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Changes in the Population Structure and Diet of the Chinese Stripe-Necked Turtle (*Mauremys sinensis*) Inhabiting a Disturbed River in Northern Taiwan

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Tien-Hsi Chen and Kuang-Yang Lue (2009) Changes in the population structure and diet of the Chinese stripe-necked turtle (*Mauremys sinensis*) inhabiting a disturbed river in northern Taiwan. *Zoological Studies* **48**(1): 95-105. The population structure and diet of the Chinese stripe-necked turtle, *Mauremys* (*Ocadia*) *sinensis*, were investigated in the Keelung River, northern Taiwan, following severe habitat disturbances. During a 2-yr levee construction and channel dredging project, the physical characteristics and riparian vegetation of the river were dramatically altered. Compared with results obtained prior to the disturbance, sex ratios were significantly skewed toward males, and the proportion of larger females significantly decreased both during and after project construction. Moreover, fewer small-sized juveniles were found following the construction disturbance. The diet of *M. sinensis* also changed, with plant materials assuming greater importance than they had prior to the disturbance. Furthermore, the mean volume of food ingested decreased both during and after the project. This tendency was more pronounced in females than males. Dietary overlap indices between the sexes during (0.591) and after (0.922) the project suggest that intraspecific food competition increased throughout the duration of the study. http://zoolstud.sinica.edu.tw/Journals/48.1/95.pdf

Key words: Habitat disturbance, Population structure, Diet, River modification, *Mauremys sinensis*.

The alteration and degradation of riverine and riparian habitats as a result of human activities is often detrimental to populations of freshwater turtles, as well as to many other aquatic organisms (reviewed in Moll and Moll 2004). Accelerating river modification is one of the major factors responsible for the worldwide decline of freshwater turtle populations, especially during the past few decades (Dodd 1990, Garber and Burger 1995, Gibbons et al. 2000, Mitchell and Klemens 2000). Riverine turtles decline because their abundance and distribution may be associated with physical and biotic characteristics, such as channel width, water depth, flow velocity, emergent vegetation, and the availability of basking/resting sites (Pluto and Bellis 1986, Buhlmann and Vaughan 1991, Fuselier and Edds 1994, Reese and Welsh 1998a, DonnerWright et al. 1999, Bodie et al. 2000, Bodie 2001). Altering these characteristics makes habitats less optimal for turtles.

Both channel and riparian areas play critical roles in the life cycle of river-dwelling turtles by providing essential microhabitat and food resources (Burke and Gibbons 1995, Reese and Welsh 1998b, Bodie 2001). Degradation of both aquatic and upland habitats associated with human activities, such as flood control projects, may lead to rapid declines in turtle populations by altering the biophysical components of the environment (Gibbons et al. 2000). In an intensively human-

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altered environment, turtle population structures also tend to become male-biased, with older age classes dominant (Garber and Burger 1995, Marchand and Litvaitis 2004).

According to the Water Conservancy Agency, Ministry of Economic Affairs, Taiwan, > 70% of the total length of the rivers in Taiwan have flood-control facilities. Despite this, the ecological impacts of habitat modification on riverine biota, including turtles, have not been adequately investigated. In a preliminary study conducted in a cemented-lined channel, modification caused detrimental impacts to the native riverine biota, including turtles, in central Taiwan (Lin et al. 2007); species diversity decreased, and the dominant species were displaced by nonindigenous ones.

During the course of river management projects, the riparian vegetation and streambed are often considerably altered, potentially depriving turtles of critical habitats, such as nesting sites, and food resources. Fragmentation accompanying riverine habitat alteration also leads to population isolation, potentially with adverse genetic effects (Dodd 1990, Bodie 2001), and makes surviving populations more vulnerable to stochastic environmental effects, such as floods, human-caused mortality, such as from the effects of adjacent roads (Gibbs and Shriver 2002), and increased predation on remaining small populations.

Following heavy flooding in 1998 along the Keelung River, northern Taiwan, a large-scale flood control project consisting of levee construction and channel dredging was carried out to prevent the adjacent suburban areas from further inundation. Prior to flooding and river modification, we had sampled turtle populations along parts of the Keelung River (Chen and Lue 1998 1999). We were then able to collect demographic and dietary information on turtles from the same population both during and after the flood control project. This comparative approach allowed us to assess the effects of river modification on critical *Mauremys sinensis* life history attributes affecting long-term survival, as well as to assess both immediate and short-term impacts on the turtle population.

MATERIALS AND METHODS

Study area

This study was conducted along a 3.5 km segment of the middle portion of the Keelung River (121°40'E, 25°05'N) in northern Taiwan. Prior to river modification, the study site comprised four pools (pools 1 to 4), separated by a series of shallow riffle zones (see descriptions in Chen and Lue 1999). The water level in the study area was highly variable, ranging in depth from 1.5 to 4 m in deep pools; occasional floods inundated the adjacent urban areas to > 10 m above normal water levels. The annual precipitation recorded at the Wutu Gauging Station (121°40'49"E, 25°04'32"N), near the study area, varied from 200.4 to 516.0 m during 1997-2000. Occasionally, there were several days with very high rainfall (300-500 mm/d) caused by typhoons. In Oct. 1998, for example, a typhoon caused extensive flooding in the Keelung River and adjacent suburban areas. A large-scale flood control project was carried out after that event. In the middle and lower sections of the river, streambed and riparian habitats were substantially modified, mainly through channel dredging and the construction of levees, flood walls, and a cement trapezoidal channel (Fig. 1). Throughout the project, channel morphology, widths, and water depths changed considerably within the Keelung River basin. According to data available from the Water Resource Agency, Ministry of Economic Affairs, Taiwan (http://gweb.wra.gov.tw/wrwebeng/index.htm), channel profiles were modified during the project, and the extent of deep pools available as refugia for turtles decreased.

Construction within the flood control project caused the aquatic and upland environment in the study area to become more uniform (original vegetation described in Chen and Lue 1999). Removal of sand and tall-stemmed plants (mainly bamboo shrubs and woody plants) in the upland area caused drastic changes in the original vegetation. After construction, only patchy herbaceous plants remained on the riverbank, and more than 1/2 of the total length of the shoreline in the study area was covered with cement or rock levees. Riparian vegetation consisted mainly of nonindigenous species such as *Brachiaria mutica* (Gramineae) and *Wedelia trilobata* (Compositae) (> 50% of the total coverage), and some other herbaceous species. Although we did not quantify many environmental parameters during the study period, it seems reasonable to suggest that many of them were also altered as a result of construction activities.

Study organism

Three native species of freshwater turtles (*Mauremys* (*Ocadia*) *sinensis*, *M. mutica*, and *Pelodiscus sinensis*) and 2 nonindigenous species (*Trachemys scripta elegans* and *Graptemys pseudographica*) were found in the study area. Prior to construction of the flood control project, most of our ecological data were derived from studies of *M. sinensis* (Chen and Lue 1998 1999).

Mauremys sinensis is distributed in Taiwan, southeastern China (including Hainan I.), and northern Vietnam (Ernst and Barbour 1989, Iverson 1992). Although this medium-sized geoemydid turtle is still the most common freshwater turtle in Taiwan (Chen et al. 2000), it is believed to be declining throughout most of its geographical range (Zhao 1998, Hendrie 2000). *Mauremys sinensis* prefers still and slow-moving waters, such as ponds, reservoirs, lakes, agricultural ditches, and low-elevation rivers (Mao 1971, Ernst and Barbour 1989; Chen and Lue 2008). The turtle is omnivorous and reproduces between Apr. and July (Chen and Lue 1998 1999). It is active year round within our study area in the Keelung River.

Animal collecting and measurements

We collected data during 2 sampling periods: (1) from May 1999 to Aug. 2000 (during the course of the construction of the flood control project), and (2) from Feb. 2001 to Apr. 2002 (after the project). Turtles were collected using home-made funnel traps (4 cm in mesh size) baited with canned cat food set along the riverbank, or by hand using a long-handled dipnet. The bait was enclosed in a wire net to prevent it from being ingested by turtles. Traps were usually checked at intervals of 1-3 d. Body size was measured as the maximum straight-line carapace length (CL) using dial calipers (to the nearest 0.1 mm). Each turtle was individually marked by notching the marginal scutes (Cagle 1939). As noted by Chen and Lue (1998), there was a high frequency of fungal infections affecting *M. sinensis* in the Keelung River. Thus, it was difficult to recognize the carapace markings on many individuals for longer than 2 yr because of shell rot; therefore, most of the turtles were independently marked during the different sampling periods. Turtles with apparent shell abnormalities were excluded from body size analyses. We determined the sex of each turtle based on the CL and the position of the cloaca in relation to the plastral notch (Ernst and Barbour 1989, McCord and Iverson 1992, Chen and Lue 1998). Because traps were frequently removed or damaged during the course of the flood control project and capture varied with weather conditions, we did not compute a catch per unit effort index nor did we compare capture results among sampling periods.

Fig. 1. Photographs of the study area (pool 1, looking upstream) showing changes in the riparian vegetation and topography of the Keelung River in (A) May 1996 (before the flood control project), (B) Aug. 1999 (during the project), and (C) Oct. 2001 (after the project).

Stomach sample analyses

Stomach samples of *M. sinensis* were collected only during the warm season (May-Nov.), as there was a high frequency of empty stomachs during the cold season (Chen and Lue 1999). Samples were obtained by gently flushing the stomach (Legler 1977, Parmenter 1980), and were preserved in 70% ethanol for further identification. Each food item was identified to the lowest possible taxon. Fragments of litter were assumed to have been accidentally ingested and were excluded from the analyses.

We determined the percentage of occurrence (F%) and percentage of total volume (V%), and computed an index of relative importance (IRI) for each food item. Food volume was estimated by removing excess moisture and then measuring the volume of water displaced in a graduated cylinder (Hart 1983). The frequency of occurrence of an item was defined as the number of samples containing that item expressed as a percentage of the total number of samples. Items found in < 1% of the samples were regarded as insignificant in dietary importance and were excluded from subsequent analyses. As a measure of dietary diversity, breadth, and overlap, the IRI was calculated for each food item using the method of Bjorndal et al. (1997).

An analysis using 1 dietary parameter alone may yield misleading results of the relative importance of specific food items (Hyslop 1980, Bjorndal et al. 1997). Therefore, we also used Shannon-Wiener's index to determine dietary diversity (Krebs 1989). Dietary breadth was calculated using the standardized Levins' measure to determine the uniformity of the food resources ingested (Levins 1968, Hurlbert 1978). Dietary overlap between groups was also assessed using Horn's measure (Horn 1966). All data were analyzed using *G*-tests with alpha = 0.05 (Sokal and Rohlf 1994).

RESULTS

Change in the distribution patterns of turtles

The distribution of *M. sinensis* in the Keelung River showed considerable changes during the study period. Prior to habitat modification, *M. sinensis* was found throughout the study area (ca. 3.5 km in total length), but during construction of the flood control project (1999-2000), we found turtles only in pool 2, which was approximately 500 m in length. After the project (2001-2002), the distribution of turtles expanded somewhat to pools 1 and 2, at approximately 1.5 km in total length (Fig. 2).

Changes in the population structure

In total, 216 and 567 *M. sinensis* were collected, marked, and measured during and after the project, respectively (Table 1). Sex ratios were significantly skewed toward males

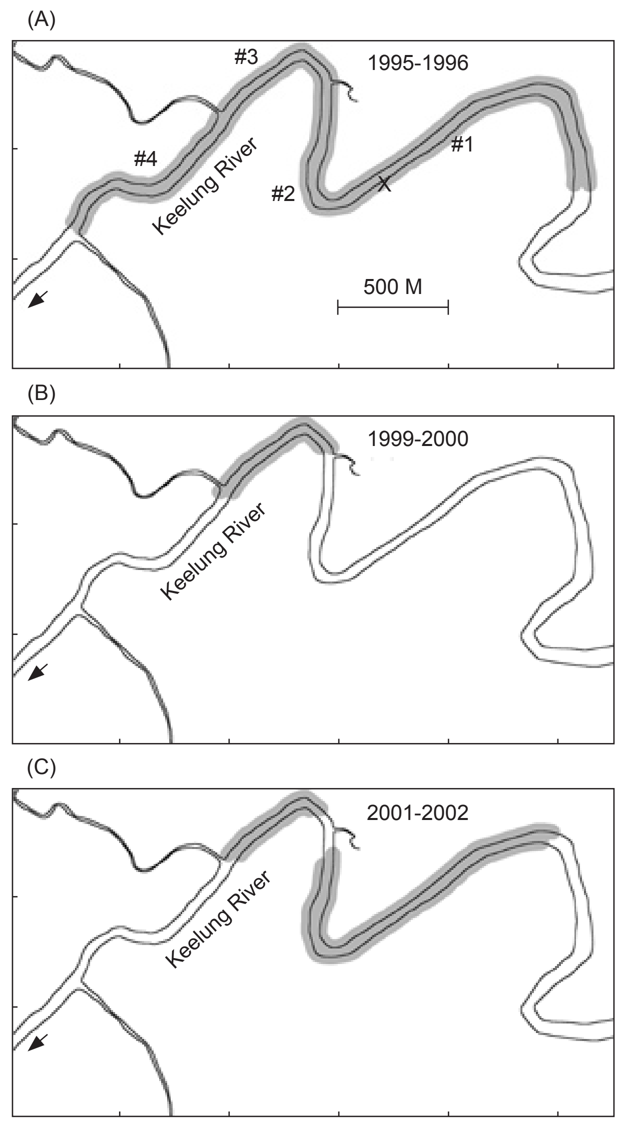

Fig. 2. Distribution of the Chinese stripe-necked turtle (*Mauremys sinensis*) in the Keelung River during (A) 1995-1996, (B) 1999-2000, and (C) 2001-2002. Numbers indicate the pool number in the study site; the "X" indicates the location where the photographs were taken in figure 1.

during both sampling periods (1999-2000: 2.7.1:1, $G = 47.35$, $p < 0.01$; 2001-2002: 2.83:1, $G = 132.88$, $p < 0.01$). Samples collected during and after the project were composed of larger-sized individuals (Fig. 3). Compared to data collected prior to the construction project, there was a significant difference in capture frequency among male, female, and juvenile turtles ($G = 219.79$, $p < 0.01$) after the project. There was no significant size difference between turtles collected during and after the project ($G = 1.44$, $p > 0.05$), however. Throughout the study period, the proportion of small juveniles (i.e., individuals with < 100.0 mm CL) was low (0.9% (2/216) during and 2.5% (14/467) after the project) compared to the total number of individuals captured.

Nests lost during the project

During the study period, 10 nests were found in 2001. All of these nests were located within the area of construction, indicating that many of the nests built in 1999 and 2000 may have been destroyed. Eight nests were placed on a sandbar on the deposition side of a meander loop (< 2 m above the water level). Three of them washed away, and 2 were inundated during the incubation period.

Changes in dietary composition

The volume of the stomach contents of both sexes of *M. sinensis* decreased after initiation of the flood control project. This tendency was more pronounced in females than in males: the mean volume of the stomach contents after the project was no more than 23.3% of that before the project (Table 2). Diet composition also differed during the 2 sampling periods (Table 3). The importance in terms of both volume and composition of plant material for both sexes increased after initiation of the flood-control project. During the project, the most important food items (as determined by the IRI) were dipteran larvae (36.5), filamentous algae (34.5) and Gramineae leaves (20.2) for males, and leaves of *W. trilobata* (69.4), and graminaceous plants (24.8) for females. The most important items after the project were leaves of graminaceous plants (63.7) and *W. trilobata* (23.3) for males, and leaves of graminaceous plants (61.0), *Solanum nigrum* (12.5), and *W. trilobata* (11.9) for females (Table 4).

In males, the dietary diversity indices were 1.91 and 1.70, whereas in females, they were 1.10 and 1.83 during and after the project, respectively. Dietary breadth indices were 0.39 and 0.10 in males, whereas the values were 0.42 and 0.13 in females during and after the project, respectively In terms of both dietary diversity and dietary breadth, *M. sinensis* was more of a generalist during the project than prior to the project, and it used more-diverse food resources. The dietary overlap index values between the sexes also increased from 0.483 (during) to 0.922 (after).

Table 1. Numbers of the Chinese stripe-necked turtles (*Mauremys sinensis*) sampled from the Keelung River during (1999-2000) and after the flood control project (2001-2002)

	Sexes		
Sampling periods	Juveniles	Males	Females
1995-1996*	136	289	233
1999-2000	1	157	58
2001-2002	8	413	146

[a]Data from Chen and Lue (1999)

DISCUSSION

Changes in distribution and population structure

Alteration and degradation of suitable habitats as a result of the flood control project seemed to have considerably restricted turtles to limited areas (deep pools) of the Keelung River, although the turtles apparently returned to some extent after the disturbance. The distribution and abundance of turtles are correlated with various river characteristics (Pluto and Bellis 1986, DonnerWright et al. 1999, Bodie et al. 2000) and available resources (Buhlmann and Vaughan 1991, Kaufmann 1992, Fuselier and Edds 1994). In our study area, habitat suitability to *M. sinensis* may have decreased, as most sections of the river channel were dredged and the riparian vegetation was removed during the flood control project. Turtles disappeared from over 2/3 of their original range apparently because of habitat modifications. The area where the turtles remained during the construction project was characterized by deeper water and patches of vegetation.

One report suggests that *M. sinensis* favors slow-moving water (Ernst and Barbour 1989). In the Keelung River, *M. sinensis* prefers deep and slow-current pools and avoids highly modified river sections (Chen and Lue 2008). During the flood control project, bedrock and barriers between deep pools were removed, thus increasing the flow velocity and decreasing the water depth in some sections of the Keelung River. Such habitat changes may have forced turtles to leave a large part of the river. Removal of riparian vegetation and covering open areas with cement eliminated many of the food resources, forcing turtles to move to more-resource-rich sections of the river. The long reproductive life and high adult survivorship of turtles are tempered by high mortality in the egg and juvenile stages, leading to low recruitment (Iverson 1991). A decrease in the proportion of small-sized individuals in the *M. sinensis* population in the middle reaches of the Keelung River suggests a lack of recruitment, which will adversely affect the long-term survival of this freshwater turtle population. Our study showed that the population structure of *M. sinensis* is skewed towards large individuals (percent of small

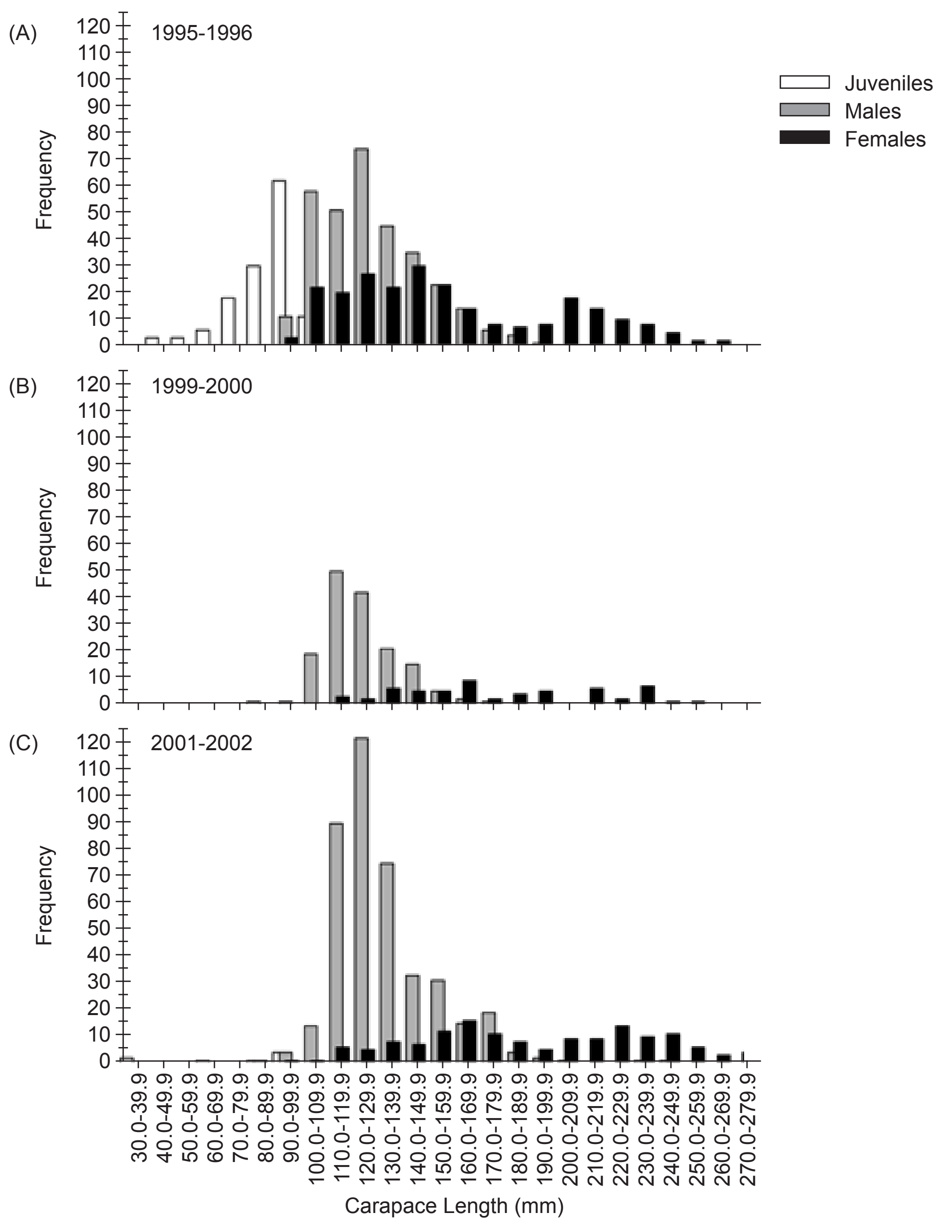

Fig. 3. Body size-class structure of the Chinese stripe-necked turtle (*Mauremys sinensis*) during (A) 1995-1996 (data from Chen and Lue, 1998), (B) 1999-2000, and (C) 2001-2002.

Table 2. Mean volumes of stomach samples from male and female Chinese stripe-necked turtles (*Mauremys sinensis*) collected from the Keelung River during 3 sampling periods (see Table 1). Numbers in brackets indicate sample sizes

	Sexes	
Sampling periods	Males	Females
1995-1996*	0.8 ml (33)	3.0 ml (32)
1999-2000	0.4 ml (46)	1.5 ml (21)
2001	0.5 ml (49)	0.7 ml (42)

*Data from Chen and Lue (1999)

juveniles: 20.7% before, 0.9% during, and 0.3% after the project), especially adult males, although the capture rate of hatchlings was low (Chen and Lue 1998). Numbers of females decreased during and after the project, suggesting that females were more sensitive to the environmental disturbance. Even after the disturbance, the recruitment of small-sized individuals was still very low (Fig. 3). In 2006, only a few adult males were collected, indicating that recruitment has remained low for several years after project completion (unpubl. data).

Buffer zones between terrestrial and aquatic habitats are important to freshwater turtle populations, especially for nesting and overwintering sites (Burke and Gibbons 1995,

Table 3. Percentage of occurrence and volume of stomach samples of the Chinese stripe-necked turtle (*Mauremys sinensis*) during 3 sampling periods (I, 1995-1996; II, 1999-2000; III, 2001). Values with T indicate significance at $p < 0.1$

	% Freq. / % Vol.					
	Males			Females		
Food items	I (*n* = 33)*	II (*n* = 46)	III (*n* = 49)	I (*n* = 32)*	II (*n* = 21)	III (*n* = 42)
Plant materials	66.7 / 45.6	93.5 / 51.7	91.8 / 92.7	81.3 / 94.8	100.0 / 99.7	100.0 / 99.0
Filamentous algae	--	41.3 / 20.8	--	3.1 / T	19.0 / 12.6	4.8 / 1.0
Gramineae	3.0 / 0.4	32.6 / 15.4	49.0 / 29.5	15.6 / 2.0	52.4 / 19.7	61.9 / 25.6
Murdannia keisak (leaves)	33.3 / 30.4	6.5 / 1.3	10.2 / 3.0	62.5 / 83.0	4.8 / T	2.4 / 0.6
Polygonum sp.	24.2 / 2.3	--	6.1 / 0.9	28.1 / 0.5	--	2.4 / 1.3
Eclipta prostrata	15.2 / 5.7	6.5 / 2.0	8.2 / 0.9	6.3 / 0.4	4.8 / T	4.8 / 1.3
Lemna aequinoctialis	--	--	--	6.3 / 8.1	--	--
Wedelia trilobata (leaves)	--	15.2 / 12.1	16.3 / 32.5	--	42.9 / 67.3	11.9 / 25.9
Ageratum conyzoides	--	--	8.2 / 1.3	6.3 / 0.4	--	9.5 / 1.6
Solanum nigrum	--	--	6.1 / 17.1	--	--	14.3 / 22.7
Ludwigia sp.	--	--	6.1 / 2.1	--	--	11.9 / 3.5
Flowers and fruits	--	--	10.2 / 4.7	--	--	19.0 / 12.5
Plant roots and shoots	27.3 / 6.8	--	4.1 / T	6.3 / 0.3	--	23.8 / 3.2
Animal materials	84.8 / 54.4	41.3 / 48.3	36.7 / 7.3	62.5 / 5.4	9.5 / 0.3	19.0 / 1.0
Gastropod	27.3 / 2.3	6.5 / 2.0	--	34.4 / 1.5	--	2.4 / T
Insecta	69.7 / 48.3	26.1 / 46.3	18.4 / 6.0	46.9 / 3.3	9.5 / 0.3	9.5 / 0.3
Ephemeridae larvae	3.0 / 0.8	--	--	--	--	--
Coleoptera	3.0 / T	--	--	3.1 / T	--	--
Diptera larvae and pupae	57.6 / 44.9	19.6 / 46.3	2.0 / 0.9	43.8 / 0.6	4.8 / 0.3	2.4 / T
Lepidoptera larvae	3.0 / 0.4	--	8.2 / 1.7	3.1 / 0.1	--	2.4 / T
Plecoptera larvae	3.0 / 0.4	--	--	9.4 / 2.5	--	--
Odonata larvae	3.0 / T	--	--	6.3 / T	--	--
Unidentifiable insects	30.3 / 2.3	17.4 / T	10.2 / 3.4	34.4 / 0.1	4.8 / T	4.8 / T
Amphipoda	0.3 / T	--	--	3.1 / T	--	--
Oligochaeta	12.1 / 3.8	2.2 / T	--	--	--	--
Hirudinea	6.1 / T	4.3 / T	2.0 / T	--	--	--
Pisces	3.0 / T	2.2 / T	18.4 / 1.3	6.3 / 0.3	--	7.1 / 0.6

[a]Data from Chen and Lue (1999).

Bodie 2001). The widespread use of upland habitats by aquatic or semi-aquatic turtles has been documented in many studies (Bennett et al. 1970, Kaufmann 1992, Burke and Gibbons 1995, reviewed in Bodie 2001). Alteration and degradation of these habitats may lead to population declines and a male-biased population structure (Dodd 1990, Reese and Welsh 1998a, Bodie et al. 2000). River-dwelling turtles, such as *M. sinensis*, directly depend on the quality of both aquatic and surrounding terrestrial habitats at all stages of their life cycle. During this study, *M. sinensis* used aquatic habitats for basking, feeding, mating, and overwintering. Terrestrial habitats are also important as nesting sites and as sources of food resources. In general, males used the aquatic habitats more consistently, whereas females spent more time on land, for example, laying eggs and ingesting terrestrial plants. Thus, adult females are more likely to be threatened by riparian habitat destruction than males. Decreased female survivorship might have resulted in the unbalanced sex ratios of the *M. sinensis* population in the Keelung River.

Reducing reproductive success by eliminating nesting habitat could quickly decrease population size and alter the demographic structure (Mitchell and Klemens 2000). In our previous study (Chen

Table 4. Dietary diversity and breadth using the index of relative importance (IRI) for the Chinese stripe-necked turtle (*Mauremys sinensis*) during 3 sampling periods (I, 1995-1996; II, 1999-2000; III, 2001). Values with T denote an IRI value of < 0.1

	% Freq. / % Vol.					
	Males			Females		
Food items	I (*n* = 33)*	II (*n* = 46)	III (*n* = 49)	I (*n* = 32)*	II (*n* = 21)	III (*n* = 42)
Plant materials						
Filamentous algae	--	34.5	--	T	5.8	0.2
Gramineae	T	20.2	63.7	0.6	24.8	61.0
Murdannia keisak (leaves)	24.6	0.3	1.3	96.1	T	0.1
Polygonum sp.	1.4	--	0.2	0.3	--	0.1
Eclipta prostrata	2.1	0.5	0.3	T	T	0.2
Lemna aequinoctialis	--	--	--	0.9	--	--
Wedelia trilobata (leaves)	--	7.4	23.3	--	69.4	11.9
Ageratum conyzoides (leaves)	--	--	0.5	T	--	0.6
Solanum nigrum (leaves)	--	--	4.5	--	--	12.5
Ludwigia sp. (leaves)	--	--	1.6	--	--	1.1
Flowers and fruits	--	--	2.1	--	--	9.1
Plant roots and shoots	4.5	--	T	T	--	2.9
Animal materials						
Gastropod	1.5	0.5	--	1.0	--	--
Insecta						
Ephemeridae larvae	T	--	--	--	--	--
Coleoptera	T	--	--	T	--	--
Diptera larvae and pupae	62.9	36.5	0.1	0.5	T	T
Lepidoptera larvae	T	--	0.6	T	--	T
Plecoptera larvae	T	--	--	0.4	--	--
Odonata larvae	T	--	--	T	--	--
Unidentifiable insects	1.7	T	1.5	0.1	T	T
Amphipoda	T	--	--	T	--	--
Oligochaeta	1.1	T	--	--	--	--
Hirudinea	T	T	T	--	--	--
Pisces	T	T	1.1	T	--	0.2
Diversity	1.59	1.91	1.70	0.33	1.10	1.83
Breadth	0.17	0.39	0.10	0.01	0.42	0.13

[a]Data from Chen and Lue (1999).

and Lue 1998), turtle nests were found in upland bamboo shrubs (up to 40 m from the water line). After channel dredging and riverbank modification, female turtles nested on newly created sandbars, usually < 2 m above the water line, where nests were more likely to be inundated or washed away during the incubation period.

Changes in the quality and quantity of available foods

Turtle densities are related to the abundance of food resources (Breininger et al. 1994). The decrease in the mean volume of stomach contents found in our study suggests a reduction or degradation of food resources. This is especially true in samples from females, in which the volume decreased 23.3% after the project compared to before the project. The total dietary volume is a function of body size. Although the decrease in diet volume may have been the result of a sampling bias due to smaller sample sizes of larger females during the control project, the mean volume did not increase in stomach samples obtained after the project. As the mean body size of female *M. sinensis* is significantly larger than that of males (Chen and Lue 1998), females require more food for growth. A deficiency in the food supply for females would be detrimental to their long-term survival. This may explain, in part, the rapid decrease in females and the subsequent male-biased population structure of *M. sinensis*.

With a reduction in food resources in a changing environment, the diet of *M. sinensis* changed remarkably. According to various foraging theories, dietary niche breadth should expand as food resource availability decreases (MacArthur and Pianka 1966, Schoener 1974, Stephens and Krebs 1986). When the food supply is limited, an animal is expected to broaden its diet and be forced to take less-preferred or less-nutritious food items (Durtsche 1992, Chen and Lue 1999). Diversity of food items was consistently high throughout the sampling periods for males, whereas food diversity increased during and after the project for females. This indicates that male *M. sinensis* depended on a variety of food resources throughout the 3 sampling periods, whereas females broadened their use of food resources in the disturbed environment. Values for dietary breadth also showed that both sexes of *M. sinensis* were using different food items during the flood-control project. The importance of animal material subsequently decreased in males. Females mainly consumed plant food, but their diet composition shifted from specializing in *Murdannia keisak* leaves to more-generalized plant items.

In our analyses of the diet, we found that the dominance of certain food items, such as *M. keisak* leaves, was substantially reduced in samples collected during 1999-2002. After clearing the riparian vegetation during the project, the early successional plants, such as the Gramineae, likely colonized and replaced the original vegetation in a short period of time. The distribution of some food resources reflects higher responsiveness to environmental disturbance than others; therefore, their relative abundances will inevitably change. As the abundance of *M. keisak* decreased after the disturbance, turtles may have been forced to consume less-favored resources, such as species of the Gramineae, which are relatively abundant in the environment. The removal of submerged and emergent plants during the project also reduced the accessibility of food resources, and therefore turtles were likely forced to depend on less-attainable food items in the uplands. Moreover, the removal of bedrocks and an increase in water turbidity likely caused a reduction in the availability of aquatic foods, such as filamentous algae, insect larvae, and snails. The reduction in primary production caused by increasing water turbidity might lead to a decline in turtle density (Wilbur 1975). The detrimental effects of habitat disturbance on food availability may have caused the decline in the population of *M. sinensis* in the Keelung River.

Implications for conservation and management

Our results show that there were detrimental effects on the population of *M. sinensis* due to rapid habitat alteration and degradation caused by a major flood-control project. The distribution of *M. sinensis* is usually associated with the quality of the habitat characteristics in the Keelung River. As habitat quality was degraded in areas of high modification, turtles were forced to move to less-disturbed areas (Dodd et al. 2006, Chen and Lue 2008). Because this construction project covered a rather long stretch of the river, turtles may have been driven to refugia within the project area. Our results showed that females were more sensitive to habitat change in terms of population structure and diet, which may negatively affect the long-term survival of the turtle population. In addition, recruitment may also have been diminished through nest destruction and direct mortality of hatchlings and juveniles by construction activities. Moreover, the reduction in food resources may have also affected the growth rates of turtles (Dodd and Dreslik 2008). A deficiency in food supply for females can lead to delayed sexual maturity, which could further skew the population's sex ratio toward males.

Without a better understanding of the effects of habitat disturbances on turtle populations, it is not easy to determine reasonable measures to minimize the damage caused by construction. Protection of critical habitats, such as feeding grounds, nesting sites, and underwater refugia of river-dwelling turtles should be thoughtfully considered in the course of planning flood-control projects to avoid long-term detrimental effects to their populations. Decreased survival of adults, especially females, will cause a serious decline in turtle populations (Congdon et al. 1994, Cunnington and Brooks 1996, Heppell 1998). Therefore, it is most important to consider the basic requirements of adult females in order to conserve turtle populations in areas slated for flood-control projects.

Pre- and post-disturbance data can provide powerful evidence concerning the ways in which turtles are affected by disturbances to their habitats. A diversity of upland habitats is important to aquatic and semi-aquatic animals inhabiting river drainages, but their biological integrity is usually ignored. Protecting diverse areas with different channel characteristics may be one of the most important factors contributing to the long-term sustainability of *M. sinensis* in the Keelung River. Vegetated riparian habitats are essential to the ecological functioning of both aquatic and terrestrial environments. The flood-control project could be modified, if necessary, to minimize further damage to the river and its riparian ecosystem. More studies of habitat alteration on river-dwelling animal populations, such as *M. sinensis*, must be conducted in order to increase public awareness of the effects of human activities on rivers.

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