3% and 69.2% respectively (Fig. 5). Volumetrically, males ate more dipteran larvae and pupae (44.9%) and *M. keisak* (30.5%) in the warm months, whereas they ingested oligochaeta (31.0%), snails (21.8%), and *E. prostrata* (17.5%) more in the cool season (Fig. 4). Females fed mainly on *M. keisak*

(83.0%) in the warm season, whereas they ate more *M. keisak* (30.4%), snails (21.0%), dipteran larvae and pupae (18.6%), and grass leaves (14.0%) in the cool season. By percent occurrence, the seasonal dietary shifts were not so obvious (Fig. 5). Percent occurrence of most food items ingested by females decreased in the cool-season sample. In males, there was a slight increase only in two major items, oligochaete and fish.

Ocadia sinensis tended to ingest fewer food items in the warm season, when turtles, especially females, exhibited lower diversity and narrower breadth in diets (Table 2); females were more generalized in the cool season. Both males and females broadened their dietary breadth from the warm to the cool season. Dietary overlap between the sexes decreased slightly from 0.51 in the cool season to 0.48 in the warm season.

Other observations.—Turtles from the cool months had empty stomachs more frequently (41.2%) than those from the warm months (13.3%). Turtles tended to ingest more litter fragments in the cool season. Volumetrically, the fragments occupied only 0.6% of the warm-season sample, whereas they composed 11.2% of the cool-season sample. Fish were rarely found in the stomachs; most fish items found were scales, flesh, and bones of large size.

TABLE 2. Dietary diversity and breadth by index of relative importance of *Ocadia sinensis* by sex and season. T denotes a value <0.1.

Food items	Males			Females		
	Warm	Cool	Overall	Warm	Cool	Overall
PLANT MATERIAL						
Filamentous algae	—	—	—	T	—	T
Grasses	T	T	T	0.6	9.9	1.5
<i>Murdannia keisak</i> (leaves)	24.9	6.2	20.6	96.1	51.9	91.1
<i>Polygonum</i> sp. (seeds)	1.4	—	0.8	0.3	—	0.1
<i>Eclipta prostrata</i> (leaves and fruits)	2.0	6.5	5.0	T	0.4	0.1
<i>Lemna aquinoctialis</i>	—	—	—	0.9	—	0.5
<i>Ageratum conyzoides</i> (leaves)	—	—	—	T	0.5	0.1
Plant roots and shoots	4.7	1.1	4.2	T	—	T
ANIMAL MATERIAL						
Gastropoda	1.4	40.3	14.0	1.0	20.9	3.2
Insecta						
Ephemeroidea larvae	T	—	T	—	—	—
Coleoptera	T	T	T	T	—	T
Diptera larvae and pupae	63.3	T	41.7	0.5	12.9	2.7
Lepidoptera larvae	T	1.3	0.4	T	0.4	T
Plecoptera larvae	T	—	T	0.4	—	0.2
Odonata larvae	T	T	T	T	—	T
Unidentifiable terrestrial insects	1.6	1.7	0.2	T	1.1	0.2
Decapoda	—	—	—	—	T	T
Amphipoda	T	T	T	T	—	T
Oligochaeta	0.6	34.2	11.2	—	1.7	0.1
Hirudinea	T	5.7	1.4	—	0.2	T
Pisces	T	3.0	0.6	T	T	T
Diversity	1.55	2.20	2.39	0.33	1.98	0.63
Breadth	0.16	0.30	0.30	0.01	0.19	0.02

DISCUSSION

Although *Ocadia sinensis* is reported to feed chiefly on various aquatic plants (Smith, 1923; Horikawa, 1934; Ernst and Barbour, 1989), our results indicate that this turtle is omnivorous rather than entirely herbivorous. *Ocadia sinensis* seems to be an opportunistic omnivore with both plant and animal matter contributing substantially to the diet (Table 1). Turtles consuming a mixture of plant and animal foods may have a greater digestive efficiency than those taking plant or animal food alone (Bjorndal, 1991). *Murdannia keisak*, a perennial herbaceous plant, was the most common component of the diet of this turtle. Since this plant was not the dominant species in our study area, its consumption was not simply because it was the most common food available in the environment. Conversely, some grasses, such as *Brachiaria mutica*, were present and abundant throughout the year, but they occurred only at low frequency in the diet of *O. sinensis*. This suggests a preference by turtles for specific food types, at least for some items.

Male and female *O. sinensis* differed greatly in the food consumed. Females ate a greater amount of plant matter than did males, both in terms of percent occurrence and volume per-

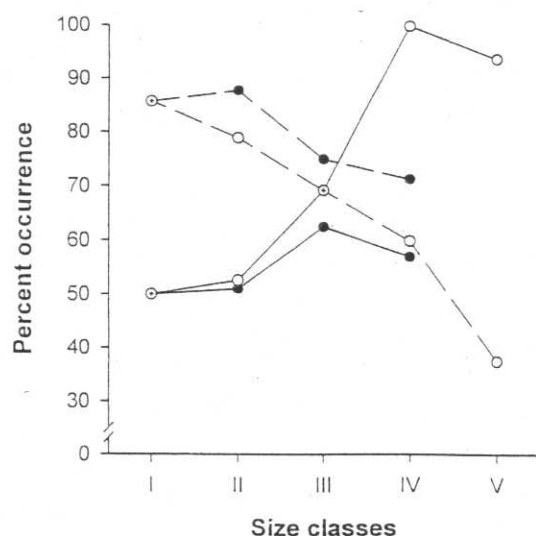


FIG. 3. Relationship between plant and animal matter of stomach samples (by percentage of occurrence) and carapace length in *Ocadia sinensis*. (○ for females, ● for males, solid lines for plant matter, and dashed lines for animal matter).

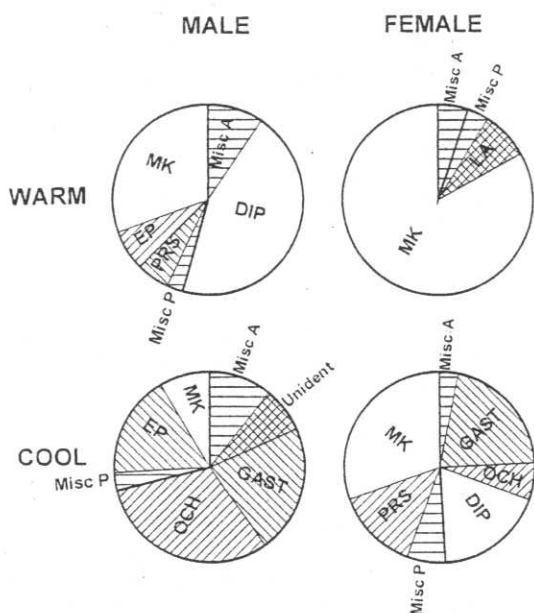


FIG. 4. Differences in the composition of the diets of *Ocadia sinensis* in volume percentage with sexes and seasons. Food items are abbreviated as follows: DIP: Dipteran larvae and pupae; EP: *Eclipta prostrata* leaves and fruits; GAST: Gastropoda; GRAM: Gramineae leaves; LA: *Lemna aquinoctialis*; Misc A: Miscellaneous animal matter; Misc P: Miscellaneous plant matter; MK: *Murdannia keisak* leaves; OCH: Oligochaeta; PRS: Plant roots and shoots; Unident: Unidentifiable terrestrial insects.

centage. Intersexual dietary differences were evident as in some other turtles (Bury, 1986; Fachin Teran et al., 1995). In turtle species with sexual size dimorphism, dietary variation between the sexes has been attributed to body size effects (Mahmoud and Klicka, 1979; Kennett and Tory, 1996). Differences in head and body size may consequently affect the dietary preference between the sexes. Since growth rate and absolute size differ greatly between the sexes in *O. sinensis* (Chen and Lue, 1998), dietary differences can be partly explained by body size effects. Male *O. sinensis* tended to take more small animal prey, such as dipteran larvae and pupae; females consumed more *M. keisak* leaves. Sexual differences in diet also have been related to differences in microhabitat use (Plummer and Farrar, 1981). Intersexual preferences in microhabitat were not investigated in our study, and further detailed studies are necessary to clarify this question.

Male *O. sinensis* fed on a balanced mixture of plant and animal food; however females showed an ontogenetic shift in diet (Table 3). Smaller females (<125.0 mm CL) fed principally on animal material, as did males. Larger fe-

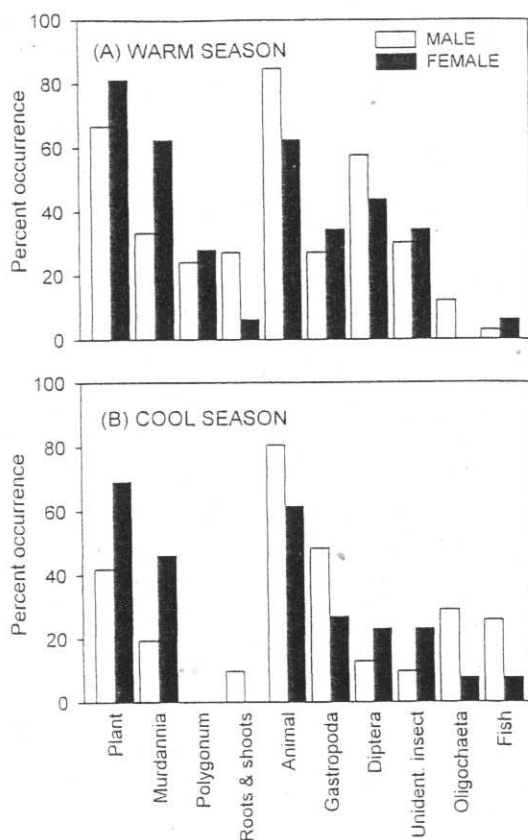


FIG. 5. Major food items (>20% by percent occurrence) of *Ocadia sinensis* stomach contents from the warm and cool season.

males ingested more plant matter of terrestrial origin than aquatic plants. The occurrence of plant items became more frequent as females grew, reaching over 90% in size classes IV and V (≥ 150.0 mm CL; Fig. 3). Ontogenetic dietary changes are common among batagurid and emydid turtles. In general, these turtles are more carnivorous as juveniles, but shift toward more herbivory as they grow older (Clark and Gibbons, 1969; Moll, 1976; Parmenter, 1980; Bury, 1986). Most of the size-correlated variation in diets in turtles can be explained on the grounds of energetic or morphological constraints (Clark and Gibbons, 1969; Mahmoud and Klicka, 1979; Parmenter, 1980). Small juveniles may have a greater demand for protein and calcium for faster growth rates (Clark and Gibbons, 1969; Parmenter and Avery, 1990). On the other hand, smaller turtles may not be able to handle or ingest plant tissues due to the smaller size of their mouths. For small turtles, consumption of animal food may compensate for the costs of prey capture. As turtles grow, the energetic return from animal matter might

TABLE 3. Major food items (>20% by percent occurrence) of *Ocadia sinensis* from different sized turtles. See text for explanation of size classes.

	Males			Females			
	II (N = 41)	III (N = 16)	IV (N = 7)	II (N = 19)	III (N = 13)	IV (N = 10)	V (N = 16)
PLANT MATERIAL	51.0	62.5	57.1	52.6	69.2	100.0	93.8
<i>Murdannia keisak</i> (leaves)	24.4	31.3	28.6	31.6	53.8	80.0	68.8
<i>Polygonum</i> sp. (seeds)	9.8	12.5	28.6	15.8	15.4	0.0	25.0
ANIMAL MATERIAL	87.8	75.0	71.4	78.9	69.2	60.0	37.5
Gastropoda	43.9	31.3	14.3	26.3	46.2	40.0	18.8
Dipteran larvae and pupae	41.5	31.3	14.3	63.2	30.8	10.0	18.8
Unidentifiable terrestrial insects	26.8	31.3	28.6	42.1	23.1	20.0	12.5
Oligochaeta	22.0	12.5	28.6	5.3	15.4	10.0	6.3

be too small to satisfy their nutritional requirements.

However, the dietary shifts we observed may not be attributed entirely to the effects of body size. The occurrence of animal and plant matter differed greatly between the sexes in size class IV (≥ 150.0 mm CL). For example, females fed on *M. keisak* more frequently than males of similar size (Table 3). This may have resulted from intersexual differences in growth patterns. The quality and quantity of foods ingested are critical to ecological energy budgets and growth models (Porter and Tracy, 1983). In *O. sinensis*, growth in males >120.0 mm CL slows down sharply, whereas it was still detectable in females >200 mm CL (Chen and Lue, 1998). Females may need the bulk of available plant foods for the ongoing growth, whereas animal foods are satisfactory for the nutrient requirements of the smaller males.

Larger turtles seem to concentrate more on plant matter for the bulk of their diet. However, the bulk of vegetable food items from large females may overshadow the importance of animal matter. Although we did not determine food volume within body size groups, larger turtles seemed to ingest a greater amount of various food items. Because the average body size of females is greater than that of males in *O. sinensis*, the importance of plant material in females may be overestimated. As in the cool-season samples of males, *E. prostrata* only represented 9.7% of the sample, although it represented 15.4% of the total volume (Fig. 4). Water trapped with the food items may cause errors in the volume estimate (Hyslop, 1980). Moreover, storage of stomach content samples in 70% ethanol may also result in dehydration in some items such as dipteran larvae and pupae.

A few authors have documented seasonal shifts in diet composition in turtles (Mahmoud, 1968; Parmenter, 1980). In those studies, the summer diet included plants and various animal prey, whereas the winter diet was composed largely of aquatic plants. Such a shift has

been generally attributed to a seasonal change in food availability (Parmenter and Avery, 1990; Lagueux et al., 1995). Our results showed that *O. sinensis* took a greater volume of animal matter in the cool season (Fig. 4). This difference may be due to differences in relative availability of plant and animal foods that fluctuate under seasonal variations in rainfall and temperature. In our study area, small aquatic snails and sewage worms are abundant in late spring. In summer, larvae of blackflies usually appear in clumps floating on the surface of water. Submerged vegetation (mostly *Brachiaria mutica* and some *Murdannia keisak*) was luxuriant during the warm months. Turtles tended to ingest greater amounts of plant items of terrestrial origin. Emergent vegetation was rare, and submergents were inundated periodically by the heavy rainfall in winter. The fluctuation of water levels and low temperature in the cool season made sources of plant food less available to turtles. Discharge in the Keelung River may vary more than 50-fold during brief periods of high rainfall. In the cool season, the temperature and rainfall usually varied weekly with approaching cold fronts. Cycles of inundation and low temperature occurred roughly on a one week period.

Mahmoud (1968) and Parmenter (1980) found that plant matter was not a scarce resource in the cool season. However, plant are less accessible to turtles in the Keelung River in the cool season. Environmental temperatures influences not only foraging behavior, but also physiological aspects of digestion (Parmenter and Avery, 1990). Digestion of plant material is generally less efficient at lower temperatures. Most turtles are opportunistic feeders, and some species are known to change their feeding habits with seasonal changes in availability of food items (Mahmoud and Klicka, 1979). Consumption of easily acquired aquatic food items may be sufficient to meet lower energy demands.

One hypothesis suggests that partitioning in diet and habitat should be lower during periods

of resource scarcity if animals disperse (Pyke, 1984; Stephens and Krebs, 1986), whereas high dietary and habitat overlap will occur during periods of scarce resources if animals do not disperse (Schoener, 1974). The movements of *O. sinensis* were limited to a small area (about 300 m) in the Keelung River (Chen and Lue, 1998), and dietary overlap between the sexes seemed to be slightly higher in the cool season. During periods of resource scarcity, such as the cool season in this study, turtles may tend to feed on any available food items. This was supported by the higher proportion of indigestible litter fragments in the cool season samples. The low diversity of food items in the warm season may be the result of high abundance of specific resources. Food preferences by turtles have been reported when resources were abundant in the environment (Parmenter, 1980; Bury, 1986).

There was a high level of dietary partitioning between the sexes in *O. sinensis*. In unproductive, nutrient-deficient environments, turtles may improve their efficiency by using available food resources. The Ouachita map turtle (*Graptemys pseudogeographica ouachitensis*), which occupies a riverine habitat with almost no aquatic vegetation and widely fluctuating water levels, feeds mainly on terrestrial plants and other materials of terrestrial origin (Moll, 1976). *Emydura krefftii* from an unproductive lentic lake also utilized foods of terrestrial origin (Georges, 1982). In our study, terrestrial food resources were taken less frequently in the unproductive cool months, when turtles tended to ingest more diverse food items of submerged origin.

There was a higher frequency of empty stomachs in the cool season; this may be a result of low food availability or metabolic depression. Turtles generally feed when body temperatures are $>20^{\circ}\text{C}$ (Mahmoud and Klicka, 1979). As the average water temperature in the cool season was nearly lower than 20°C , turtles may forage less frequently during the cool months.

The occurrence of fish probably represents consumption of carrion. Our stomach-flushing technique may have underestimated the frequency of fish in the diet, as most fish items had been partly digested. Only some scales and bones were flushed. Fish were seldom found in stomach samples, whereas sardine-baited traps attracted both sexes of *O. sinensis*, suggesting that this species may feed on fish occasionally.

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