CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A COMPILATION PROJECT OF THE IUCN/SSC TORTOISE AND FRESHWATER TURTLE SPECIALIST GROUP

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Malayemys macrocephala (Gray 1859) – Malayan Snail-Eating Turtle, Rice-Field Terrapin

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> **CHELONIAN RESEARCH MONOGRAPHS** Number 5 (Installment 12) (2018): Account 108



Published by Chelonian Research Foundation and Turtle Conservancy



in association with IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Global Wildlife Conservation, Turtle Conservation Fund, and International Union for Conservation of Nature / Species Survival Commission











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SUMMARY. – The Malayan Snail-eating Turtle, *Malayemys macrocephala* (family Geoemydidae), is a small (carapace length generally under 200 mm) aquatic turtle native to the west-central Indochinese Peninsula and northern Malay Peninsula. Shortly after description, the species was synonymized with *M. subtrijuga* and only recently regained taxonomic acceptance. Sexual dimorphism is pronounced, with females growing considerably larger than males. Individuals have large heads and other specializations for a diet of predominantly molluscs. The species frequently inhabits rice fields, canals, and other lowland habitats modified by human activity. Clutches of 10 eggs or fewer are laid early in the dry season and the eggs may take several months to hatch. Despite considerable exploitation in the past, and moderate levels of collection and other threats at present, the species appears to remain relatively abundant and widespread. Additional research, including field surveys and population monitoring, in addition to abatement of water pollution and continued reduction of exploitation, are recommended conservation measures.

DISTRIBUTION. – Thailand, Malaysia. Extends from northern Thailand through northern Peninsular (West) Malaysia; possibly also occurs marginally in western Laos, western Cambodia, and southeastern Myanmar.

SYNONYMY. – Geoclemys macrocephala Gray 1859, Clemmys macrocephala, Emys macrocephala, Damonia macrocephala, Geoclemmys macrocephala, Malayemys macrocephala, Emys megacephala Gray 1870 (nomen nudum), Damonia megacephala.

SUBSPECIES. - None currently recognized.

STATUS. – IUCN 2018 Red List: Not Evaluated (NE); TFTSG Draft Red List: Least Concern (LC, assessed 2018); CITES: Appendix II.

Taxonomy. — Malayemys macrocephala was originally described as Geoclemys macrocephala by Gray (1859) based on two specimens originating from "Siam" and sent to the British Museum (now the Natural History Museum) by Henri Mouhot. Following its description, the species was initially reassigned to a number of other genera (i.e., Clemmys, Emys, Geoclemmys, and Damonia; TTWG 2017) before Hubrecht (1881) questioned the species' validity. Hubrecht (1881) argued that the physical description and figure provided by Gray (1859) matched specimens and descriptions of Emys subtrijuga, a species previously named by Schlegel and Müller (1845). Thereafter, Gray's specific epithet macrocephala was considered a junior synonym of the earlier name subtrijuga (Hubrecht 1881; Bourret 1941). The synonymized taxon typically appeared in scientific works as Damonia subtrijuga until Lindholm (1931), aware that Damonia was already in use for a genus of dipteran insect, proposed the generic name *Malayemys*. Most authors adopted this change, although *Damonia* continued to sporadically appear in literature afterward (e.g., Bourret 1941; Nutaphand 1979). *Malayemys* was for a long time considered monotypic, with *M. subtrijuga* (sensu lato) the sole member of the genus (Ernst and Barbour 1989; Iverson 1992; Stuart et al. 2001).

This arrangement persisted until Brophy (2002, 2004) re-examined morphological variation within *Malayemys*. Based on differences in head stripes and shell characters, Brophy (2004) concluded that the genus consisted of two distinct allopatric groups, each of which he considered a distinct species. *Malayemys subtrijuga* was restricted to populations in eastern Thailand, Cambodia, Vietnam, Laos, and Java, while *M. macrocephala* was resurrected for populations in northern, central, and southern Thailand and northern Peninsular Malaysia (Brophy 2004, 2005). This revision was subsequently accepted by others (Fritz



Figure 1. Adult Malayemys macrocephala from Phetchaburi Province, Thailand. Photo by F. Ihlow.

and Havaš 2007; TTWG 2007b). Of the two syntypes (BMNH.1947.3.4.51–52) of *M. macrocephala* in the collection of the Natural History Museum, Brophy (2004) designated the larger specimen, BMNH.1947.3.4.52, as the lectotype; he also restricted the type locality to Thanyaburi, Pathum Thani Province, north of Bangkok, in the Chao Phraya River Basin of central Thailand.

Ihlow et al. (2016) analyzed mitochondrial DNA, microsatellite loci, and morphology of snail-eating turtles from Thailand and Cambodia. Their analyses identified three distinct groups within *Malayemys*: *M. macrocephala*, *M. subtrijuga*, and a third more genetically divergent clade that they described as the new species *M. khoratensis*. This new species was also nearly simultaneously described as *M. isan* by Sumontha et al. (2016), but *M. isan* was published later (Thomson and Lambertz 2017). In their mitochondrial DNA, M. macrocephala and M. subtrijuga displayed a history of introgression and relatively low differentiation (uncorrected p-distances of 1.45% for cyt b and 1.09% for partial ND4 gene). However, the nuclear gene pools of all three taxa were unique, indicating reproductive isolation (Ihlow et al. 2016). Consistent differences in morphology were also apparent (Ihlow et al. 2016; Sumontha et al. 2016). As a result, three species of Malayemys (M. macrocephala, M. subtrijuga, and M. khoratensis) were included in the most recent checklist of chelonian taxonomy (TTWG 2017). However, the checklist authors were not unanimous in accepting this arrangement, including disagreement over the status of M. macrocephala. TTWG (2017) recommended a more comprehensive study of the molecular and morphological variation of the genus, incorporating both the type specimens and samples from across the entire known distribution of



Figure 2. *Malayemys macrocephala*. Left: Carapace of an individual from Uthai Thani Province, Thailand. Right: Plastron of an individual from Phetchaburi Province, Thailand. Photos by F. Ihlow.



Figure 3. Malayemys macrocephala. Top: Profile of an adult from Uthai Thani Province, Thailand. Bottom: Individuals with two nasal stripes (*left*) and four nasal stripes (*right*). Photos by F. Ihlow.

Malayemys. Although we believe that sufficient evidence currently exists to recognize *M. macrocephala* as a separate species, we also agree with the authors of the checklist on the need for further research. In order to maintain taxonomic stability until additional data become available, we follow the taxonomy of TTWG (2017) for this account.

While M. macrocephala is presently recognized as a full species, much of the available information on the species is found under other names (e.g., Damonia subtrijuga and Malayemys subtrijuga) due to the long period of synonymy (e.g., Smith 1931; Taylor 1970; Nutaphand 1979; Srinarumol 1995). Furthermore, previous literature may also include a mix of material from the currently accepted species (e.g., Bourret 1941; Ernst and Barbour 1989; Iverson 1992; Stuart et al. 2001). In some cases, it may be possible to determine which species is covered by a work through localities or representations (photographs or descriptions) of specimens; when these details are lacking in the text, the species identification may be ambiguous. For this account, we endeavored to identify which of the currently valid species appeared within our references and have presented species-specific data whenever possible. We use the specific

taxonomic name where information refers to a single species; when the source material could not be restricted to one species, we use only the generic name.

Phylogenetically, Malayemys is included in the Old World Pond Turtles (family Geoemydidae), but past analyses have offered differing affinities for the genus within this group. Previous morphological and karyotypic studies placed Malayemys with the macrocephalic genera Chinemys (now = Mauremys) and Geoclemys (Loveridge and Williams 1957; Hirayama 1984; Gaffney and Meylan 1988), within a complex including Chinemys and Ocadia (now both = Mauremys) and Hieremys (now = Heosemys) (McDowell 1964), or intermediate between the other geoemydids and the family Emydidae (Carr and Bickman 1986). However, similarities in morphology can occur through convergent evolution in groups that are not closely related (e.g., the cranial osteology of duraphagous turtles; Joyce and Bell 2004). Based on analyses of mitochondrial and nuclear DNA, Spinks et al. (2004) presented a phylogeny in which Malayemys is the sister clade to Orlitia. This relationship has since been supported by additional molecular studies (Thomson and Shaffer 2010; Guillon et al. 2012).

Description. — The morphology of *M.macrocephala* has been previously described, based primarily on Thai specimens, by Gray (1859), Günther (1864), Flower (1899), Smith (1931), Taylor (1970), Nutaphand (1979), Brophy (2002), and others. *Malayemys macrocephala* is



Figure 4. Juvenile *Malayemys macrocephala* from central Thailand. Photo by F. Ihlow.

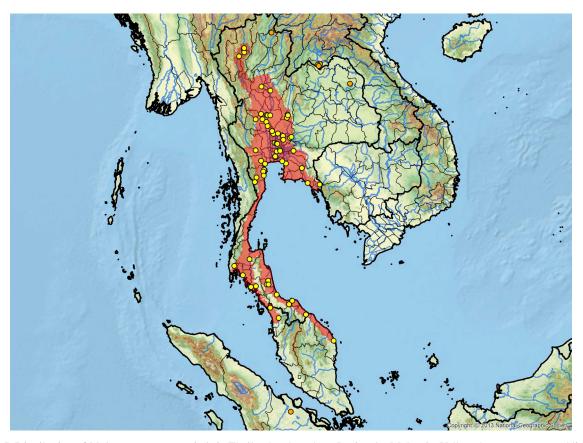


Figure 5. Distribution of *Malayemys macrocephala* in Thailand and northern Peninsular Malaysia. Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992) plus more recent and authors' data; orange dots = uncertain native or trade or introduced specimens; red shading = projected historic distribution. Distribution based on GIS-defined level 10 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al. 2009; TTWG 2017), and adjusted based on authors' subsequent data.

a relatively small species; adults generally remain under 200 mm in straight carapace length (SCL). The sexes display dimorphism in body size, with females growing larger than males (Srinarumol 1995; Brophy 2006). Based on measurements of museum specimens, Brophy (2006) calculated the mean $(\pm 1 \text{ SD})$ maximum SCL of mature males to be 117.21 ± 9.55 mm (n = 15), while adult females averaged significantly larger at 148.60 ± 20.23 mm (n = 21). The means of maximum SCL for adult males (n = 14)and females (n = 25) measured by Srinarumol (1995) were 112.20 ± 9.83 mm and 155.48 ± 27.91 mm, respectively. The largest reported male attained a midline SCL of 156 mm (Ihlow et al. 2016). Females may exceed 200 mm in SCL, but such specimens are rare. Das (2010) gave the maximum SCL as 300 mm, but the basis for this statement is unknown and is probably erroneous. The greatest recorded size of a female was 220 mm in midline SCL (Srinarumol 1995; Ihlow et al. 2016). The heaviest males known to us were under 500 g, while very large females can surpass 1300 g in body mass (Ihlow, unpubl. data).

In addition to differing in their smaller maximum body size, males can be distinguished from females by proportionally narrower and flatter shells, thicker tail bases, shorter plastra, and V-shaped anal notches. Females have comparatively wider and higher shells, thinner tail bases, longer plastra, and shallower rounded anal notches. Differences in shell shape are due to allometric growth; the shells of males increase more in length relative to width or height during growth, while most aspects of the shell grow proportionally in females (Brophy 2006). Unlike many turtle species, a plastral concavity does not develop in males.

Juvenile Malayan Snail-eating Turtles are similar in appearance to adults, but have proportionally higher shells. Full-term (24-week-old) embryos from eggs collected in central Thailand had a mean maximum SCL of 33.3 mm (n = 7; Pewphong et al. 2013). Mean dimensions of twelve hatchlings measured by Srinarumol (unpubl. data) were 32.80 ± 2.57 mm in maximum SCL, 23.02 ± 2.59 mm in maximum straight carapace width, and 29.20 ± 2.59 mm in maximum straight plastron length (SPL). The mean mass of 48 hatchlings was 8.04 ± 1.61 g, and both sexes are similar in size at hatching (Srinarumol 1995). The tail is short at all stages of life.

The carapace of M. macrocephala is tricarinate. Keels are distinct in younger animals but may be reduced to a discontinuous series of knobs in old adults. The lateral

keels seldom extend past the third costal scutes. The scutes of the shell are very thin. The first vertebral scute is usually greater in length than width and tapered posteriorly, while the remaining vertebrals are typically broader than long (Ihlow et al. 2016). The underlying eight neural bones are unusually wide. The anterior neurals are typically longer than the posterior ones, but the great width of the bones is maintained throughout the entire series.

The color of the carapace ranges from chestnut to mahogany brown with a cream or yellow rim. The scutes of the carapace tend to be darker along the keels and the posterior seams of the marginal scutes, while recent growth is usually lighter in color. The dark marks along the seams of the marginals form narrow dark bars on the lower side of those scutes not adjacent to the bridge (Ihlow et al. 2016).

The immovable plastron is shorter and narrower than the carapace; for 51 individuals with a mean midline SCL of 124.7 mm, the mean maximum SPL was 102.3 mm and the mean straight plastron width at the broadest position was 81.9 mm (Ihlow et al. 2016). Attachment of the plastron to the carapace is through strong buttresses and sutures. The humero-pectoral seam is posterior to the entoplastron. The plastron is yellow with a large dark blotch on each scute; occasionally, these markings may expand and connect into a broad line on either side of the plastron or an almost completely dark ventral side. Two dark blotches are present on the bridge.

The head is proportionally large and becomes relatively enormous in large, old females. However, even in the largest specimens, the head remains somewhat elongate compared to other macrocephalic turtle species (e.g., some *Graptemys* species). The snout projects slightly beyond the mouth.

The skull of Malayemys displays a number of specializations for durophagy, many of which are shared by other molluscivorous turtles (Srinarumol 1995; Joyce and Bell 2004). Both the postorbital and quadratojugal bars are broad and strong, and the quadratojugal bar is only slightly emarginated from below. The supraoccipital crest is large and serves as an attachment for extremely powerful jaw-closing musculature (Srinarumol 1995). There are two uniquely derived traits among the characters of the cranial bones of Malayemys: contact of the inferior process of the parietal with the maxilla and contact between the pterygoid and the articular facet of the quadrate (Joyce and Bell 2004). The coronoid process of the mandible is large and very high (McDowell 1964; Joyce and Bell 2004) and the symphysis is developed into a strong, blunt hook. The alveolar surfaces of both jaws are greatly expanded to form crushing areas. However, the jaws do not occlude when closed and are unable to cut (Srinarumol 1995). According to Iwasaki et al. (1996), the flattened tongue of M. macrocephala is triangular with a rounded apex and is similar to the tongues of other geoemydid turtles.

Head coloration is dark brownish-gray to black with several distinctive white to yellow stripes and spots present on each side of the head, with some marks stretching onto the neck. A supraorbital stripe begins on top of the snout, passes above the eye, and continues along the temporal region. An infraorbital stripe runs down the lateral aspect of the snout, curves gradually under the eye, and extends through the corner of the mouth (Brophy 2004; Ihlow et al. 2016). In M. macrocephala, the infraorbital stripe is relatively wide at the loreal seam between the eye and nostrils but typically does not extend far above the suture and very seldom connects with the supraorbital stripe (Brophy 2004; Ihlow et al. 2016). Beyond the mouth, the infraorbital stripe generally continues roughly parallel to the supraorbital stripe, but may be broken. A postocular stripe (typically broken or consisting of a line of spots) begins behind the orbit and runs between and parallel to the supraorbital and infraorbital stripes (Ihlow et al. 2016). In M. macrocephala, four or fewer nasal stripes are present below the nostrils (Brophy 2004; Ihlow et al. 2016). The lower jaw is also marked by a pair of light stripes. The legs and soft skin are gray with light colored markings.

Distribution. — The range of *M. macrocephala* covers the west-central Indochinese Peninsula and northern Malay Peninsula. Most of the species' distribution is within the borders of Thailand, with slight extension into northern Peninsular Malaysia and potentially marginally into other surrounding countries (Cambodia, Laos, and Myanmar). In Thailand, the species inhabits the majority of the country, including the northern, central, southeastern, and southern regions. Malayan Snail-eating Turtles are found in the Chao Phraya River Basin, the lower drainage of the Mae Klong River, and the lowlands along the Gulf of Thailand (Smith 1916; Taylor 1970; Brophy 2006; Ihlow et al. 2016).

On the Malay Peninsula, *M. macrocephala* has been recorded from the southern provinces of Thailand, below the Isthmus of Kra, into northern Malaysia (Brophy 2006). In Peninsular (West) Malaysia, *M. macrocephala* is present in the states of Perlis and Kedah on the northwestern coast (Auliya 2007; E.O. Moll, pers. comm.) and Terengganu and possibly Kelantan on the northeastern coast (Sharma and Tisen 2000). *Malayemys macrocephala* does not occur in the lowlands of the rest of Peninsular Malaysia; the reason for its absence from this seemingly suitable area is unclear (Smith 1930).

Malayan Snail-eating Turtles have been identified in Sakon Nakhon Province of northeastern Thailand (Ihlow et al. 2016) and reported from markets in nearby parts of western Laos (Suzuki et al. 2015). These sites are located within the drainage of the Mekong River, outside the confirmed range of *M. macrocephala*. At present, it is unclear whether these specimens indicate that *M. macrocephala* naturally occurs along the middle reaches of the Mekong or if the species was introduced from another area through trade (Suzuki et al. 2015; Ihlow et al. 2016).

Win Maung and Win Ko Ko (2002) and Platt et al. (2012) included *M. macrocephala* in the turtle fauna of Myanmar. Due to the proximity of known localities in southern Thailand, the species could potentially inhabit southeastern Myanmar (Platt et al. 2000; Brophy 2005). However, uplands along the border of Thailand and Myanmar represent a biogeographic barrier to lowland turtle species such as M. macrocephala (Thirakhupt and van Dijk 1995). Presently, there is little evidence for the occurrence of this species in Myanmar, although S.G. Platt (pers. comm.) has seen photographs reportedly portraying a specimen captured during a fish survey in southern Myanmar, but no locality data have yet been published. Without further information, the origin of the individual cannot be verified, and the possibility that it was a released trade specimen cannot be excluded. Therefore, the occurrence of M. macrocephala in Myanmar presently remains tentative, and the species' potential distribution within the country is unknown.

Habitat and Ecology. — *Malayemys macrocephala* lives in freshwater habitats, both natural and anthropogenic, at elevations ranging from near sea level around Bangkok to roughly 300 m in the Mae Ping Valley of northern Thailand. The species is restricted to lowlands and has not been found in the streams of any hill areas (Thirakhupt and van Dijk 1995). Most lowland areas in Thailand and Malaysia have been heavily impacted by humans through agriculture and development. No studies of habitat preference compared to availability have been conducted, but M. macrocephala is typically associated with warm, shallow, slow-moving or still waters with dense vegetation. Known habitats include flooded rice fields, khlongs (canals), irrigation ditches, ponds, swamps, seasonal wetlands, floodplains, and the margins of large rivers (Thirakhupt and van Dijk 1995; Cox et al. 1998; Chan-ard et al. 1999; Stuart et al. 2001). Malayan Snail-eating Turtles are frequently observed in the waters of Buddhist temples and urban parks (Pauwels et al. 2003; Sukmasuang et al. 2007; Bundhitwongrut et al. 2008; Sukmasuang et al. 2009; Chansue 2012) as a result of introductions during religious ceremonies (see Threats to Survival). Malayemys macrocephala shares some lowland habitats with Amyda ornata, Cuora amboinensis, Heosemys annandalii, Heosemys grandis, and Siebenrockiella crassicollis (Annandale 1916; Thirakhupt and van Dijk 1995; Eiamampai 2002; TTWG 2017).



Figure 6. Habitats of *Malayemys macrocephala*. Top Left: Semi-natural freshwater wetland in the vicinity of Bueng Boraphet Non-Hunting Area, Nakhon Sawan Province, Thailand. Photo by F. Ihlow. Top Right: Shallow lake in northern Thailand. Photo by F. Ihlow. Bottom Left: Khlong (canal) in Pattum Thani Province, Thailand. Photo by F. Ihlow. Bottom Right: Rice fields in Kedah State, Malaysia. Photo by E.S.H. Quah.

Across the distribution of *M. macrocephala*, the climate is tropical and dominated by monsoons, resulting in a seasonal pattern of wet and dry periods. Northern Thailand experiences three seasons: a rainy season (July-October) when the most precipitation occurs, a cool dry season (November-February) when air temperatures decrease slightly and rainfall is the least, and a hot dry season (March-June) when maximum air temperatures can rise to 40°C (Maxwell 2004; Poolpak et al. 2008). Moving southward, annual precipitation increases, the length of the dry period shortens, and air temperatures become less variable (Maxwell 2004). Southern Thailand and Peninsular Malaysia are hot and humid throughout the year, with two rainy seasons: the northeast monsoon (November-February) and the slightly drier southwest monsoon (May-August). While the eastern lowlands receive substantial rains during the northeast monsoon, the western lowlands are comparatively less influenced by this weather pattern due to a rain shadow from the mountains in the center of the peninsula. Convective rains fall throughout the region during the two inter-monsoon periods (Suhaila et al. 2010). In central Thailand, M. macrocephala shows seasonal patterns in activity, being most active during the rainy season and cool dry season. Local Thai people have reported that Malayan Snail-eating Turtles bury into the mud when temporary waterbodies disappear during the hot dry season and estivate until the next monsoon rains begin (Ihlow, unpubl. data).

Malayemys macrocephala is usually characterized as a slow, bottom-walking, aquatic species. Cloacal temperatures of turtles in Bangkok ranged from 27–32°C during the cool dry season and were identical to the temperatures of the surrounding shallow water microhabitats (Thirakhupt and van Dijk, unpubl.data). We are unaware of any extensive research on daily activity or movement patterns. Malayan Snail-eating Turtles have been reported to be nocturnal (Chan-ard et al. 2015), but active individuals may also be seen during the day. Mudde (1991) discovered a single animal at night in a pool near Krabi in southern Thailand, but found no trace of turtles in this pool during the daytime. Specimens have occasionally been observed foraging by the light of street lanterns in Bangkok (Thirakhupt and van Dijk, pers. obs.).

Malayemys macrocephala appears to be highly molluscivorous. Srinarumol (1995) was able to identify the remains of two gastropod species, *Filopaludina sumatrensis* and *Brotia costula*, in the stomach contents of 10 (5 males and 5 females) Malayan Snail-eating Turtles from Pathum Thani Province, Thailand. Individuals were also observed consuming *Pomacea canaliculata*, a South American snail species that is invasive in Thailand (Srinarumol 1995). According to Cox et al. (1998), males primarily feed upon aquatic snails, whereas large females will also eat freshwater mussels. However, a comprehensive dietary analysis has not yet been conducted, so the exact composition of the diet and the actual degree of any possible ontogenetic changes or differences based on sex are uncertain. Leeches, crabs, shrimp, small fish, worms, and insects have also been reported as foods (Taylor 1970; Nutaphand 1979; Manthey and Grossmann 1997; Cox et al. 1998; Auliya 2007; Chanard et al. 2015).

While foraging, the turtle systematically examines surrounding objects, including every available nook and cranny. Prey appears to be recognized by olfaction. Feeding is slow and methodical. When *Malayemys* consumes a mollusc, the turtle uses its tongue to turn the prey until it achieves a position suitable for crushing the hard shell between its jaws (Schmidt 1959). After crushing, the turtle washes away the shell fragments by flushing movements of the throat, and then the soft body is swallowed (Gans 1969). This procedure works well for snails but is less successful with freshwater mussels whose mantle adheres to the shell. Swallowed shell fragments and snail opercula may be eliminated through regurgitation or defecation.

Nesting occurs between November and February (i.e., the cool dry season) in northern and central Thailand, but usually takes place between mid-December and March (occasionally extending into April depending on weather conditions) in southern Thailand (P. Meewattana, pers. comm.). Females excavate nests along the edges of khlongs and ponds or on the ridges between rice fields (Pewphong et al. 2013). Nest cavities are 70–110 mm in greatest diameter and 70–150 mm in depth (Keithmaleesatti et al. 2010).

The eggs are brittle-shelled and elliptical. Flower (1899) reported an egg with dimensions of 32 x 20 mm laid on 17 April in Thailand. Fertile eggs (n = 12) measured by Thirakhupt and van Dijk (unpubl. data) had mean dimensions of 40.7 \pm 2.6 mm by 21.9 \pm 1.2 mm and a mean mass of 10.9 \pm 2.8 g. Srinarumol (1995) found eggs (n = 83) to have similar lengths (range = 32.5-45 mm) and masses (range = 6.3-15.4g); the diameters of these eggs were not provided. A mean clutch size of 3.86 ± 1.08 eggs (range = 3–6 eggs, n = 22) was reported by Srinarumol (1995) from nests in Phetchaburi Province, Thailand. Nutaphand (1979) gave the clutch size as 5-10 eggs, presumably also based upon Thai specimens. Pewphong et al. (2013, 2016) obtained 712 eggs from 126 clutches in Phra Nakhon Si Ayutthaya Province, Thailand, resulting in a mean clutch size of 5.65 eggs. No information is available on clutch frequency or relative clutch mass in the wild, but Böhm (2017) reported that a female in captivity laid two clutches in a season, each comprised of two eggs, and with a relative clutch mass (clutch mass/post oviposition female body mass) of approximately 0.036. The following year, this same female produced four clutches, totaling 13 eggs, while being kept under the same conditions (Ettmar, unpubl. data).

The mean internal temperature of nests surveyed between December and February in central Thailand was $28.47 \pm$

 3.80° C (range = $20.5-36.5^{\circ}$ C), which was lower than the average ambient air temperature (Pewphong et al. 2013). Incubation periods and rates of hatching have been studied in eggs collected from the wild and artificially incubated. However, the reported incubation lengths and hatch rates may not be representative of natural nests due to the passage of indeterminate lengths of time between nesting and collection and the effects of controlled incubation conditions. Eggs collected by Srinarumol (1995) hatched after an average of about 165 days (range = 97-292 days) at 28-30°C. There was wide variation in the duration of incubation with the first and last hatchlings from a single clutch emerging as much as four months apart. Hatch rate during the study was 58.5%. There was no significant size or mass difference between eggs that hatched and those that did not, but mean hatchling mass was positively correlated with mean egg mass (Srinarumol 1995). Pewphong et al. (2013, 2016) incubated eggs at three different constant temperatures: 26°C, 29°C, and 32°C. At 29°C, the mean incubation period was 115 ± 20.3 days with a range from 78-150 days (Pewphong et al. 2013). The length of incubation was similar at 26°C and slightly shorter at 32°C, but the differences were not statistically significant. Further, while the growth rate of embryos was significantly greater at 32°C than at either 26°C or 29°C, the incidence of deformities also increased significantly (Pewphong et al. 2013).

Sex determination in *M. macrocephala* is temperaturedependent and follows TSD Pattern Ia. Pewphong et al. (2016) found that significantly more males were produced than females at 26°C. Incubation at 32°C resulted in significantly more females than males. The pivotal temperature was 29°C (Pewphong et al. 2016).

Young Malayan Snail-eating Turtles grow relatively quickly. Two hatchling M. macrocephala raised in captivity by Ettmar (unpubl. data) grew to a mean SCL of 55.5 mm (an increase of nearly 55%) and a mean mass of 31.0 g (an increase of around 200%) by one year of age. Srinarumol (1995) found that the mean growth rate of males was significantly lower than that of females during the first five years of life under captive conditions. For males and females, respectively, mean SCL increased by 44% and 73% in the first year, 25% and 26% in the second year, 18% and 21% in the third year, 14% and 16% in the fourth year, and 12% and 13% in the fifth year. At five years old, the mean SCL of males (n = 5) was 103.79 ± 8.55 mm and the mean SCL of females (n = 11) was 127.75 ± 15.53 mm (Srinarumol 1995). While growth under natural conditions has not yet been thoroughly investigated, available data support juveniles growing at similar rates in the wild. An average increase of 75 mm SCL occurred among nine wild juveniles over their first three years (Thirakhupt and van Dijk, unpubl. data).

The smallest sizes of individuals successfully sexed by Brophy (2006) and Ihlow et al. (2016) using tail morphology were 68 mm maximum SCL and 74 mm midline SCL, respectively. Brophy (2006) considered males less than 80 mm maximum SCL and females under 100 mm maximum SCL to be juveniles, while larger individuals were assigned to either subadult or adult classes. The smallest maximum SCL of a male considered to be an adult was 100.3 mm and the smallest female classified as adult was 114.4 mm in maximum SCL (Brophy 2006). However, it is unknown whether these sizes represent the typical body sizes at which individuals become capable of reproduction. Based on average growth rates, these sizes may be reached within five years in captivity (Srinarumol 1995). It is possible that maturity in the wild can also be attained by five years of age, but this has yet to be confirmed through any studies.

Thirakhupt and van Dijk (pers. obs.) have found leeches to almost always be present on the shells and soft skin of wild Malayan Snail-eating Turtles. However, only three of 50 specimens examined by Ihlow (pers. obs.) bore leeches. Endoparasites include nematodes (Oxyuridae and Rhabditidea) and flukes (Digenea) of the digestive system (Srinarumol 1995). Nematodes occur frequently and can constitute a considerable volume of the contents flushed from the gastrointestinal tracts of wild-caught specimens (Srinarumol, unpubl. data). A blood fluke, Hapalorhynchus snyderi, was described based on specimens isolated from wild-caught turtles from Malaysia (Platt and Sharma 2012). Unidentified blood parasites have also been detected in animals from Thailand (Ihlow, unpubl. data). Nearly all animals living in semi-captivity in Bangkok temple ponds suffer from shell rot, often quite severe, frequently perforating the bone altogether. Animals from the wild show a much lower incidence of shell disease (Thirakhupt and van Dijk, pers. obs.).

Water Monitors (*Varanus salvator*) have been observed consuming Malayan Snail-eating Turtles in the urban parks of central Thailand (Bundhitwongrut et al. 2008; Kulabtong and Mahaprom 2015). Monitor lizards probably also eat *M. macrocephala* eggs. The remains of *M. macrocephala* were recorded in the scats of Hairy-nosed Otters (*Lutra sumatrana*) in southern Thailand (Kanchanasaka and Duplaix 2011). Reliable sources have informed us that Large-billed Crows (*Corvus macrorhynchos*) also actively kill and consume this species (Thirakhupt and van Dijk, unpubl. data).

Population Status. — Historically, *M. macrocephala* was reported to be common around Bangkok (Flower 1899; Smith 1916; Smith 1931) and in the lower Phatthalung River of Peninsular Thailand (Annandale 1916). More recent literature has reiterated the apparent abundance of *M. macrocephala* (Taylor 1970; Thirakhupt and van Dijk 1995; van Dijk and Palasuwan 2000; Pauwels et al. 2003; Chanard et al. 2015). In the early 1990s, a mark-recapture study was undertaken within an area of rice fields transected by a regular network of deep khlongs in Pathum Thani Province,



Figure 7. *Malayemys macrocephala* for sale at a market in Lamphun Province, Thailand. Photo by F. Ihlow.

Thailand; over several months, roughly 400 Malayan Snaileating Turtles were caught, with a low number of recaptures, in an area of less than 10 km² (Srinarumol, unpubl. data).

To date, no further systematic surveys have been undertaken to estimate the sizes or trends of any populations. However, informal observations suggest that the number of *M. macrocephala* is stable or only modestly declining. This species is the only native turtle in Thailand that one can expect to encounter in the wild and viable populations seem to exist at the present. In particular, Malayan Snaileating Turtles appear to be reasonably common in central Thailand within the Chao Phraya River Basin. Substantial reproduction has been reported, based on the large numbers of nests in this area (Keithmaleesatti et al. 2010; Pewphong et al. 2013, 2016). Current information on M. macrocephala in southern Thailand and Malaysia is limited. While populations in the area are thought to be fairly secure at the present time, anecdotes from reliable sources suggest that the species could be less common there now than in the past (Ihlow, unpubl. data).

Threats to Survival. — Local consumption of M. macrocephala occurs in Thailand (van Dijk and Palasuwan 2000). The use of turtles as food has been practiced for a long time in the region (van Dijk 1998). At archeological sites in northeastern Thailand, the remains of *Malayemys* have been found in association with prehistoric human settlements (Higham and Kijngam 1982). Flower (1899) remarked that Thai and Chinese contemporaries in Thailand ate Malayan Snail-eating Turtles. During the 20th century, exploitation of *M. macrocephala* was extremely high prior to 1992 (see Conservation Measures Taken). Today, modest local trade exists, with *M. macrocephala* offered in the food markets of some villages and cities (Thirakhupt and van Dijk 1995; Pauwels et al 2003; Ihlow et al. 2016). However, at present, most consumption in Thailand appears to occur through subsistence collection in lower-income rural areas. Large turtles (over 150 mm in SCL) are generally preferred for food as they provide greater quantities of meat; due to the sexual dimorphism of this species, these individuals are frequently adult females.

Malayan Snail-eating Turtles have also been traded internationally as food and components of traditional medicines. High volumes of Malayemys have been recorded in the markets of China and other East Asian countries (Lee et al. 2004; Cheung and Dudgeon 2006). Although historical export data are unavailable, it is likely that large quantities of M. macrocephala were sent to China from Thailand prior to the early 1990s. In Malaysia, collection of M. macrocephala has reportedly been mostly for export, rather than domestic use. The species was not present in local trade before the mid-1990s (Sharma 1999) and E.O. Moll (pers. comm.) saw only three specimens, via the animal trade, while working in Malaysia. However, Sharma and Tisen (2000) observed a number of *M. macrocephala* at an exporter in Perlis awaiting shipment to China in the late 1990s. Although legal international trade is presently regulated (see Conservation Measures Taken), illegal trade continues. During seizures of illegally traded turtles in Thailand, M. macrocephala was recorded in 11% of cases between 2008 and 2013 (Chng 2014). The species is transported by both air and overland routes (Chng 2014).

Small Malayan Snail-eating Turtles, which typically are not utilized for food, are often used for other purposes.



Figure 8. *Malayemys macrocephala* eggs for sale at a morning market in Phitsanulok Province, Thailand. Photo by P. Meewattana.

All sizes of *M. macrocephala* are frequently sold by street vendors and in markets near Buddhist temples in Thailand, in association with religious beliefs (Srinarumol 1995; Manthey and Grossmann 1997; van Dijk and Palasuwan 2000; Bundhitwongrut et al. 2008; Chansue 2012; Ihlow et al. 2016). The animals are purchased and then subsequently released into the ponds of temples and parks, actions that are believed to confer merit onto the practitioners. Unfortunately, little regard is typically given to ensure that the turtles are placed into appropriate areas. When released into habitats with sufficient prey and shelter, the turtles may survive (Bundhitwongrut et al. 2008), but many quickly perish after succumbing to illness or starvation under unsuitable conditions in crowded temple ponds (Srinarumol 1995; Budischek et al. 2007; Chansue 2012). Merit releases also have the potential to introduce M. macrocephala into areas outside of the species' native distribution.

In the past, young Malayan Snail-eating Turtles regularly entered the global pet trade from Thailand. Although M. macrocephala continues to appear in foreign pet markets (e.g., Sy 2015), this trade has diminished recently and currently appears to be very limited. The decline can be partially attributed to conservation efforts, but is also likely due to low demand because of the generally poor survival of this species in captivity (see Captive Husbandry). Snail-eating turtles remain available in the domestic pet trade of Thailand. During 2006 and 2007, low numbers of Malayemys were available from pet traders in the Chatuchak Weekend Market of Bangkok (Shepherd and Nijman 2008). Specimens of Malayemys were present during 25% of visits to the dealers between 2004 and 2013 (Nijman and Shepherd 2015). However, turtles native to Thailand are not a major focus at Chatuchak and most trade consists of exotic species. While Shepherd and Nijman (2008) and Nijman and Shepherd (2015) did not distinguish between M. subtrijuga and M. macrocephala, most observations of snail-eating turtles at Chatuchak by T. Bundhitwongrut (pers. comm.) have consisted of the latter species. Still, overall, the pet trade does not appear to have ever posed a serious threat to this species.

The eggs of *M. macrocephala* are eaten in some areas. Rural people in central Thailand believe that the eggs provide nutritional benefits and enhance the libido of men (Tunsaringkarn et al. 2012, 2013). Currently, a moderate level of local trade in eggs exists in Thailand. During the nesting season, rice farmers actively search for nests along the edges of fields and gather the eggs. The eggs are either retained for personal use or sold commercially. During the early 1990s, two turtle eggs were valued equal to three chicken eggs. In Phetchaburi Province, collectors noted a gradual decline in the number of nests and the number of eggs per nest, resulting in egg collection becoming less profitable (Thirakhupt and van Dijk, unpubl. data). However, in Phra Nakhon Si Ayutthaya Province, collection of eggs is currently regulated by a local management plan. In this area, the farmers have agreed to limit harvesting to certain time periods and the annual number of eggs collected is reported to have remained stable (Kitana et al. 2015).

Habitat destruction has been considered a problem in some places. Sharma and Tisen (2000) mentioned draining of the seasonally inundated *Melaleuca* freshwater swamps as an issue in Malaysia. Yet, compared with many other turtle species, habitat loss is less of a threat to *M.macrocephala* due to its ability to inhabit flooded agricultural fields and irrigation ditches. In fact, the species might have benefited in some areas during the historical spread of rice agriculture through the anthropogenic creation of new water bodies. Modern agricultural methods can create hazards for Malayan Snaileating Turtles, however. As an example, the replacement of traditional buffalo-drawn plows with mechanized plows increases the risk of turtles being crushed or mutilated during soil tilling (van Dijk and Palasuwan 2000).

Degradation of freshwater habitats by pollution is a large and growing problem in parts of Southeast Asia. The river basins of the Chao Phraya and Mae Klong, for example, are heavily polluted through agricultural runoff, inadequate sewage treatment in rural areas, industrial waste, and urban effluent (Dudgeon 2008; Poolpak et al. 2008). Because large numbers of M. macrocephala occur in areas of rice cultivation, many Malayan Snail-eating Turtles are likely exposed to agrochemicals. Components of some fertilizers and pesticides, such as heavy metals and organochlorines, are extremely persistent in the environment and can be biomagnified by molluscs (Boonlue et al. 2011; Dummee et al. 2012). These compounds may then be transferred to Malayan Snail-eating Turtles through their diet. Keithmaleesatti et al. (2010) analyzed the blood, eggs, and nest soil of M. macrocephala in Phra Nakhon Si Ayutthaya Province, Thailand for organochlorine pesticides. Although the use of these pesticides (e.g., DDT) had been officially banned in Thailand for decades (Poolpak et al. 2008), significant amounts of pesticide residue were found in the soil and eggs, the latter likely contaminated through maternal transfer of yolk (Keithmaleesatti et al. 2010). While the current impact of pollution on M. macrocephala is largely unknown, heavy metals and organochlorines have the potential to adversely affect reproduction and development in turtles (Kitana et al. 2008; Keithmaleesatti et al. 2010).

Other threats appear to be relatively minor, localized, or speculative at the present. Turtles can become entangled and drown in abandoned monofilament fishing nets (van Dijk and Palasuwan 2000); in areas with extensive networks of roads, individuals may be injured or killed by vehicular traffic (e.g., Ihlow et al. 2016); and van Dijk and Palasuwan (2000) reported that Malayan Snail-eating Turtles were fashioned into stuffed curios for tourists in Thailand. Severe droughts can cause water bodies to shrink or even disappear, directly (through overheating and dehydration) and indirectly (through increased susceptibility to collection or predation) resulting in mortality. Recently, concerns have been raised over the possible future effects of climate change on *M. macrocephala*, as high incubation temperatures have the potential to increase developmental abnormalities (Pewphong et al. 2013) and skew the sex ratio (Pewphong et al. 2016) of embryos under laboratory conditions. However, the degree to which climatic changes will impact *M. macrocephala* in the wild and how the species could respond remain unknown.

Conservation Measures Taken. – Malayemys macrocephala does not appear on the most recent IUCN Red List. However, Malayemys subtrijuga (sensu lato, including M. macrocephala) was assessed as Least Concern by the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (TFTSG) in 1996, and therefore not included on the IUCN Red List at that time, but assessed as Vulnerable in 2000 (TTWG 2017). A draft assessment conducted by the TFTSG in 2011 evaluated M. macrocephala as Vulnerable (TTWG 2017), but a second provisional evaluation in 2018 has returned it to Least Concern status (Rhodin et al. 2018). Since 2005, international trade in M. macrocephala has been regulated through listing of the species on Appendix II of CITES. Trade statistics, derived from the CITES Trade Database maintained by UNEP-WCMC (2016), reveal that little legal international trade was reported between 2005 and 2015.

In 1992, all *Malayemys* in Thailand received legal protection through the Wildlife Preservation and Protection Act, B.E. 2535 (1992) under the scientific name in use at the time, M. subtrijuga. While limited local exploitation was allowed, trade was prohibited. Prior to this law, over 100 specimens of Malayemys could be observed during a visit to the markets of Bangkok; afterwards, the number of these turtles sold in markets declined dramatically (Thirakhupt and van Dijk, pers. obs.). However, protection under this Thai act is afforded only to specific taxonomic names and is not automatically adjusted for nomenclatural changes. Thus, recognition of *M. macrocephala* as a separate species resulted in the loss of official protection (TTWG 2007a). Similarly, M. subtrijuga (erroneously spelled as Malayems substrijuga) is protected by the Wildlife Conservation Act 2010 of Malaysia, but M. macrocephala is not listed. Yet, although not technically protected in either country, M. macrocephala still receives a measure of practical protection in both countries through the listing of M. subtrijuga, due to the long period of synonymy and close similarity in appearance between the two taxa.

Economic and cultural changes have also reduced the consumption of M.macrocephala.In recent decades, Thailand and Malaysia have undergone rapid development, creating

diversified economies and reducing the need for subsistence use of natural resources (van Dijk and Palasuwan 2000). Concerns over the potential for parasites in snail-eating turtles have also led to negative views among the public towards eating these turtles. Subsequently, the use of *M. macrocephala* as food has declined in Thailand, particularly in major urban areas, such as Bangkok, where poverty is relatively low.

While large numbers of *M. macrocephala* continue to be sold for Buddhist merit releases, the monks responsible for the turtles at various temples discourage the release of Malayan Snail-eating Turtles because they often die within a short time (Thirakhupt and van Dijk, pers. obs). Various organizations, including the Wildlife Fund Thailand, Tourism Authority of Thailand, and Love Turtles Club, have conducted educational campaigns to increase public understanding of the issues surrounding merit releases. In addition, the Love Turtles Club, a volunteer group organized through the veterinary medicine department of Chulalongkorn University, has negotiated with monks for the removal of turtles from temple ponds, conducted health assessments and treatments, and then released the turtles into the wild (Chansue 2012).

Although the vast majority of the lowlands in Thailand and Malaysia have been modified by humans, some small areas of protected habitat exist. *Malayemys macrocephala* has been documented from the following conservation areas within Thailand: Bueng Boraphet Non-Hunting Area (Eiamampai 2002), Kaeng Krachan National Park (Pauwels and Chan-ard 2006), and Nong Thung Thong Non-Hunting Area (Storer 1978). *Malayemys macrocephala* may also be the species of *Malayemys* reported from Khao Ang Rue Nai Wildlife Sanctuary by Inthara et al. (2004).

In Malaysia, Jambu Bongkok Forest Reserve protects a portion of the *Melaleuca* swamps occupied by *M*. *macrocephala* (Sharma and Tisen 2000). Despite the relatively poor coverage of protected areas across the range of the species, the ability of *M. macrocephala* to inhabit irrigated rice fields means that large expanses of habitat remain available.

Environmental regulations, which restrict or outlaw use of specific pesticides, and national standards for water quality have been established by both Thailand and Malaysia. However, these laws are generally poorly enforced (Dudgeon 2008). Smuggling of banned pesticides from other countries has been reported and the illegal use of these chemicals in agriculture continues to be an issue (Poolpak et al. 2008).

Conservation Measures Proposed. — At present, *M. macrocephala* does not seem to be seriously threatened in its survival. However, collection and trade continue to occur, while many aspects of the species' population biology are still unknown. The removal of adult turtles (in particular, mature females) from a population is directly detrimental to reproductive output and recruitment. As a result, the use of

large females as food should be discontinued in rural areas where this exploitation continues to occur. The demand by Buddhist practitioners for Malayan Snail-eating Turtles continues to promote substantial indiscriminate collection and trade. Further efforts should be made to discourage the use of turtles in merit releases. Excessive collection of eggs should also be prohibited. Amending the wildlife conservation laws in Thailand and Malaysia to explicitly include *M. macrocephala* would increase protection and awareness for the species.

Other threats should also be controlled. In particular, greater action should be taken to remediate polluted waters and prevent future contamination. Improvements to wastewater and stormwater systems, enforcement of water quality standards on factories and other point-source polluters, and implementation of responsible agrochemical application practices among farmers (especially the elimination of illegal pesticide use) should be pursued where needed. In addition, the few remaining natural lowland habitats in Thailand and Malaysia should continue to be safeguarded.

Field surveys should be undertaken to investigate the possible presence of *M. macrocephala* in Myanmar, northeastern Thailand, and western Laos in order to establish the actual extent of the species' distribution, identify possible threats in these areas, and determine the need for any local conservation actions. Additional ecological and demographic research is also essential. Currently, little is known about the species at the southern edge of its range. Long-term studies on the abundance and density of M. macrocephala are needed at sites across the species' known distribution in both Thailand and Malaysia. This research would allow for monitoring of the sizes and trends of populations, enabling more accurate assignment of the species to an IUCN Red List category. Until additional evidence becomes available, we recommend leaving the listing of M. macrocephala at Least Concern as proposed in the 2018 draft assessment by the TFTSG, although a case could possibly be made for listing it as Near Threatened, as has been proposed for M. subtrijuga (Rhodin et al. 2018).

Captive Husbandry. — *Malayemys* has a reputation for being extremely difficult to establish in captivity long-term. Numerous *M. macrocephala*, mostly small individuals (Pritchard 1979), were imported into the United States and Europe between the 1950s and 1980s. However, few of these individuals survived longer than a few months (Hausmann 1959; Dawson, unpubl. data). This high mortality has often been attributed to the specialized diet of the species and the difficulty of providing a reliable supply of freshwater snails (Nutaphand 1979; Thieme 1980). Breeding sufficient numbers of these snails requires large facilities, while snails collected from the wild can be vectors of parasites and may be unavailable during the winter in temperate climates. However, other important factors contributing to the mortality rate were the generally poor body condition of imported animals (Bader 1962), typically heavy parasite loads and high sensitivity to stress of wild-caught individuals (Gurley 2003; Auliya 2007), and relatively limited husbandry and veterinary knowledge of the time. Despite the low rate of survival, successful captive maintenance over many years has occasionally occurred (e.g., Bader 1962; S. Szymanski, pers. comm.). The published longevity record for *Malayemys* (likely *M. macrocephala*) is 14 years and 2 months for a wild-caught adult obtained in 1975 by a private individual in the United States (Slavens and Slavens 2003).

Captive turtles have been reported to eat a variety of live freshwater snails, including genera available in the aquarium trade (e.g., Cipangopaludina, Lymnaea, Melanoides, Planorbarius, and Pomacea). Individuals may also accept fresh and frozen/thawed whole snails and snail meat sold for human consumption (e.g., Pila). Some authors (e.g., Schuch 1959) have reported the refusal of any foods except for freshwater snails. Others have successfully offered additional foods, including small terrestrial snails (Cepea), slugs, mealworms, superworms, mosquito larvae, tubifex worms, earthworms, shrimp, crabs, leeches, small mussels, aquatic insects, minced meat (e.g., pinky mice, chicken heart, and beef heart), fish, prepared gelatin foods, and commercial pellets (Bader 1958, 1962; Jes 1970; Friedel 1971; Petzold 1975; Nutaphand 1979; Thieme 1980; Böhm 2017; W. Sachsse, S. Szymanski, and S. Nickl, pers. comm.).

Snail-eating turtles may be housed in plastic tubs, stock tanks, or aquariums. Individuals are best kept separately to minimize stress. If multiple individuals are placed together, the space should be large and feature numerous visual barriers (Gurley 2003). Enclosures should contain many non-abrasive hiding places (e.g., live or artificial plants and driftwood) and a basking site partially below the water level (Bader 1958; Sachsse 1967; Friedel 1971; Petzold 1975; Gurley 2003). Provision of a terrestrial section that allows burying into substrate or hiding beneath vegetation is advisable (Petzold 1975). While Friedel (1971) reported that individuals never left the water, Böhm (2017) saw both sexes out of the water for considerable periods of time, basking under UVB spot lights during the day and sometimes resting on land during the night. Recommended water depths range from 10 cm (Bader 1958) to roughly 50 cm (Friedel 1971; Petzold 1975) with proposed depths often not much greater than the shell length of the turtle. Suggested ranges for water temperature include 22-26°C (Bader 1962), 24-26°C (Gurley 2003), 28-32°C (Auliya 2007), and 30-32°C during the day with a drop to 28°C at night (Thirakhupt and van Dijk, unpubl. data). Water acidity and mineral content have seldom been reported, but the species has been successfully kept in water with a pH of slightly above 7.0 and a conductivity of 450 µS/cm (Böhm 2017).

Newly acquired animals should be guarantined, evaluated for health and stabilized if necessary, and then acclimated to captive conditions. Gurley (2003) advocated for prophylactic treatment against intestinal nematodes. Although snail-eating turtles appear to tolerate unclean habitats in the wild, successful keeping seems to require hygienic conditions at all times (Bader 1959). Accordingly, good water quality should be maintained through filtration and regular water changes (Böhm 2017). In captivity, Malayemys is prone to diseases of the shell and skin. Scratches or minor injuries may develop into major infections. Shell rot can be difficult to treat. This disease generally begins by penetrating through the seams between the scutes and can quickly spread across the shell, causing severe bone destruction (Thieme 1980; Nöllert 1982). Cysts of the skin may also occur but heal quickly if the affected turtles are kept dry for a few days (S. Szymanski, pers. comm.).

Captive reproduction of Malayemys is extremely rare. The factors stimulating the reproductive cycle and breeding activity in M. macrocephala are still largely unknown. In the wild, the species experiences seasonal variations in food availability, precipitation, water levels, and temperature. Replicating some of these conditions (e.g., simulating a dry season to encourage estivation) may be important for the health and reproduction of turtles under human care. Böhm (2017) recently reported the first captive breeding of M. macrocephala in Europe. Copulation was observed following the introduction of a female (160 mm in maximum SCL) and male (107 mm in maximum SCL) that were typically housed separately. Roughly four weeks after copulation, the female laid two eggs. A second clutch of two eggs followed about four weeks after the first nesting. In both instances, the eggs were buried in moist substrate beneath a heat lamp in the warmest spot in the enclosure (32°C surface temperature). The eggs were artificially incubated in coco peat substrate at varying temperatures between 26-30°C and 80-90% relative humidity. Banding of the eggs occurred after approximately two weeks. Following a mean incubation period of 139.7 days (range = 133-144 days), three of the four eggs hatched. This pair also successfully reproduced the following year; nine of 13 eggs had already hatched, and two seemingly fertile eggs were still incubating, as this manuscript was under review (Ettmar, unpubl. data).

Current Research. — Research on the population biology and reproductive strategy of *M. macrocephala* is ongoing at Chulalongkorn University in Thailand. In addition to the systematic studies (see Taxonomy) and status surveys (see Conservation Measures Proposed) previously mentioned, worthwhile future projects include studies of the interrelationships between *M. macrocephala* and aquatic snails, the latter including species of economic importance as pests in rice culture and medical importance as intermediate hosts of bilharzia-causing *Schistosoma* blood flukes. The potential service provided to humans by *Malayemys* through the biological control of snails harmful to agriculture (Carlsson et al. 2004) and snail-transmitted diseases (Hopkins 1973; Srinarumol 1995) deserves further consideration.

Acknowledgments. - This work began many years ago as an account for Malayemys subtrijuga (sensu lato). The unpublished manuscript was sometimes cited by other authors as van Dijk and Thirakhupt (in press); however, taxonomic changes and other challenges delayed actual publication. The current version was produced through revision of the original text by the first three authors. We thank the editors of Conservation Biology of Freshwater Turtles and Tortoises (in particular, Anders G.J. Rhodin) for their guidance and patience during this long process. Thanks to Thunya Chanard, Balász Farkas, Teddy Good, Edward O. Moll, Peter Mudde, Peter C.H. Pritchard, Nipon Srinarumol, Tran Triet, and numerous Thai countryside people for contributing specimens, literature, and information for the original manuscript. For the updated text, we gratefully acknowledge the additional contributions and assistance of Thanakhom Bundhitwongrut, Michael Cota, Noppadon Kitana, Sunchai Makchai, Pratheep Meewattana, Sebastian Nickl, Steven G. Platt, Evan S.H. Quah, and Steffen Szymanski. We thank Evan S.H. Quah and Pratheep Meewattana for photos.

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Citation Format for this Account:

DAWSON, J.E., IHLOW, F., ETTMAR, S., VAN DUK, P.P., AND THIRAKHUPT, K. 2018. Malayemys macrocephala (Gray 1859) – Malayan Snaileating Turtle, Rice-field Terrapin. In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., Pritchard, P.C.H., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(12):108.1–16. doi: 10.3854/ crm.5.108.macrocephala.v1.2018; www.iucn-tftsg.org/cbftt/.