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Biodiversity, Exploitation, and Conservation of Turtles in the Tonle Sap Biosphere Reserve, Cambodia, with Notes on Reproductive Ecology of *Malayemys subtrijuga*

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Abstract. – We investigated the biodiversity, exploitation, and conservation status of turtles in the Tonle Sap Biosphere Reserve (TSBR) of Cambodia from June 2000 through October 2001. We confirmed the occurrence or former occurrence of 4 native species of turtles (*Batagur baska*, *Cuora amboinensis*, *Heosemys annandalii*, and *Malayemys subtrijuga*) in TSBR and discuss the possible occurrence of 4 others, including 2 native species (*Amyda cartilaginea* and *Pelochelys cantorii*) and 2 exotics (*Trachemys scripta* and *Pelodiscus sinensis*). Large numbers of turtles were being unsustainably harvested from TSBR at the time of our study. Most harvested turtles were destined for urban markets in Cambodia and international wildlife markets in Vietnam and southern China, with very few kept by fishermen for household consumption. We regard any attempts to eliminate the subsistence harvest of turtles as impractical in Cambodia but recommend a complete ban on the extraction of turtles and other wildlife resources from the 3 core areas of TSBR. Incidental to our investigation of turtles in TSBR, we collected data on sexual size dimorphism and reproductive biology of *M. subtrijuga*. Our findings indicate that female *M. subtrijuga* are larger than males, and females may construct underwater nests as floodwaters begin to recede in the early dry season.

Key Words. – Reptilia; Testudines; Geoemydidae; Trionychidae; turtles; distribution; exploitation; protected areas; conservation; Cambodia

Species inventories of particular regions are essential data sets for conservation and resource management (Oliver and Beattie 1993), and acquiring baseline data on the distribution and status of even common species is important (Dodd and Franz 1993; Gibbons et al. 1997). Furthermore, knowledge of alpha-level diversity (MacArthur 1965) is fundamental to understanding community and ecosystem dynamics (McDiarmid 1994). Although mainland Southeast Asia is considered a hot spot of turtle and tortoise diversity (van Dijk 2000), its chelonian fauna has not been well studied (Stuart and Platt 2004). This is especially true in Cambodia where decades of civil unrest, political instability, and military conflict have until recently prevented fieldwork. Consequently, the distribution and ecology of chelonians in the country are incompletely known (Holloway 2000; van Dijk 2000; Stuart and Platt 2004), and pre–World War II publications (e.g., Smith 1931; Bourret 1941) remain the principal source of information (Campbell et al. 2006). In particular, there is a notable paucity of data on the chelonians inhabiting Tonle Sap (Campbell et al. 2006). Such data are urgently needed given the widespread and intensive exploitation of chelonians now underway in Cambodia to supply commercial wildlife markets in China and, to a lesser extent, Vietnam (Martin and Phipps 1996; Holloway 2000; Tana et al. 2000; Stuart and Platt 2004). Indeed, some species (e.g., *Batagur baska*; Platt et al. 2003a) could disappear before even basic ecological studies can be undertaken.

To address this deficiency, we here present the results of an investigation into the occurrence, conservation status, and exploitation of freshwater turtles in the Tonle Sap Biosphere Reserve (TSBR) of Cambodia, and make conservation recommendations based on our findings. Incidental to this investigation we collected data on sexual size dimorphism and reproductive biology of the Malayan snail-eating turtle (*Malayemys subtrijuga*) in TSBR. Except for the studies of Srinarumol (1995) and Brophy (2006) on the closely related *Malayemys macrocephala* (until recently considered conspecific with *M. subtrijuga*; Brophy 2004) in Thailand, and general comments by others (Smith 1931; Bourret 1941; Nutaphand 1979; Pritchard 1979; Ernst and Barbour 1989; Cox et al.

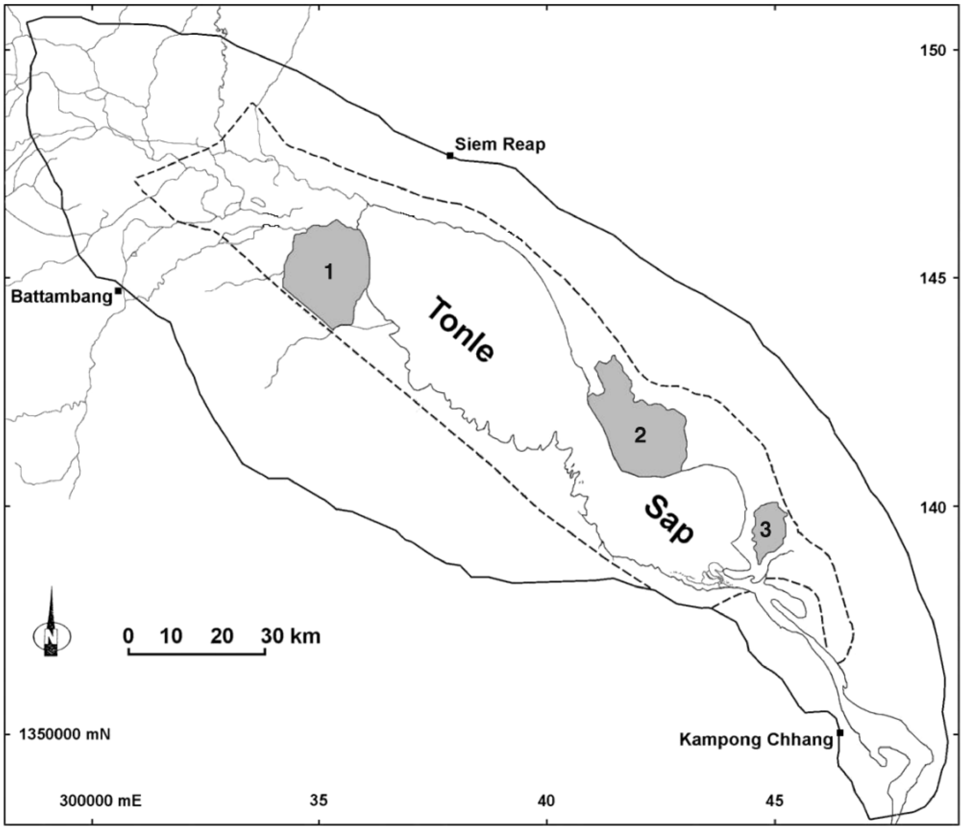

Figure 1. Map of Tonle Sap Biosphere Reserve, Cambodia. Solid line denotes boundary of transition zone, and buffer zone is encompassed by dashed line. Core areas are shaded and numbered (1. Prek Toal, 2. Moat Khla–Boeng Chhmar, 3. Stoeng Sen).

1998), little is known concerning the ecology of *M. subtrijuga*.

STUDY AREA

Tonle Sap (Fig. 1), located in the central plain of Cambodia, is the largest permanent freshwater lake in Southeast Asia (Scott 1989; Campbell et al. 2006). The Tonle Sap floodplain (defined as that area within the 10-m above-sea-level contour line surrounding Tonle Sap; Giesen 1998) extends approximately 250 km from northwest to southeast and is up to 100 km wide (Scott 1989). The Tonle Sap River connects Tonle Sap with the Mekong River near Phnom Penh, the capital of Cambodia. During the dry season (December to mid-May) the Tonle Sap covers an area of 250,000 to 300,000 ha and has a mean depth of < 1 m. Shortly after the onset of the wet season in late May the Tonle Sap River reverses flow and carries water from the Mekong into Tonle Sap, resulting in extensive inundation of the surrounding floodplain. At the height of the wet season (September), mean water depth increases to 8–10 m, and Tonle Sap expands to approximately 1.3 million ha (Scott 1989). Floodwaters begin to recede in late November and the lowest water levels occur during April and early May (Scott 1989).

Tonle Sap is surrounded by extensive seasonally flooded wetlands. Approximately 80% of the floodplain is covered by swamp scrubland characterized by semi-continuous stands of trees and shrubs up to 4 m in height (Campbell et al. 2006). Swamp forest (Campbell et al. 2006) consisting of trees 7 to 15 m tall covers $< 10\%$ of the floodplain. This swamp forest occurs primarily along the lakeshore and riverbanks and remains flooded for up to 8 months. Additionally, large tracts of emergent herbaceous and floating vegetation are scattered throughout the floodplain (McDonald et al. 1997). Significant areas of natural vegetation have been degraded or destroyed by fuelwood cutting and conversion to rice fields, and the area of inundated forest (both swamp scrubland and swamp forest associations) is thought to have declined from more than 1 million hectares in the 1930s to 360,000 ha by the late 1990s (Campbell et al. 2006).

One-hundred-sixty communes inhabited by an estimated 1.02 million people are located on the periphery of Tonle Sap, and about 170 floating villages, ranging in size from 2 to over 100 households, occur on the lake and move in accordance with seasonally fluctuating water levels (Giesen 1998). Rice farming, fuelwood collection, fish culture, and subsistence and commercial fishing are the principal economic activities in these communities (Giesen 1998; Gum 1998). Commercial fishing is concentrated in administrative fishing lots leased by concessionaires from the government; these lots encompass extensive areas of the lake and surrounding wetlands (Giesen 1998). Fishing lots are enclosed with bamboo fences that extend for many kilometers and concessionaires strictly control access for the duration of the fishing season (October through May).

In 1997, Tonle Sap was designated a biosphere reserve in the United Nations Educational, Scientific, and Cultural Organization's (UNESCO's) Man and the Biosphere Program (Campbell et al. 2006). Biosphere reserves consist of strictly protected, inviolate core areas surrounded by buffer and transitional zones where sustainable resource extraction and human occupancy are permitted (Hough 1988). Three core areas (Prek Toal, Moat Khla–Boeng Chhmar, and Stoeng Sen) totaling 70,837 ha were established in TSBR (Campbell et al. 2006). In contrast to the standard UNESCO model, subsistence and commercial fishing are permitted in core areas of TSBR. The 3 core areas are surrounded by buffer and transition zones totaling 510,768 and 899,652 ha, respectively (Campbell et al. 2006). The natural and social dimensions of the Tonle Sap ecosystem are described in greater detail elsewhere (Scott 1989; MacDonald et al. 1997; Platt et al. 2004b; Poole 2005; Campbell et al. 2006).

METHODS

We conducted fieldwork in TSBR from June 2000 through October 2001. During this period, we visited floating villages on the lake, and agricultural villages and larger towns on the lake periphery, where we conducted open-ended interviews (sensu Martin 1995) with fishermen, farmers, and other knowledgeable individuals. Such individuals are generally recognized as an excellent source of information on the local chelonian fauna (Thirakhupt and van Dijk 1994; Platt et al. 2004a). Our informants were questioned regarding the local occurrence of turtles, harvest levels, capture methods, and general knowledge of turtles. In accordance with the format of an open-ended interview, we asked each informant a series of questions that included standard questions prepared in advance and others that arose during the course of conversation (Martin 1995). We measured, photographed, and if possible salvaged any available specimens; the latter were deposited in the Field Museum of Natural History (FMNH). Stuart and Platt (2004) provide FMNH numbers and specific locality data for salvaged specimens.

We sexed *Cuora amboinensis* and *Heosemys annandalii* according to plastral morphology; males are characterized by a prominent plastral concavity, which is absent in females (Ernst and Barbour 1989). The sex of *M. subtrijuga* was determined on the basis of tail morphology; subadult and adult males have much longer and thicker tails than females (Ernst and Barbour 1989; Brophy 2006). Additionally, we accompanied villagers into the field to search for turtles and nests, inspect habitat, and observe capture methods. Geographic coordinates were determined with a Garmin® GPS 48.

To investigate trade, we conducted surveys of wildlife markets in major towns surrounding TSBR, including Siem Reap, Battambang, Kampong Thom, and Kampong Chhang. At each market we determined what species were offered for sale, and queried vendors regarding species composition and volume of trade, prices, and origin and destination of the turtles offered for sale. We also attempted to locate and interview middlemen who purchased turtles in rural villages for later sale in wildlife markets.

The degree of sexual size dimorphism in *M. subtrijuga* was quantified with a compressed sexual size dimorphism index (SDI) (Lovich and Gibbons 1992). SDI is a dimensionless number calculated by dividing the mean size of the larger sex by the mean size of the smaller sex and then adding or subtracting one from this value depending on whether males or females, respectively, are the larger sex (Lovich and Gibbons 1992). Although SDI may be based on mass or some measure of body length, we selected carapace length (CL) as the appropriate variable because body mass often exhibits considerable variation among animals of similar body length owing to the presence of eggs in gravid females, recent ingestion of large meals, and overall body condition (Lovich and Gibbons 1992).

To obtain eggs and explore allometric relationships between female body size and clutch parameters of *M. subtrijuga*, we purchased locally captured adult females directly from fishermen in floating villages or from wildlife markets in Siem Reap. These turtles were housed in plastic wading pools at the Wildlife Conservation Society Siem Reap Field Station. We held turtles for 21–24 days to insure that oviductal eggs were fully shelled and then induced oviposition by injecting oxytocin into the pectoral muscles at a dosage of 2.0 units/100 g of body mass (Ewert and Legler 1978). Following injection, each female was placed in a water-filled 20-L bucket with a wire-mesh grate positioned approximately 5 cm above the bottom; this allowed eggs to fall through but prevented accidental trampling by the female. A second injection was administered within 24 hours to insure that the complete clutch was deposited. Eggs were removed from the buckets within an hour of laying; length and width were measured with dial calipers ($\pm$ 0.1 mm SD), and mass was determined with Pesola scales ($\pm$ 0.5 g SD). We buried each clutch in a shallow (ca. 7–10 cm deep) hole excavated in clay soil at the field station to simulate a likely natural incubation regime. After recovering eggs, we released females in a protected wetland at the nearby Angkor Wat World Heritage Site. Mean values are presented as $\pm$ 1 SD. Results were considered significant at $p \leq 0.05$.

RESULTS AND DISCUSSION

We confirmed the present or former occurrence of 4 native species of turtle (*Batagur baska*, *Cuora amboinensis*, *Heosemys annandalii*, and *Malayemys subtrijuga*) in TSBR and discuss the possible occurrence of up to 4 others, including 2 native species (*Amyda cartilaginea* and *Pelochelys cantorii*) and 2 exotics (*Trachemys scripta* and *Pelodiscus sinensis*). Our efforts should be regarded as preliminary and continued fieldwork will likely verify the occurrence of additional species (e.g., *Siebenrockiella crassicollis*) in TSBR.

Geoemydidae

Batagur baska. — The shells of 2 adult *B. baska* found buried in lake sediments are displayed at the Department of Fisheries office in Siem Reap. According to local villagers, small numbers of *B. baska* were present in Tonle Sap during the early 1900s, but these large river turtles are now locally extirpated. A summary of the historic distribution and current conservation status of *B. baska* in Cambodia is provided by Platt et al. (2003a).

Cuora amboinensis. — We examined 13 specimens during this survey, including 6 living turtles and 7 shells. Our sample consisted of 9 females, 2 males, and 2 carapaces that lacked plastrons and could not be sexed. Mean CL and plastron length (PL) were 183.8 ± 22.6 mm SD (range = 136.0–206.0 mm; $n = 8$) and 176.0 ± 9.9 mm SD (range = 160.1–194.0 mm; $n = 11$), respectively. The largest specimen that could be sexed was a female. Villagers regard *Cuora amboinensis* as the least common of the 3 species of turtles that are regularly harvested in TSBR.

Cyclemys atripons. — Wildlife exporters reported that distinctively marked *Cyclemys*, later described as *Cyclemys atripons*, which began appearing in the pet trade during the early 1990s originated from Tonle Sap (Iverson and McCord 1997). However, we found no evidence for the occurrence of *Cyclemys atripons* in TSBR and concur with Iverson and McCord (1997) that the trade specimens in question most likely originated from "hill regions" (probably the Cardamom Mountains) of southwestern Cambodia.

Heosemys annandalii. — We examined 18 specimens during this survey, including 15 living turtles and 3 carapaces. Mean CL and PL were 382.3 ± 40.5 mm SD (range = 310.0–444.6 mm; $n = 18$) and 321.8 ± 28.2 mm SD (range = 282.3–360.0 mm; $n = 15$), respectively. Males (CL = 412.1 ± 22.4 mm SD; range = 372.0–444.6 mm; $n = 8$) were larger than females (CL = 364.0 ± 41.8 mm SD; range = 330.2–420.0 mm; $n = 4$); although, meaningful statistical comparisons were not possible because of our small sample size. According to fishermen, females become sexually mature upon attaining a body mass of about 4 kg. Villagers keep *H. annandalii* for extended periods beneath floating dwellings by securing a length of cord through a small hole drilled in the posterior margin of the carapace. These turtles are fed kitchen refuse and glean excess food from commercial cage fisheries until sold to a visiting turtle buyer.

Malayemys subtrijuga. — Our survey indicated that *M. subtrijuga* is the most frequently harvested turtle in the TSBR. We examined and measured 360 *M. subtrijuga* in local markets and held by fishermen, a sample that included 326 living turtles and 34 carapaces; many more were observed in local markets. Mean CL and PL were 147.3 ± 39.3 mm SD (range = 77.0–236.7 mm; $n = 360$) and 123.9 ± 34.3 mm SD (range = 62.3–199.0 mm; $n = 326$), respectively. Our sample of *M. subtrijuga* included 248 females and 78 males (1:3.1 males:females), a sex ratio that differed significantly from parity ($\chi^2 = 88.6$, df = 1, $p < 0.001$). The skewed sex ratio of our sample is thought to result from the preferential harvest and sale of larger turtles, most of which are females (see below), and probably does not reflect the actual sex ratio among wild populations.

Trachemys scripta elegans. — To our knowledge, photographs obtained by Peter Paul van Dijk of a single adult *T. scripta elegans* reportedly captured in the lake during the mid-1990s constitute the only record of this invasive species in TSBR (P.P. van Dijk, *pers. comm.*). Additional evidence for the occurrence of established *T. scripta elegans* populations was not forthcoming during our survey. However, because large numbers of imported juveniles are used in Buddhist release ceremonies (D. Emmett, *pers. comm.*), future establishment of *T. scripta elegans* in TSBR is a possibility. Feral populations are now established in both temperate and tropical regions of Asia, including Thailand (Cox et al. 1998), Indonesia (Platt et al. 2001), South Korea (Platt and Fontenot 1992), and Taiwan (Chen and Lue 1998).

Trionychidae

Amyda cartilaginea and Pelochelys cantorii. — Evidence for the occurrence of softshell turtles in TSBR is equivocal and somewhat conflicting. According to some villagers, softshell turtles occur only in small tributaries of the lake; whereas, fishermen inhabiting the Prek Toal and Moat Khla core areas maintained that softshell turtles are present in the lake, although rarely captured. In contrast, fishermen near Siem Reap considered softshell turtles rather common and reportedly captured 10–20 every fishing season. The identity of these softshell turtles remains unclear. We obtained the photograph of a dried plastron and carapace (CL ca. 15 cm) from a small softshell turtle captured in the Stoeng Chreuw River, a tributary of Tonle Sap (F. Goes, *pers. comm.*) but, owing to its dried condition and lack of distinguishing characteristics discernible in the photograph, were unable to reliably identify this specimen. Either or both *A. cartilaginea* and *Pelochelys cantorii* could occur in TSBR. We examined specimens of *A. cartilaginea* in Kampong Thom that reportedly originated in the uplands surrounding Tonle Sap, and *Pelochelys cantorii* is known from the main channel of the Mekong River (Stuart and Platt 2004).

Until voucher specimens are forthcoming, we include *A. cartilaginea* and *P. cantorii* as provisional members of the TSBR chelonian fauna.

Pelodiscus sinensis. — Although we are unaware of any records of wild-caught *Pelodiscus sinensis* from Tonle Sap, this nonnative species is being commercially reared by fish farmers at floating villages on the lake. We visited 2 families and learned of at least 6 others in Choeng Khneas Village who were engaged in *Pelodiscus sinensis* culture. Families at Prek Toal were also said to be rearing these turtles; 200–300 turtles were kept by each family. *Pelodiscus sinensis* are obtained as hatchlings from Thailand and, according to farmers, reach a marketable size in about 14 months. The turtles are housed in floating bamboo cages and undoubtedly some escape into the lake. Interestingly, one farmer indicated that about half of the hatchlings he initially purchased later "disappeared." Although we found nothing to suggest the occurrence of feral populations in TSBR, it is possible that *Pelodiscus sinensis* will become established in the future as a result of such escapes.

Exploitation and Conservation

Villagers in TSBR and the surrounding region harvest turtles and their eggs for both subsistence and commercial purposes. Holloway (2000) estimated that up to 90% of villagers living around Tonle Sap are engaged in regular turtle harvesting. Collecting is conducted throughout the year, although our informants stressed that during periods of maximal water levels turtles become difficult to find after dispersing into flooded vegetation. Our interviews indicate that a significant portion of the turtles captured in TSBR are taken incidental to commercial fishing, usually when turtles enter bamboo fish traps (*lorb raw*). These traps consist of extensive networks of bamboo fencing that often extend for several kilometers and funnel fish into strategically placed enclosures which then hold the catch until removed by fishermen. The bamboo fences function as large-scale drift fences (Gibbons and Semlitsch 1981) that intercept any species of turtle as well as fish. Turtles (primarily *M. subtrijuga*) are also opportunistically captured by farmers working in rice fields during the planting (May to July) and harvesting (November) seasons.

In addition to incidental capture, a variety of turtle-specific harvesting methodologies are employed, most of which appear to be nonselective with regard to species. Foremost is the use of a smaller version (*lorb teal*) of the bamboo trap with accessory fencing described above that is designed to capture turtles rather than fish. Fishermen also use sharpened sticks to probe for *H. annandalii* and *M. subtrijuga*, which reportedly aestivate buried in the mud during the dry season. Fires are often used at this time to remove dried herbaceous vegetation and expose concealed turtles. Notably, several *M. subtrijuga* that we examined exhibited discolored carapacial scutes consistent with past fire injuries. Some villagers reported that hunting dogs are particularly effective at locating turtles during the dry season, especially *M. subtrijuga* and *Cuora amboinensis*. When waters begin to rise in May and June, fishermen use headlights to search beneath fruiting trees at night for turtles that congregate to feed on falling fruit. Several individuals described scattering *Ipomea* leaves and stems on the waters surface to attract turtles, although this method is not regarded as very effective.

Malayemys subtrijuga eggs are collected from December through March. Although microsites vary, females reportedly use the same general nesting areas each year, and hunters locate nests by following tracks and drag marks in the mud. Dogs are occasionally used to find nesting females, in which case both the eggs and female are harvested. Small, dome-shaped bamboo enclosures are placed around some nests to capture emerging hatchlings.

Annual harvest levels are difficult to quantify, but large numbers of turtles were apparently being collected in TSBR at the time of our study. One collector estimated that over 800 kg turtles/season were opportunistically taken in a single *lorb raw*, and capture rates given by other fishermen ranged from 1 to 5 turtles/d. The overwhelming consensus among fishermen is that turtles are less abundant today, large individuals (particularly *H. annandalii* and *Cuora amboinensis*) are becoming rare, and more effort is required to catch fewer turtles than in the past. One collector stated that in the early 1980s it was possible to harvest as many as 150 turtles in a single night; whereas, now 2 to 3 turtles/d are considered a good catch. A middleman in Siem Reap indicated that daily purchases of up to 300 kg of turtles were commonplace during the late 1980s, but at the time of our survey only 10 to 20 kg turtles/d were being supplied by fishermen. Based on our examination of 391 turtles held by fishermen and in local markets, *M. subtrijuga* comprises the bulk (92%) of turtles harvested from TSBR, followed by small numbers of *H. annandalii* (4.6%) and *Cuora amboinensis* (3.3%). Similarly, Holloway (2000) found that *M. subtrijuga* was the most common turtle in urban markets in Cambodia; undoubtedly many of these originated from TSBR. Egg collecting seems to be a rather specialized activity practiced by fewer villagers, and consequently less data are available; however, several collectors reported harvesting 40 to 50 *M. subtrijuga* eggs each month during the December to March nesting season.

In the past, turtles were an important subsistence food for inhabitants of Tonle Sap. Now, however, most turtles are instead sold to commercial buyers with few being retained for household consumption. Holloway (2000) concluded that villagers regard turtles as an important source of disposable income and estimated that 95% of captured turtles are sold to middlemen. Although prices paid to collectors vary (Holloway 2000), at the time of our investigation villagers received US$0.75 to 2.00 for an adult *M. subtrijuga*, and slightly more (US$2.50) for *H. annandalii* and *Cuora amboinensis*. Given the daily wage for a laborer during the same period was about US$2.00, there is an obvious economic incentive to collect and sell turtles to commercial buyers.

There is a large demand for turtles in the domestic markets of Cambodia. Cooked turtles, principally *M. subtrijuga,* are widely available in markets of the larger towns and cities, and gravid females are considered a special delicacy. Cooked turtles are presented whole with the plastral bridge broken to expose the viscera and eggs for inspection by customers. Turtle shells are also used in traditional Khmer medicine, being an important component of a postpartum tonic for women. Smaller (CL $<$ 10 cm) and hence less valuable *M. subtrijuga* are sold for use in Buddhist release ceremonies. Purchasing and releasing captive turtles (and other animals) is a common practice in Southeast Asia and believed to be a means by which an individual can earn karmic merit towards a higher incarnation during a future life (Annandale and Shastri 1914). *Malayemys subtrijuga* eggs are available in local markets during the nesting season. These are regarded as a delicacy and eaten raw, and thought by some to function as a male aphrodisiac (Holloway 2000). In addition to the domestic consumption of turtles, large numbers are exported to neighboring countries, principally China and Vietnam (Holloway 2000; Stuart et al. 2000b; Tana et al. 2000). Although many of the turtles leaving Cambodia undoubtedly emanate from TSBR (Holloway 2000), international trade was beyond the scope of our investigation and has been dealt with by others (Martin and Phipps 1996; Holloway 2000; Tana et al. 2000).

We regard the current level of commercial turtle harvesting in TSBR as unsustainable and consider it a serious threat to the continued viability of regional populations. Life history traits of turtles severely constrain the ability of populations to respond to chronic overharvesting (Congdon et al. 1993), and even a low-intensity subsistence take has the potential to decimate turtle populations (Thirakhupt and van Dijk 1994; Platt et al. 2003b). Indeed, it is doubtful whether any level of turtle harvest can be truly sustainable (Thorbjarnarson et al. 2000). Owing to long-standing traditions of cheloniophagy in Khmer culture and weak regulatory infrastructure, we consider any attempt to halt the subsistence consumption of turtles in Cambodia as impractical. Instead, efforts should be made to decommercialize the trade, perhaps through measures such as banning the sale of cooked turtles in urban markets. Most importantly, we reiterate our earlier recommendations with regard to Siamese crocodile (*Crocodylus siamensis*) conservation and urge a complete ban on the extraction of wildlife resources, particularly fish, from the 3 core areas of TSBR (Platt et al. 2004b). In addition to decimating turtles, fishing activities in TSBR core areas also threaten the viability of crocodile and homalopsine water snake populations (Stuart et al. 2000a; Platt et al. 2004b). Each TSBR core area is thought to be large enough to support viable populations of turtles and, given sufficient time for recovery, may function as a source-sink system (Hanski and Simberloff 1997) in which turtles (and other wildlife) produced in the core area (source) disperse into the buffer and transition zones (sink) where sustainable harvest is allowed. Our recommendations are in keeping with the traditional UNESCO model that discourages all forms of extractive resource use in the core areas of biosphere reserves (Hough 1988). Notably, TSBR appears unique among biosphere reserves in continuing to allow the extraction of fish and wildlife from core areas.

Implementing effective protection of TSBR core areas will prove challenging for several reasons. First, core areas are encompassed within administrative fishing lots, and concessionaires will no doubt be reluctant to relinquish their right to harvest wildlife in these areas owing to the potentially significant economic loss this entails. Second, the government departments charged with implementing conservation measures are chronically underfunded and field personnel often lack basic equipment, such as functioning boats and communication gear. Third, the size of the core areas (70,837 ha) is large relative to the number of personnel tasked with protection. Moreover, patrolling in TSBR is difficult because many areas are accessible only on foot during the dry season. Nonetheless, effective protection of core areas is absolutely essential to insure the long-term sustainability of resource use in TSBR (Platt et al. 2004b).

Unlike the harvest of living turtles, we do not regard egg collecting as a threat to turtle populations in TSBR. Turtle nests are widely dispersed and difficult to locate, and egg collecting is a specialized activity practiced by relatively few people who undoubtedly find only a small percentage of available nests each year. Moreover, turtles typically experience high rates of mortality among eggs and hatchlings, and these life stages are the least valuable demographic component of most populations (Iverson 1991; Congdon et al. 1993). In general, egg collecting only threatens turtle populations when nesting activity is concentrated at specific sites, such as sandbars along rivers or coastal beaches (Thorbjarnarson et al. 2000).

Finally, hydrological changes resulting from proposed dam construction on the upper Mekong and its tributaries (Osborne 2000) could alter the future prospects of turtle populations in TSBR. Predicted impacts of dam construction include wetland loss and an altered flooding cycle with a dry season flow 50% greater than under natural conditions (Chapman and He 1996; Dudgeon 2000). These changes could negatively affect turtle populations through habitat loss, a reduction in prey availability, and an increased loss of nests to flooding (Roberts 1993; Dudgeon 2000; Hogan et al. 2004; Platt et al. 2004b).

Reproductive Ecology of Malayemys subtrijuga

The mean CL of female and male *M. subtrijuga* was 158.0 $\pm$ 38.2 mm SD (range = 87.0–236.0 mm; $n = 248$) and 132.8 $\pm$ 25.1 mm SD (range = 93.0–199.4 mm;

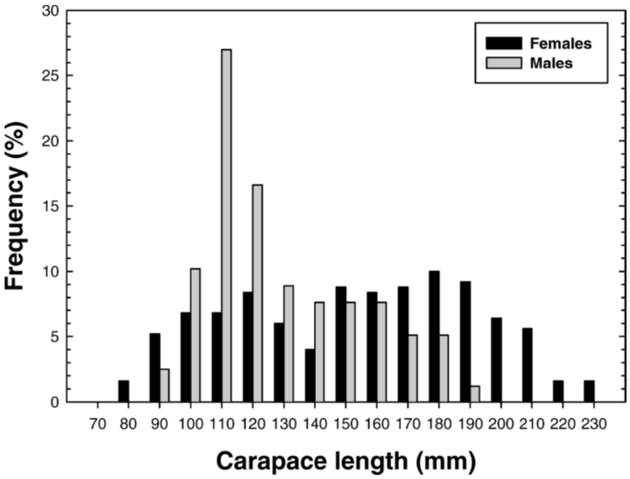

Figure 2. Size-class distribution of female ($n = 248$) and male ($n = 78$) *Malayemys subtrijuga* from Tonle Sap Biosphere Reserve, Cambodia.

$n = 78$), respectively. A frequency distribution (Fig. 2) indicated females were larger than males and the mean CL of females was significantly greater than that of males ($t = 5.4$, df $= 324$, $p < 0.001$). We calculated a SDI of $+ 0.18$ for *M. subtrijuga*. Somewhat greater SDI values of $+ 0.27$ and $+ 0.39$ were calculated for *M. macrocephala* (Brophy 2006). Brophy (2006) suggested that sexual size dimorphism in *Malayemys* is due to different selective pressures faced by females and males; selection for increased fecundity favors larger body size among females; whereas, the advantages of early sexual maturity outweigh the risks of small body size in males. Because male and female *M. macrocephala* apparently consume different foods (Srinarumol 1995; Brophy 2006), character displacement to reduce potential competition (Brown and Wilson 1956; Slatkin 1984) may also be an important evolutionary factor selecting for different adult body sizes (Brophy 2006). However, Shine (1989) cautioned that ecological differences between the sexes are likely a consequence rather than the cause of observed patterns of sexual size dimorphism.

We obtained 30 female *M. subtrijuga* (CL = 153.0–230.0 mm) from local sources during early January 2001. These turtles were injected with oxytocin and we recovered 129 eggs from 22 females; 8 females failed to deposit a clutch. The CL of the smallest female that deposited a clutch was 162.2 mm. Mean clutch size and clutch mass were 5.8 ± 1.7 eggs SD (range = 3–10) and 88.6 ± 34.7 g SD (range = 37.0–170.0 g), respectively. Our estimates of clutch size and mass should be considered conservative because in some instances females injected with oxytocin may only deposit a partial clutch (Congdon and Gibbons 1985). However, we administered 2 injections of oxytocin to each female, and it is therefore likely that complete clutches were recovered from most turtles. Moreover, inguinal palpation of females following clutch deposition failed to detect additional eggs. Mean egg length, width, and mass were 41.2 ± 2.7 mm SD (range = 35.3–47.5 mm), 23.8 ± 1.7 mm SD (range = 21.0–27.7 mm), and 15.1 ± 3.3 g SD (range = 9.0–22.0 g), respectively.

Mean clutch size in our study was significantly greater (analysis of variance, df = 1, 42; $F = 21.79$; $p < 0.001$) than the mean of 3.8 ± 1.0 eggs SD (range = 3–6; $n = 22$) reported for *M. subtrijuga* [*M. macrocephala*; Brophy 2004] in Thailand (Srinarumol 1995). The range of 5–10 eggs given by Nutaphand (1979) for *M. subtrijuga* is comparable to our study. According to unsubstantiated reports from fishermen in TSBR, *M. subtrijuga* may deposit as many as 20 eggs in a clutch. The range of linear egg dimensions that we found encompasses, and is somewhat greater than, values reported by others (Smith 1931; Ewert 1979; Srinarumol 1995).

We found no correlation between female CL and clutch size ($r = 0.22$; $p = 0.31$; Fig. 3), but because *M. subtrijuga* deposits multiple clutches during a single nesting season (Srinarumol 1995), it is possible that total annual fecundity is significantly related to body size. There was a significant positive correlation between female CL and both egg mass ($r = 0.82$; $p < 0.001$) and clutch mass ($r = 0.63$; $p < 0.001$) indicating that egg size increases with increasing female body size (Fig. 3). Hatchling size in *M. macrocephala* is positively correlated with egg mass (Srinarumol 1995) and a growing body of literature suggests that fitness advantages accrue to larger hatchlings (Miller et al. 1987; Janzen et al. 2000, but see also Congdon et al. 1999). Theoretical models of optimal clutch size predict a trade-off between clutch size and egg mass because energy allocated to reproduction must be divided among both (Brockelman 1975; Stearns 1992). However, we found no correlation between clutch size and egg mass ($r = 0.09$; $p = 0.68$), suggesting that such a trade-off did not occur among the *M. subtrijuga* females in our sample.

We incubated 128 *M. subtrijuga* eggs, of which 4 (3.1%) hatched successfully on 10 May 2001 after an incubation period of 99 days. Two hatchlings were killed and eaten by village dogs; morphometric measurements of the 2 remaining hatchlings were: CL = 37.6 and 37.2 mm; PL = 28.0 and 27.8 mm; and mass = 10.5 and 10.0 g. Ewert (1979) reported a mean CL for 11 hatchlings of 35.3 mm. Poor hatching success among our sample of clutches is believed to be due to 3 factors. First, village dogs repeatedly penetrated the perimeter fence at the field station, unearthed clutches, and consumed eggs. Second, extraneous calcium deposits were noted on many eggs at the time of oviposition that probably formed because females had retained eggs for longer than normal; an undetermined period elapsed from the time females were captured until we obtained them in local markets, and we held turtles for an additional 21–24 days. Extraneous calcium deposits are thought to cause decreased embryo viability by reducing eggshell porosity and gas exchange (Wink et al. 1990). Third, our incubation regime may have been inadequate for a turtle that appears to deposit clutches

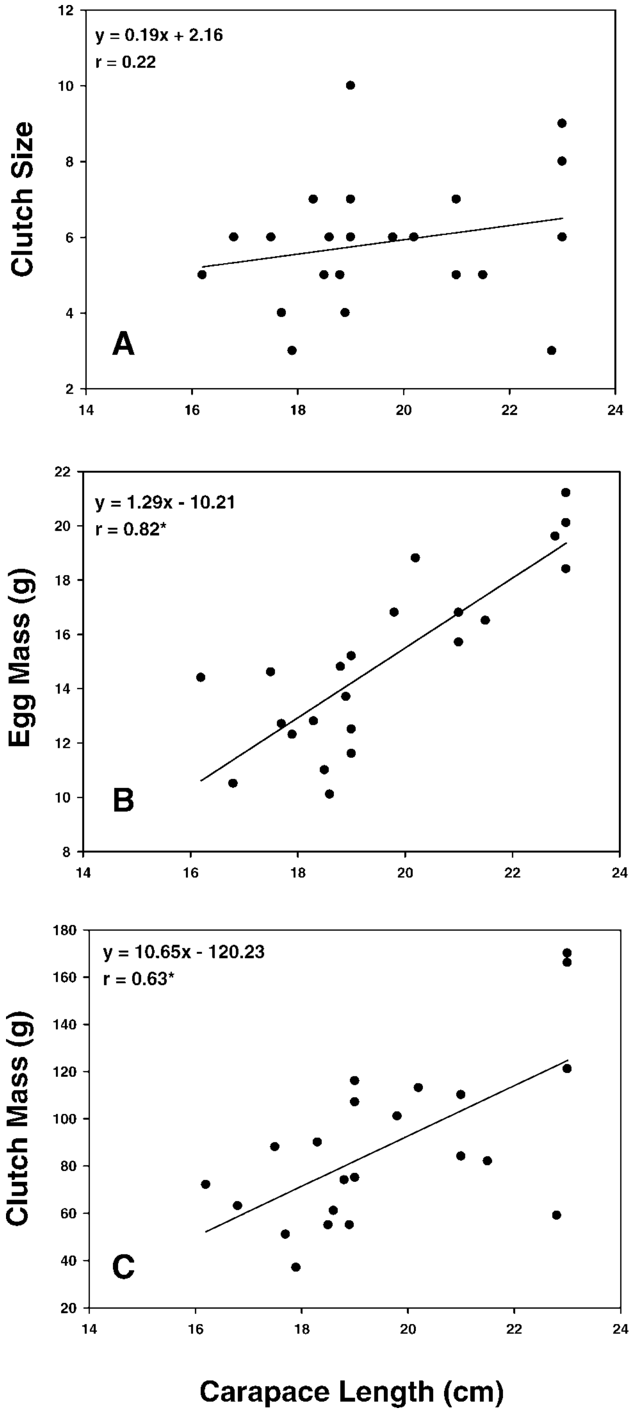

Figure 3. Relationship between the carapace length of female *Malayemys subtrijuga* and (A) clutch size, (B) egg mass, and (C) clutch mass (* $p < 0.001$).

underwater (see below). Our results and information obtained from fishermen suggest that neonate *M. subtrijuga* emerge from the nest at the beginning of the wet season.

With the assistance of local egg collectors, we located 5 *M. subtrijuga* nests during field surveys in March 2001. Four nests were found along Long Aung Creek (lat 13°14.27′N, long 103°37.77′E) within the Prek Toal core area. These nests were located 5 to 10 m apart under a dense canopy of *Vitex* sp. A fifth nest was found on a low ridge (lat 13°14.33′N, long 103°39.62′E) near Prek Toal Village, covered in a dense growth of herbaceous vegetation (*Sorghum* sp., *Sesbainia* sp., and *Polygonum* sp.). Nests were constructed in partially flooded, waterlogged clay substrates, and holes were 10 to 12 cm deep. An egg collector removed 1 clutch and the other 4 nests were robbed by macaques (*Macaca fascicularis*) prior to our visit. According to egg collectors, other predators of *M. subtrijuga* nests include otters (*Lutra* spp.), greater coucals (*Centropus sinensis*), and water monitors (*Varanus salvator*).

Egg collectors stated that *M. subtrijuga* deposits clutches from December through March. This is consistent with our observation of gravid females in local markets as early as mid-December. The initiation of nesting coincides with the end of the wet season when elevated water levels in Tonle Sap slowly begin to recede. Our observations of nests in partially flooded, waterlogged soil and the presence of gravid females during a period when water levels remain high and exposed nesting substrates are limited raises the interesting possibility that *M. subtrijuga* may construct underwater nests. Underwater nesting has been reported for several other tropical turtles (e.g., *Chelodina rugosa* and *Dermatemys mawii*) that, like *M. subtrijuga*, inhabit seasonal environments and nest during the late wet and early dry seasons (Kennett et al. 1993; Polisar 1996). Kennett et al. (1993) suggested that underwater nesting evolved in response to the unpredictable availability of dry nest sites in seasonal habitats that undergo extensive flooding. Clearly this question with regards to *M. subtrijuga* merits further investigation.

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