CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

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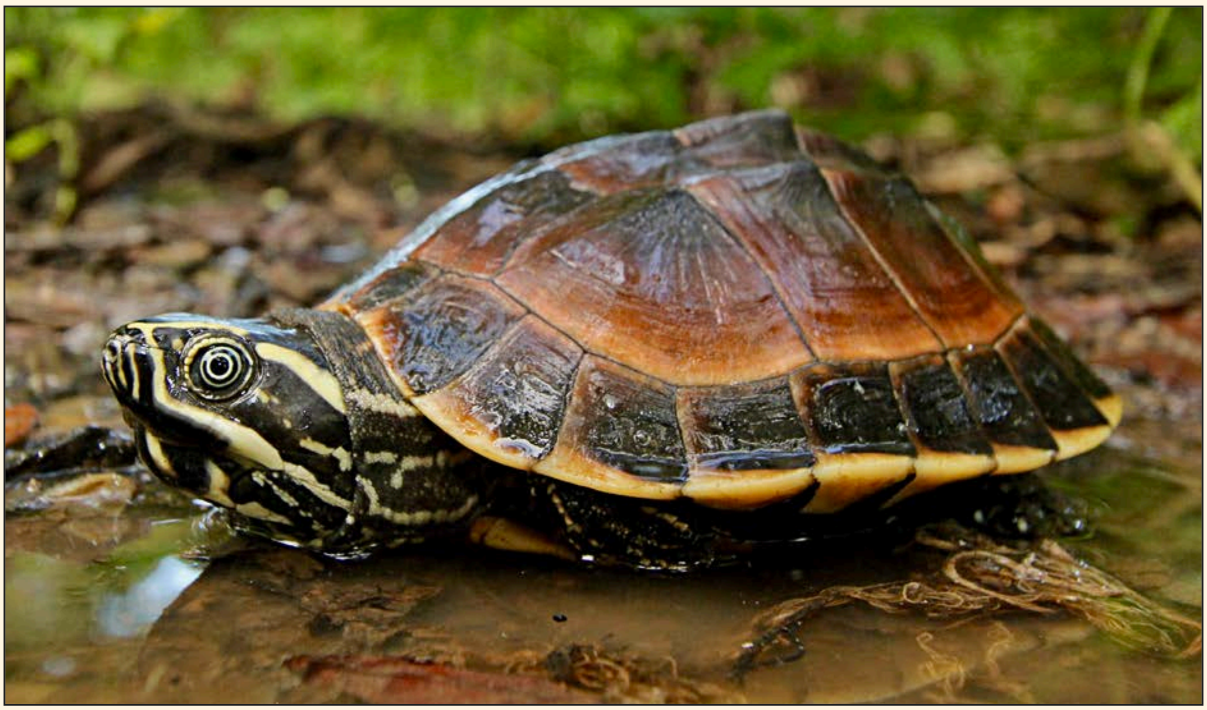

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Malayemys subtrijuga (Schlegel and Müller 1845) – Mekong Snail-Eating Turtle

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Summary. – The Mekong Snail-eating Turtle, *Malayemys subtrijuga* (family Geoemydidae), is a small (carapace length typically under 200 mm, but reaching up to 236 mm) freshwater turtle inhabiting wetlands, rice fields, and other seasonal lowland habitats in Southeast Asia. The species has an unusual distribution: a disjunct population on the island of Java in Indonesia, which could be either a centuries-old anthropogenic introduction or a naturally occurring relict, and an extensive occurrence across the lower Mekong River drainage of the southeastern Indochinese Peninsula. The species exhibits sexual dimorphism in body size, with females growing considerably larger than males. Individuals have enlarged heads and other specializations for a diet consisting largely of molluscs. Clutches of up to 10 eggs are laid during the dry season (December–March in Cambodia), and incubation is timed so that hatchlings emerge at the beginning of the wet season. Many aspects of the species' natural history remain poorly known. Although considerable habitat is available, populations throughout the species' distributional range appear to have declined as a result of exploitation. Reduction in the level of collection and additional research and management are needed for the conservation of this species.

Distribution. – Cambodia, Indonesia, Laos, and Vietnam. An isolated population is present on the Indonesian island of Java. The species occurs in lowland areas throughout Cambodia, southern Laos, and southern Vietnam.

Synonymy. – *Emys subtrijuga* Schlegel and Müller 1845, *Damonia subtrijuga*, *Geoclemys subtrijuga*, *Cistudo gibbosa* Bleeker 1857 (*nomen nudum*), *Emys nuchalis* Blyth 1863, *Bellia nuchalis*, *Damonia crassiceps* Gray 1870, *Damonia oblonga* Gray 1871.

Subspecies. – None currently recognized.

Status. – IUCN 2020 Red List: Vulnerable (VU A1d+2d, assessed 2000); TFTSG Draft Red List: Near Threatened (NT, assessed 2018); CITES: Appendix II.

Taxonomy. — The nomenclatural history of *Malayemys subtrijuga* is complex, with considerable confusion and synonymy. Schlegel and Müller (1845) described *Emys subtrijuga* based on specimens collected on Java in the early 1820s, while the island (now part of Indonesia) was a colony in the Dutch East Indies. Heinrich Kuhl and Johan Conrad van Hasselt obtained three turtles, probably from the region of Bantam (= Banten) in western Java, and sent the mounted specimens to the Rijksmuseum van Natuurlijke Historie (RMNH; currently, Naturalis Biodiversity Center) in Leiden, Netherlands (Schlegel and Müller 1845). Heinrich Boie, then curator of herpetology at the RMNH, identified these specimens as *Emys trijuga* in an unpublished manuscript (Hubrecht 1881; Brophy 2002, 2004; Hoogmoed et al. 2010). Subsequently, Temminck and Schlegel (1834) used the name *E. trijuga* in a brief initial account of the specimens.

Emys trijuga had been described by Schweigger (1812) based on a shell collected from Java by Jean-Baptiste Leschenault de La Tour and deposited in the Muséum National d'Histoire Naturelle (MNHN) in Paris (Cuvier 1819). Unfortunately, this specimen was thereafter lost, and the name *E.* (= *Melanochelys*) *trijuga* became erroneously associated with a different species from the Indian subcontinent (Bour and Schmidtler 2014). This circumstance led Schlegel and Müller (1845) to reexamine the RMNH specimens and describe *E. subtrijuga*. However, before its disappearance, the MNHN specimen was painted by Nikolaus Michael Oppel, and this artwork has recently been made accessible (Bour and Schmidtler 2014). While Oppel's depiction reveals that both epithets likely refer to the same taxon, Bour and Schmidtler (2014) emphasized the extensive nomenclatural chaos that would ensue if *E. trijuga* was recognized as having priority over *E. subtrijuga*. Instead, Bour and Schmidtler (2014) recommended the designation of a neotype for *E. trijuga* in order to maintain nomenclatural stability, and this approach is supported in the upcoming checklist of turtle taxonomy (TTWG, in press). *Emys herrmanni*, also described by Schweigger (1812) and formerly considered

Figure 1. Adult *Malayemys subtrijuga* from Tonle Sap Lake Biosphere Reserve, Battambang Province, Cambodia. Photo by F. Ihlow.

a *nomen dubium* synonymous with *E. subtrijuga* (TTWG 2017), is actually a subjective synonym of *E. trijuga* (Bour et al. 2017).

Uncertainty has also existed over the identity and depository of the syntypes of *E. subtrijuga* (Brophy 2004; Hoogmoed et al. 2010). In the mid-nineteenth century, the Zoological Department of the British Museum (BMNH; presently, Natural History Museum) in London attempted to acquire the type specimens of species described by Solomon Müller (Gray 1872). Gray (1873) registered a skeleton obtained from "Mus. Leyden," and this specimen (BMNH 1947.3.4.53) has been reported as the type of *E. subtrijuga* (Iverson 1992; NHM 2014). According to the BMNH catalog, the specimen was purchased from "Mr. Franks." This entry likely refers to Gustav Adolph Frank, a natural history dealer in Amsterdam who frequently exchanged specimens with the RMNH (see Jansen and van der Mije 2015). However, after reviewing the taxonomy of the species, Brophy (2004) concluded that the specimen in the BMNH should not be designated as the type because neither Gray (1873) nor Boulenger (1889) explicitly identified the skeleton as a type specimen. In addition, Hubrecht (1881) detailed the history of the specimens described by Schlegel and Müller (1845) and stated unequivocally that all three remained at the RMNH in Leiden. Brophy (2004) examined the RMNH specimens, assigning a lectotype (RMNH.RENA 6082)

Figure 2. Carapace and plastron of adult *Malayemys subtrijuga* from central Cambodia. Photos by J.E. Dawson.

Figure 3. Head of *Malayemys subtrijuga* from Tonle Sap Biosphere Reserve, Battambang Province, Cambodia. Photo by J.E. Dawson.

based on its morphology and condition compared to the other specimens (RMNH.RENA 6084, 6085). Hoogmoed et al. (2010) provided a photograph of the lectotype along with a brief overview of the work by Hubrecht (1881) and Brophy (2004).

Perhaps partly due to the disorder surrounding the names *E. trijuga* and *E. subtrijuga*, other authors gave different binomials to subsequent Javan specimens. Bleeker (1857) listed a new species, *Cistudo gibbosa*, from Batavia (= Jakarta). Pieter Bleeker donated a specimen bearing this name to the BMNH (Boulenger 1889), which is now catalogued as BMNH 1863.12.4.38 (NHM 2014). However, Bleeker (1857) failed to publish a description with the proposed name; therefore, *C. gibbosa* is a *nomen nudum*. Blyth (1863) described *Emys nuchalis* based on specimens that he had received from the Batavian Society in 1844, after previously mistaking these specimens for *E.* (= *Siebenrockiella*) *crassicollis*. The specimens were housed by the Asiatic Society of Bengal (Theobald 1868) and later incorporated into the collection of the Zoological Survey of India (ZSI 824–826; Das et al. 1998). Finally, Gray (1871) described *Damonia oblonga* from a specimen (BMNH 1947.3.5.30; NHM 2014) acquired from Batavia by Edward Gerrard, Jr. Over time, these names have been relegated to junior subjective synonyms (TTWG 2017).

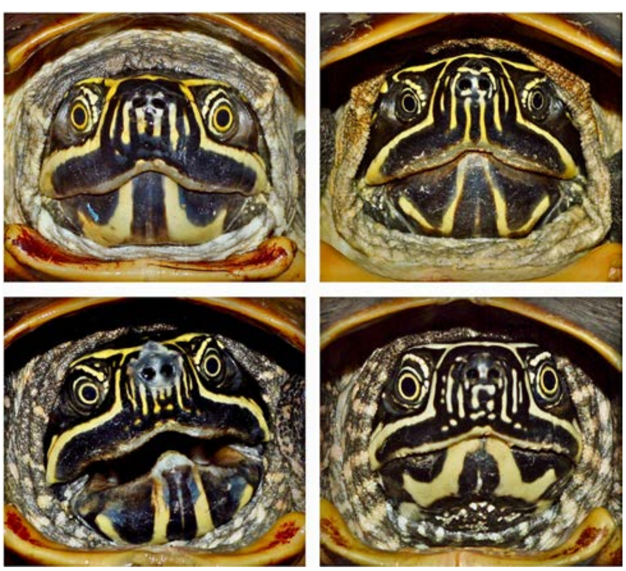

Figure 4. Frontal views of *Malayemys subtrijuga* from central Cambodia, showing variation in the number and form of nasal stripes. Photos by J.E. Dawson.

Hubrecht (1881) argued that *Geoclemys macrocephala*, described by Gray (1859), was also synonymous with *E. subtrijuga*. Gray (1859) based his description on specimens from Thailand, but Hubrecht (1881) judged the text and figure in Gray's work to also agree perfectly with specimens from Java. Boulenger (1889) followed suit but reassigned *E. subtrijuga* to the genus *Damonia*. Smith (1931) added *Damonia crassiceps*, described by Gray (1870) from a drawing sent from China by John Reeves, to the synonyms of *D. subtrijuga*. Sumontha et al. (2016) contended that this identification was incorrect, but did not suggest an alternate taxonomy (TTWG 2017).

Lindholm (1931) proposed a new generic name, *Malayemys*, after noting that *Damonia* had already been used earlier for a genus of dipteran insect. Afterwards, most authors adopted this change, although *D. subtrijuga* continued to appear sporadically (e.g., Bourret 1941a). *Malayemys* was accepted to be monotypic, with *M. subtrijuga* as the sole representative (Ernst and Barbour 1989; Iverson 1992; Stuart et al. 2001), until Brophy (2002, 2004) examined morphological variation within the genus. 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 to be a full species. *Malayemys subtrijuga* was restricted to the populations of Java and the Mekong River drainage of the Indochinese Peninsula (Cambodia, Laos, Vietnam, and northeastern Thailand), while *M. macrocephala* was resurrected as the name for populations in the rest of Thailand and peninsular Malaysia (Brophy 2004, 2005).

Through analyses of mitochondrial DNA, microsatellite loci, and morphology, Ihlow et al. (2016) identified three distinct groups within *Malayemys*: *M. macrocephala*, *M. subtrijuga*, and a third group from the Khorat Plateau in northeastern Thailand. This area of the Lower Mekong Basin had previously been included in the distribution of *M. subtrijuga* (Brophy 2002, 2004, 2005). Levels of mitochondrial divergence between turtles from the Khorat Plateau and the other two groups resembled other distinct turtle species, while the divergence between *M. subtrijuga* and *M. macrocephala* was relatively low. In addition, *M. subtrijuga* and *M. macrocephala* displayed a history of mitochondrial introgression. However, the absence of nuclear admixture indicated that all three groups were reproductively isolated from each other, and diagnostic morphological characters enabled consistent identification (Ihlow et al. 2016).

As a result, Ihlow et al. (2016) agreed with Brophy (2002, 2004), in recognizing *M. subtrijuga* and *M. macrocephala* as separate species, but also described the Khorat Plateau population as a new species, *M. khoratensis*. Nearly simultaneously, Sumontha et al. (2016) described the same taxon as *M. isan* based on morphology and indicated that it also occurred in adjacent areas of northern Laos. However, Thomson and Lambertz (2017) provided evidence that, according to the International Code of Zoological Nomenclature, Ihlow et al. (2016) fulfilled the criteria for publication before Sumontha et al. (2016). Accordingly, *M. khoratensis* has nomenclatural priority as the valid name for the Khorat Plateau species (TTWG 2017).

In the most recent checklist of chelonian taxonomy, three species of *Malayemys* (*M. subtrijuga*, *M. macrocephala*, and *M. khoratensis*) were recognized (TTWG 2017). However, the authors of the checklist 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 *Malayemys* (TTWG 2017). Although we believe that sufficient evidence exists to recognize three separate species, we agree on the need for further research. In order to maintain taxonomic stability until additional data become available, we follow the taxonomy of the TTWG (2017) for this account.

Previous literature often includes a combination of material from the three currently accepted species (e.g., Bourret 1941a; Ernst and Barbour 1989; Iverson 1992; Stuart et al. 2001). In some cases, it may be possible to determine which species is covered through localities or representations (photographs or descriptions) of specimens, but identification may be ambiguous when these details are lacking. 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.

Figure 5. Carapaces and plastra of juvenile captive-bred *Malayemys subtrijuga*. Scale bar = 10 mm. Photos by S. Szymanski.

Malayemys is included in the Old World pond turtles (family Geoemydidae) and is most closely related to the genus *Orlitia* (Spinks et al. 2004; Thomson and Shaffer 2010; Guillon et al. 2012). Dawson et al. (2018) reviewed prior hypotheses regarding the phylogenetic position of *Malayemys*.

Description. — *Malayemys subtrijuga* is a relatively small chelonian species, reaching a maximum midline straight carapace length (SCL) of 236.7 mm (Platt et al. 2008), although most individuals do not exceed 200 mm SCL. Adults from across the species' distribution appear to reach similar sizes, and sexual size dimorphism is evident, with females larger than males (Table 1). Individuals from central Cambodia had a sexual size dimorphism index (SDI; Lovich and Gibbons 1992) of + 0.18, slightly lower than SDI values reported for *M. macrocephala* (Platt et al. 2008). The largest known male that has been reported was 199.4 mm in midline SCL, while the midline SCL of the largest known female was 236.0 mm (Platt et al. 2008); an unsexed shell of 236.7 mm SCL was probably a female as well.

Data on body mass in the wild have seldom been reported; measurements from trade specimens held for long periods can be unreliable as these turtles may be severely underweight. A wild female in Cambodia with a midline SCL of 114.5 mm had a mass of 251 g (Ihlow and Dawson, unpubl. data). Bezuijen et al. (2009) provided information on two captives reportedly caught a short time prior by local people in Cambodia; the mass of one individual with a maximum SCL of 137 mm was 303 g, while another turtle that was 187 mm in maximum SCL had a mass of 1000 g. For individuals in good body condition under human care, mature males may reach approximately 500 g, while large females can exceed 1100 g (Dawson, unpubl. data; S. Szymanski, pers. comm.).

In addition to the difference in body size, males have longer tails with thicker bases than females (Platt et al. 2008). Males also possess relatively narrower shells and more V-shaped anal notches of the plastra, while females have comparatively rounder shells and shallower, wider anal notches (Auliya 2007; Ihlow et al. 2016). In *M. macrocephala*, these differences in shell shape are the result of allometric growth (Brophy 2006). Brophy (2002) found allometry to be less evident in *M. subtrijuga*, although the lack of statistical significance may have been a reflection of inadequate sample

Table 1. Mean ± 1 SD (range, *n*) straight carapace length (SCL) reported for *Malayemys subtrijuga* across the geographic range of the species. Brophy (2002) reported maximum SCL, while Platt et al. (2008) reported midline SCL. Indochinese populations represented by Lower Mekong Basin (= samples from Cambodia and Vietnam) and Tonle Sap Lake (= samples from central Cambodia, within Lower Mekong Basin).

	Males			Females			
Location	Mean SCL	Range	*n*	Mean SCL	Range	*n*	Source
Java Island, Indonesia	127.2 ± 15.7	(101.0–151.8)	15	152.8 ± 19.8	(118.0–182.4)	14	Brophy 2002
Lower Mekong Basin	126.3 ± 18.7	(103.5–149.9)	6	163.6 ± 22.2	(121.4–207.0)	16	Brophy 2002
Tonle Sap Lake	132.8 ± 25.1	(93.0–199.4)	78	158.0 ± 38.2	(87.0–236.0)	248	Platt et al. 2008

sizes. Unlike many turtle species, a plastral concavity does not develop in males.

Young have proportionally deeper shells than adults (Bourret 1941b), but they are otherwise similar in appearance. Even in hatchlings, the tail is short. Two hatchlings from Cambodia were 37.6 and 37.2 mm in midline SCL, 28.0 and 27.8 mm in maximum straight plastron length (SPL), and 10.5 and 10.0 g in mass (Platt et al. 2008). The mean maximum SCL of six hatchlings captive-bred in Europe was 37.7 mm ± 1.5 mm, while the mean straight carapace width was 27.5 mm ± 2.27 mm, and the mean mass was 10.4 ± 1.35 g (range = 8–11.9 g; S. Szymanski, pers. comm.). These measurements are similar to those reported for hatchling *M. macrocephala* (reviewed by Dawson et al. 2018).

The carapace is tricarinate in *M. subtrijuga*, with one keel along the midline of the vertebral scutes and two parallel keels near the mesial margins of the costal scutes (Pritchard et al. 2009). The lateral keels seldom continue beyond the third costals. While the dorsal ridges are distinct in younger animals, they may be reduced to a discontinuous series of knobs in old adults. The first vertebral scute is usually longer than wide and tapered posteriorly, while the remaining vertebrals are typically greater in width than in length (Ihlow et al. 2016). The underlying neural bones are unusually broad. Anterior neurals are typically longer than the posterior ones, but the great width of the bones is maintained throughout the entire series. The margins of the carapace are not serrated (Pritchard et al. 2009). The keratinous layer of the shell is very thin. Carapace coloration 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 undersides of the rear marginals (8–12) are marked with narrow blackish bars (Ihlow et al. 2016).

The plastron lacks a hinge and is immovable. Based on specimens of both sexes in central Cambodia, Platt et al. (2008) reported that the mean maximum SPL was 123.9 ± 34.3 mm (range = 62.3 – 199.0; *n* = 326), compared to a mean midline SCL of 147.3 ± 39.3 mm (range = 77.0 – 236.7 mm; *n* = 360). From Ihlow et al. (2016), the mean ratios between maximum SPL and midline SCL were 1:1.20 in females (*n* = 10) and 1:1.22 in males (*n* = 15). However, the data set of Ihlow et al. (2016) did not cover very large specimens. The entoplastron is anterior to the humero-pectoral seam. Two specimens from Vietnam, examined by Pritchard et al. (2009), exhibited sexual variation in the epiplastra and pygal notch. A medial depression is present midway along the lateral margin of the xiphiplastron in both sexes (Pritchard et al. 2009). The apex of the two xiphiplastral bones is noticeably flattened and slightly irregular, with an angle of approximately 120° (Pritchard et al. 2009). The plastron is attached to the carapace through strong buttresses and sutures. Where the carapace and plastron meet at the bridge, the anterior peripheral bones may have a slight upturned lip (Pritchard et al. 2009). The plastron is yellow in color, with a large dark blotch on each scute. These blotches may occasionally expand and connect, forming a broad line on either side of the plastron or even an almost completely dark ventral side. Two dark blotches are present on the bridge.

The head is large, becoming relatively enormous in old individuals. A very large (210 mm SCL) female, measured by P.C.H. Pritchard (pers. comm.) at a market in Siem Riep, Cambodia, had a head width (HW) of 54 mm. Yet, compared to other macrocephalic turtle species (e.g., some *Graptemys* species), the head remains relatively elongate, and the snout projects slightly beyond the mouth. Furthermore, unlike broad-headed *Graptemys*, evidence for sexual dimorphism in head width is lacking. While Auliya (2007) indicated that males have narrower heads than females, this statement may not have accounted for the difference in body size between the sexes. In central Cambodia, males with a mean midline SCL of 93.7 ± 18.0 mm (range = 71.2–141.3 mm; *n* = 31) had a mean HW of 22.7 ± 3.3 mm (range = 18.2–32.1 mm), while females with a mean midline SCL of 101.9 ± 25.5 mm (range = 70.7–158.6 mm; *n* = 33) had a mean HW of 24.6 ± 5.2 mm (range = 18.7–35.7 mm). The head widths of males and females were not significantly different after controlling for body size through an analysis of covariance, $F(1,61) = 1.043$, $p = 0.311$ (Dawson, unpubl. data). However, the samples in this study were limited to relatively small individuals, so further research incorporating larger adults is required to confirm this finding.

The skull of *Malayemys* displays a number of specializations for durophagy, many of which are shared by other molluscivorous turtles (Joyce and Bell 2004). Both the postorbital and quadratojugal bars are broad and strong; the quadratojugal bar is only slightly emarginated from below. The extremely powerful jaw-closing musculature attaches to a large supraoccipital crest. 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 (Dawson, pers. obs.). The hyoid apparatus of *Malayemys* is similar in shape to those of other members of Geoemydidae, and becomes well-ossified in adults, as occurs in most aquatic species in the family (Richter et al. 2008).

The color of the head is dark brownish-gray to black, with several distinct white or yellow stripes and spots, including some that extend onto the neck. These markings distinguish *M. subtrijuga* from its congeners (Brophy 2004; Ihlow et al. 2016; Sumontha et al. 2016). A supraorbital stripe begins on the top of the rostrum and passes over the eye, before extending onto the temporal region of the head and running just above the tympanum. An infraorbital stripe extends down the side of the snout, sharply angles back below the orbit, and passes just below the tympanum parallel to the supraorbital stripe (Brophy 2004; Ihlow et al. 2016). The infraorbital stripe is relatively narrow in *M. subtrijuga* and extends above the loreal seam between the eye and nose, usually connecting with the supraorbital stripe on the snout (Brophy 2004; Ihlow et al. 2016). A conspicuous postocular stripe appears behind the eye and passes across the tympanum, parallel to the supraorbital and infraorbital stripes (Ihlow et al. 2016). In *M. subtrijuga*, at least four, and typically six or more, thin nasal stripes are present below the nostrils (Brophy 2004; Ihlow et al. 2016). A pair of light markings exist on the lower jaw. Two distinct yellowish rings are present on each eye (Ihlow et al. 2016). The feet have extensive webbing between the toes (Auliya 2007). The legs and soft skin are gray in color with many light lines and spots.

Distribution. — As currently recognized, *M. subtrijuga* has an unusual disjunct distribution on the island of Java in Indonesia and the southeastern Indochinese Peninsula. The first specimens known to science were collected from Java (Schweigger 1812; Schlegel and Müller 1845). Bantam, the type locality mentioned by Schlegel and Müller (1845), is currently located in Banten Province, Indonesia. Subsequent Javan records originated from sites in the present-day Indonesian provinces of Jakarta (Bleeker 1857; Blyth 1863; Gray 1871; Ouwens 1914; De Rooij 1915), West Java (Barbour 1912; Kopstein 1938; Brophy 2005), Central Java (Hamidy et al. 2019), and East Java (Brophy 2005). Most of these localities are situated in the northern coastal plain adjacent to the Java Sea.

On the Indochinese Peninsula, *M. subtrijuga* ranges throughout most of the lowlands of Cambodia and the southern portions of Laos and Vietnam. To the west, the species is replaced by *M. macrocephala*, which occurs in central Thailand and the northern Malay Peninsula (Dawson et al. 2018). Populations in northeastern Thailand and neighboring Laos, formerly assigned to *M. subtrijuga* (Brophy 2004, 2005), are currently recognized as a distinct species, *M. khoratensis* (Ihlow et al. 2016; Sumontha et al. 2016).

Malayemys subtrijuga was recorded from Cambodia (as *Geoclemys macrocephala*) by Gray (1861) initially, who reported on a specimen in the British Museum that had been collected by Henri Mouhot. Since then, most records in Cambodia have come from the Mekong River and its floodplains, including Tonle Sap Lake (Bourret 1939, 1941b; Bezuijen et al. 2009; Stuart and Platt 2004; Platt et al. 2008; Ihlow et al. 2016). The species is also known from other localities in the Lower Mekong Basin, such as the northern lowlands (Hartmann et al. 2013; Geissler et al. 2019) and the northeastern province of Ratanakiri (FMNH 263050; Grant and Resetar 2019). Outside of the Mekong River drainage, a captive specimen, reportedly caught locally, was noted from the Sre Ambel River along the southern coast (Stuart and Platt 2004).

In Laos, *M. subtrijuga* has been documented in the southwestern province of Champasak, with records from wetlands along the Mekong River, extending from the Nam Lepou River (which forms part of the Laos-Cambodia border) north to the Bolaven Plateau (Stuart 1998, 1999; Stuart and Platt 2004; Duckworth and Timmins 2015; Brakels 2018). Snail-eating turtles have also been reported from Khammouan and Savannakhet provinces in central Laos (Stuart 1999; Stuart and Platt 2004; Brakels 2018; Scott et al. 2018). However, the identity of *Malayemys* in this area is presently uncertain, as this population could potentially represent *M. khoratensis*, which occurs both upstream in the Mekong River and in the tributaries draining adjacent Thailand (Ihlow et al. 2016; Sumontha et al. 2016).

Malayemys subtrijuga is found in southern Vietnam (Nguyen et al. 2005; Nguyen et al. 2009; Hendrie et al. 2011; Vassilieva et al. 2016) in the Mekong Delta (Safford et al. 1998; Stuart 2004; Stuart and Platt 2004; Brophy 2005; Ngo and Hoang 2008; Hoang and Le 2010) and adjacent lowlands drained by the Sai Gon-Dong Nai river system (Siebenrock 1903; Le 2007). The species has also been reported from Phu

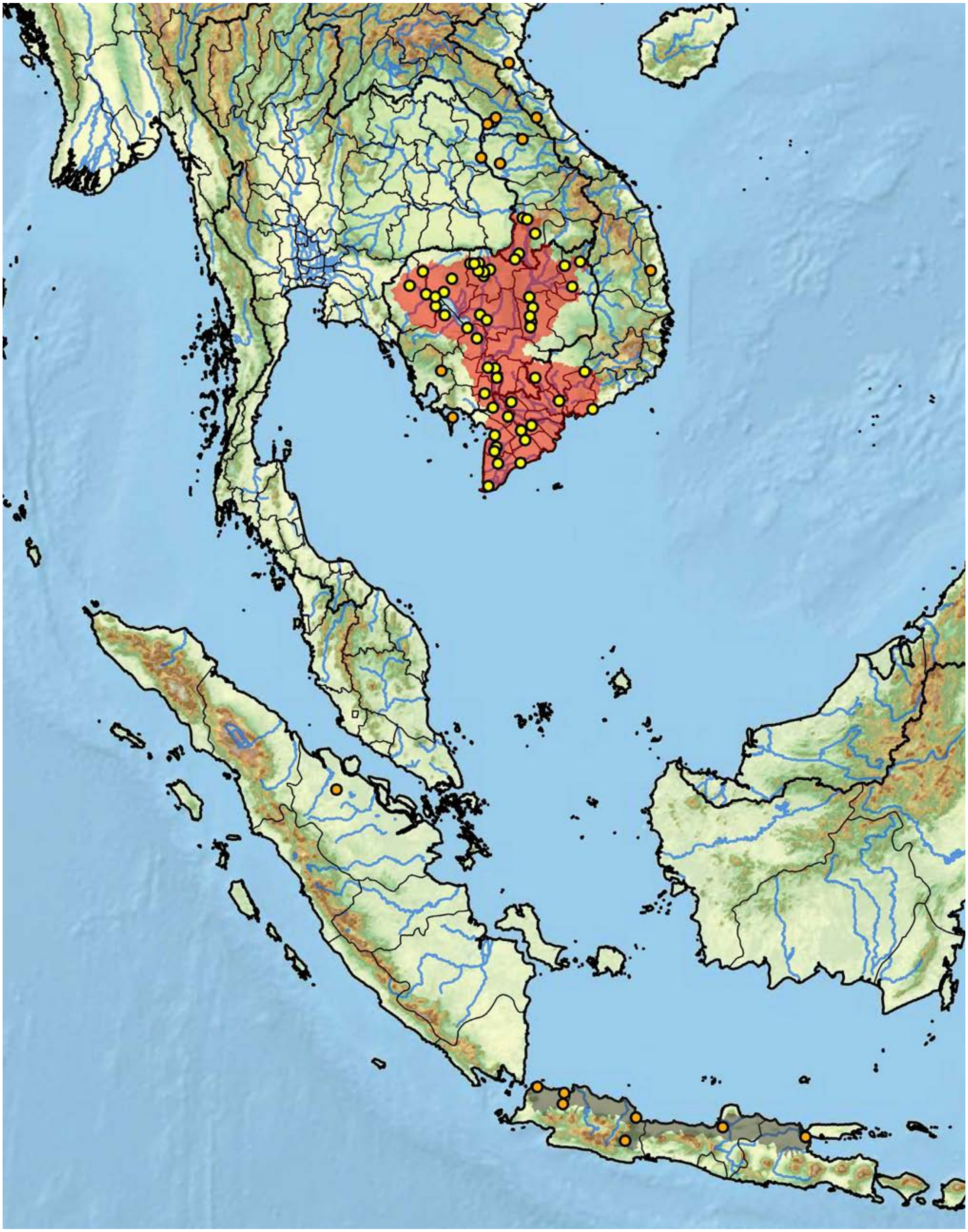

Figure 6. Distribution of *Malayemys subtrijuga* in Southeast Asia (Laos, Cambodia, Vietnam, and Java, Indonesia). Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992) plus more recent and authors' data; orange dots = uncertain native, introduced, misidentified, or trade specimens; red shading = presumed native historic indigenous range; gray shading = possibly historically introduced populations. Distribution based on GIS-defined level 12 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, in press), and adjusted based on authors' subsequent data.

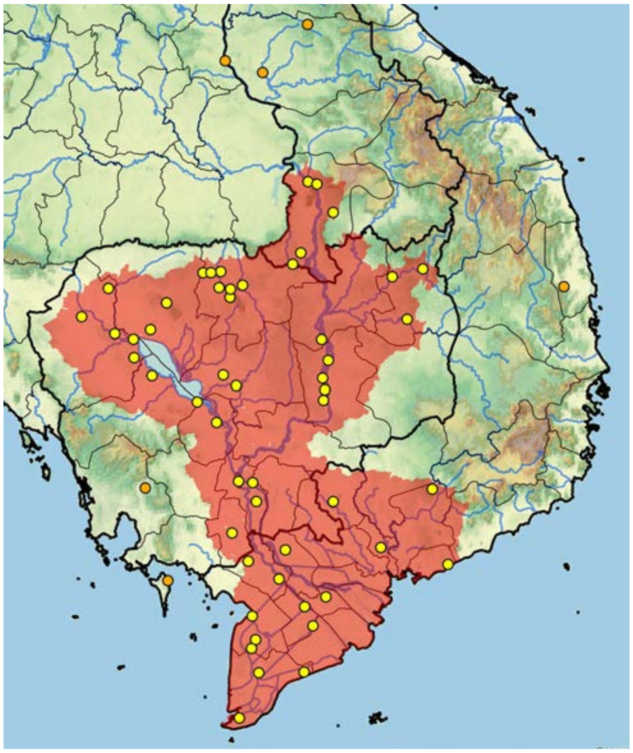

Figure 7. Detailed view of the distribution of *Malayemys subtrijuga* on the Indochinese Peninsula (Laos, Cambodia, and Vietnam). Map details and dot colors as in Fig. 6.

Quoc Island (Dang et al. 2006). Farther north, a specimen of *M. subtrijuga* was captured from a stream in Binh Dinh Province (Duong et al. 2014). However, while photographs in Duong et al. (2014) confirm a correct identification of the species, it seems likely that this individual was released or escaped from captivity. *Malayemys subtrijuga* has also been reported from Quang Binh Province of central Vietnam (e.g., Nguyen et al. 2009), but this record is doubtful (Ziegler et al. 2006), and recent inventories have removed the species from the herpetofauna of the area (Nguyen et al. 2011).

A span of roughly 1,600 km separates the southern tip of Vietnam from Java, and *M. subtrijuga* is apparently absent from the intervening islands of Sumatra and Borneo (Brophy 2005). Although a few museum specimens and published records (e.g., Iverson 1992; Iskandar 2000; Samedi and Iskandar 2000; Auliya 2007; Teynié et al. 2010) have been attributed to these islands, Brophy (2005) considered these localities to be questionable and likely based on misidentified, mislabeled, or imported specimens. Supporting this view, no snail-eating turtles were observed during an extensive survey of the turtle trade on Sumatra, and trappers and dealers on the island were unfamiliar with *M. subtrijuga*, despite being specifically asked and shown photographs of the species (Shepherd 2000).

Several authors have discussed the enigmatic biogeography of *M. subtrijuga* (e.g., Barbour 1912; Dammerman 1929; Brophy 2005). Dammerman (1929) was the first to suggest that *M. subtrijuga* may have been anthropogenically introduced to Java. Brophy (2005) concluded that introduction was most likely, based on the seeming current rarity of the species on Java, the potential for transport of the species during movements of humans between mainland Southeast Asia and Java, the overlap between large port cities and the distribution of the species on Java, the apparent requirement for the species to pass through either Sumatra or Borneo to reach Java, and the morphological similarity of specimens from the Mekong River drainage and Java.

Recently, Hamidy et al. (2019) sequenced two mitochondrial genes of 11 *M. subtrijuga* specimens, consisting of field-collected turtles from Java and captive individuals from a breeder on Sumatra. These sequences were compared with data for Indochinese populations submitted to GenBank by Ihlow et al. (2016). Little divergence was found, leading Hamidy et al. (2019) to regard *M. subtrijuga* as having been introduced to Indonesia. However, mitochondrial DNA evolves slowly in chelonians (Avise et al. 1992), indicating that analyses relying solely on mitochondrial genes may be unsuitable for resolving the history of recent divergences. Ihlow et al. (2016) observed that mitochondrial divergence between *M. macrocephala* and *M. subtrijuga* was low (uncorrected *p*-distances of 1.45% for cyt *b* and 1.09% for ND4) and suggestive of introgression. The species were validated only through analyses of 12 microsatellite loci, which revealed distinct nuclear gene pools (Ihlow et al. 2016). Thus, the findings of Hamidy et al. (2019) are inadequate to fully settle the status of *M. subtrijuga* on Java.

It is also possible that *M. subtrijuga* is a naturally occurring relict on the island (Brophy 2005). Climatic oscillations earlier in the Quaternary produced changes in temperature, precipitation, and vegetation patterns, along with sea level fluctuations that exposed land between the islands of the Sunda Shelf and mainland Southeast Asia (Heaney 1991; Bain and Hurley 2011). Paleoclimatic projections of climatic niche models suggest that environmental conditions in some parts of the exposed continental shelf, Sundaland, might have been suitable for *Malayemys* (Ihlow et al. 2016). *Malayemys subtrijuga* could have colonized Java from the Indochinese Peninsula during a period when the land masses were connected and subsequently became isolated on the island as seas rose to present levels. If *M. subtrijuga* reached Java by this mechanism, it is possible that the species either managed to somehow bypass the neighboring areas of Sumatra and Borneo or later went extinct on these islands as climatic conditions changed. The route of *M. subtrijuga* may have been through a savanna corridor that is hypothesized to have extended through central Sundaland, largely skirting most of Sumatra and Borneo, except for the extreme southern portion of the latter (Wuster et al. 2019). This scenario could explain why *M. subtrijuga* was not identified by

Pritchard et al. (2009) among the fragments of turtle remains recovered from Pleistocene deposits of human refuse at an archaeological site in northern Borneo.

While Brophy (2005) considered an introduction to be more probable than a natural occurrence of *M. subtrijuga* on Java, he did note that some other fauna share similar patterns of distribution. Species occurring on both Java and the Indochinese Peninsula, but which appear to be absent (or represented by only a few isolated records) from Sumatra and Borneo, include the Eastern Russell's Viper, *Daboia siamensis* (Thorpe et al. 2007), the Burmese Python, *Python bivittatus* (Barker and Barker 2008), the White-lipped Pit Viper, *Trimeresurus albolabris* (David and Vogel 2000; Giannasi et al. 2001), and the Leopard, *Panthera pardus* (Meijaard 2004). Given the characteristics of these species and their limited values for consumption or trade, it seems highly improbable that they would have also been intentionally introduced by humans in the past. At present, neither explanation for the presence of *M. subtrijuga* on Java can be dismissed. A comprehensive phylogeographic analysis of the species is needed to elucidate the origins of the Javan population and clarify relationships among the populations (TTWG 2017).

Habitat and Ecology. — *Malayemys subtrijuga* inhabits heavily-vegetated, soft-bottomed, lentic waters in lowland areas. The upper elevational limit for the species appears to be approximately 200 m above sea level (asl). Reported elevations of known localities range from near sea level (Hoang and Le 2010) to around 120 m asl (Brakels 2018).

To date, no studies on habitat preference relative to availability have been conducted. However, *M. subtrijuga* has been documented from a variety of habitats, both natural and anthropogenic, including permanent marshes, streams, riparian areas of rivers, lake margins, ponds, canals, temporary wetlands, flooded grasslands, wet rice paddy fields, seasonally inundated shrublands, peat swamp forests, and mixed deciduous forests (Tirant 1884; Reijst 1949; Safford et al. 1998; Stuart 1998, 1999, 2004; Stuart and Platt 2004; Dang et al. 2006; Le 2007; Hoang and Le 2010; Hartmann et al. 2013; Ihlow and Dawson 2016b; Vassilieva et al. 2016; Brakels 2018; Geissler et al. 2019; Hamidy et al. 2019). Sympatric chelonians variously occurring in these habitats include *Amyda ornata*, *Cuora amboinensis*, *Cyclemys oldhamii*, *Heosemys annandalii*, *Heosemys grandis*, and *Siebenrockiella crassicollis* (Platt et al. 2008; Le 2007; Brakels 2018).

Although principally found in freshwater habitats, *M. subtrijuga* may occasionally occur in more saline environments. In the Mekong Delta of Vietnam, individuals have been captured approximately 6 km inland from the South China Sea in tidally influenced brackish canals with an average salinity of approximately 1.8% (Hoang and Le 2010). However, the mechanisms and limits of salinity tolerance in *M. subtrijuga* have not yet been determined.

The climate throughout the distribution of *M. subtrijuga* is tropical with seasonal variations in precipitation. Although Java is hot and humid year-round, much of the island experiences wet and dry seasons and is classified as a tropical monsoon climate under the Köppen-Geiger system (Beck et al. 2018). In the Jakarta area, the daily maximum air temperature is around 32°C throughout the year and the mean annual precipitation is approximately 1,700 mm. Between December and March, rainfall averages over 150 mm per month, whereas mean monthly rainfall is less than 100 mm between June and September (Siswanto et al. 2016). Moving eastward on Java, the dry season becomes more prominent, and the Köppen-Geiger classification changes to tropical savanna climate (Fukui 1956).

Southeastern Indochina also has a tropical savanna climate (Beck et al. 2018), and the dry season is very distinct. In central Cambodia, the monthly maximum temperature peaks around 35°C in March and April, then falls throughout the wet season to roughly 31°C between September and December (Meynell et al. 2014). The wet season generally lasts from May to October, while drier conditions predominate from roughly November to April; mean annual precipitation is around 1,500 mm or more (Bezuijen et al. 2009; Meynell et al. 2014). Temperatures and timing of the seasons are similar elsewhere in Indochina. In southern Laos, one third of the roughly 2,000 mm of mean annual precipitation occurs in August (Meynell et al. 2015). Mean precipitation exceeds 2,250 mm annually in the Mekong Delta of southern Vietnam, but peak rainfall occurs in September and October, and a pronounced dry season extends from December to March (Safford et al. 1998).

The low-lying habitats of *M. subtrijuga* are prone to flooding in the wet season (Meynell et al. 2015; Siswanto et al. 2016). An annual flood pulse along the Mekong River reverses the flow of the Tonle Sap River, filling Tonle Sap Lake in central Cambodia. The resulting inundation increases the lake's size by roughly five-fold (Balzer et al. 2005; Platt et al. 2008; Meynell et al. 2014). Heavy rains also lead to seasonal flooding of the Mekong Delta (Safford et al. 1998; Hoang and Le 2010).

Malayemys subtrijuga is typically considered to be a slow bottom-walking species, rather than a powerful agile swimmer. Nevertheless, reliable sources in central Cambodia have reported observations of individuals swimming far from shore in the middle of Tonle Sap Lake (Ihlow, unpubl. data). The activity and movement patterns of *M. subtrijuga* have not been extensively studied. To our knowledge, the only available quantitative data come from a short-term telemetry project conducted in central Cambodia. Nine turtles, tracked through flooded forest over ten consecutive days of the wet season, had highly variable daily movements, ranging from a

Figure 8. Habitats of *Malayemys subtrijuga*. **A**: Rice fields, Preah Vihear Province, Cambodia. **B**: Seasonally flooded shrubland, Tonle Sap Biosphere Reserve, Battambang Province, Cambodia. **C**: Prek Spot stream, Tonle Sap Biosphere Reserve, Battambang Province, Cambodia. **D**: Permanent pond, Kulen Promtep Wildlife Sanctuary, Preah Vihear Province, Cambodia. **E**: Shallow pond near Po Chruk village, Preah Vihear Province, Cambodia. **F**: Bau Sau wetland, Cat Tien National Park, Dong Nai Province, Vietnam. Photos by F. Ihlow (A,D,E) and J.E. Dawson (B,C,F).

few meters up to 1.8 km (Ihlow and Dawson 2016b). As water levels rise in the wet season, the ability to travel relatively long distances over short time periods may allow individuals to migrate into recently inundated areas and exploit newly available resources. According to local people, turtles are found in flooded rice fields in central Cambodia only from August to December, coinciding with the maximum extent of Tonle Sap Lake, and spend the remainder of the year in forests around the lake (Balzer et al. 2005). Conversely, individuals appear to estivate when bodies of water shrink and disappear during seasonal periods of low rainfall. On Java, individuals reportedly bury into the mud in the late dry season and remain there until the next monsoon rains begin (Reijst 1948). Similarly, local people in central Cambodia reported that the species estivates during the dry season (Platt et al. 2008).

Due to a lack of comprehensive studies thus far, a detailed composition of the diet of *M. subtrijuga* is unavailable. However, the species seems to be largely molluscivorous. In central Cambodia, one individual had the operculum of a snail lodged in its mouth upon capture, while three additional opercula were recovered from the feces of other recently caught individuals (Dawson and Ihlow, unpubl. data). To our knowledge, taxonomic identification of the snails eaten by *M. subtrijuga* in the wild has rarely been attempted. All of the above mentioned opercula were from members of the Viviparidae (F. Köhler, pers. comm.), a gastropod family that is diverse and abundant in Southeast Asia (Köhler et al. 2008). However, whether *M. subtrijuga* preys upon species of snails in direct proportion to their abundance or instead has dietary preferences for certain kinds is unknown. Besides snails, *Malayemys* has been reported to occasionally consume other foods, including worms, shrimp, and bivalves (Bourret 1941a; Stuart et al. 2001).

Often inhabiting waterbodies with low visibility, *Malayemys* appears to recognize prey by olfaction, and a foraging individual will examine nearby objects and crevices systematically. Feeding is slow and methodical. When *Malayemys* consumes a snail, the prey is turned using the tongue until a position suitable for crushing the hard shell between the turtle's jaws is achieved (Schmidt 1959). Then, prior to swallowing, the turtle holds the crushed mollusc in its mouth and uses movements of the throat to create currents of water that flush away the fragments of shell (Gans 1969). Any remaining shell fragments and snail opercula pass through the digestive system.

Nesting of *M. subtrijuga* occurs during the dry season. Information on the reproductive ecology of the species is almost nonexistent for Java. However, because of differences in the timing of seasons, nesting in Java and Indochina may happen at different times of the year. Kopstein (1932) reported that a female caught in the western part of Java laid an egg on 26 October. In contrast, egg collectors in central Cambodia stated that oviposition occurs from December to March (Platt et al. 2008). This period is consistent with observations of fresh eggs and gravid females in Cambodian markets during December and January (Platt et al. 2008; P.C.H. Pritchard, pers. comm.). Hatching of a nest near Sisophon, western Cambodia, occurred in late April just after the first days of rainfall (C. Held, pers. comm.), suggesting that nesting had occurred at the onset of the dry season. Meynell et al. (2015) reported egg laying in southern Laos to begin in March and April. Presumably based on individuals from the Mekong Delta, Bourret (1941a) reported that *Malayemys* nests in April.

Malayemys subtrijuga is known to nest above water, based on several observations from central and western Cambodia reported to Ihlow (unpubl. data). Platt et al. (2008) speculated that *M. subtrijuga* may also be capable of nesting underwater, because egg deposition appears to begin in central Cambodia while water levels of Tonle Sap Lake are still elevated. Underwater nesting has been documented in other chelonians inhabiting seasonal wet and dry environments (Kennett et al. 1993; Polisar 1996), so the possibility of this behavior in *M. subtrijuga* deserves further investigation. Five nests examined by Platt et al. (2008) in central Cambodia were located along creeks under a thick canopy of woody plants (*Vitex* sp.) or on a low ridge covered by dense herbaceous vegetation (*Sorghum* sp., *Sesbainia* sp., and *Polygonum* sp.). The nest cavities were between 100–120 mm in depth and constructed in partially-flooded, water-logged clay substrates (Platt et al. 2008). A single nest found near Sisophon, western Cambodia, was located on the slope of a small incline adjacent to a temporarily flooded area. The nest cavity was approximately 100 mm deep (C. Held, pers. comm.).

The eggs of *M. subtrijuga* have hard chalky shells (Kopstein 1932). For Java, dimensions are only available for a single, potentially infertile, egg that measured 41.5 x 24.5 mm (Kopstein 1932). Platt et al. (2008) found that eggs from central Cambodia had a mean length of 41.2 ± 2.7 mm (range = 35.3–47.5 mm; n = 129), a mean width of 23.8 ± 1.7 mm (range = 21.0–27.7 mm), and a mean mass of 15.1 ± 3.3 g (range = 9.0–22.0 g). Bourret (1941a) reported similar lengths (range = 40–45 mm) and widths (range = 20–25 mm) for *Malayemys* eggs. Two days before hatching, one egg from a nest in western Cambodia had a mass of 8 g (C. Held, pers. comm.). In captivity, eggs measured shortly after deposition had a mean length of 44.9 ± 2.8 mm (range = 40.1–51.3 mm; n = 37), a mean width of 23.6 ± 1.8 mm (range = 18.3–26.6 mm), and a mean mass of 15.8 ± 2.6 g (range = 9.6–19.6 g; S. Szymanski, pers. comm.).

In central Cambodia, Platt et al. (2008) induced oviposition in 22 females and calculated the mean clutch mass to be 88.6 ± 34.7 g (range = 37.0–170.0 g) and the mean clutch size to be 5.8 ± 1.7 eggs (range = 3–10). However, the data reported by Platt et al. (2008) should be considered conservative estimates, because while complete clutches were most likely obtained, it is possible that some eggs were not deposited through induction. A nest in western Cambodia contained four eggs (C. Held, pers. comm.). In captivity, females have laid clutches of 1–4 eggs (S. Szymanski, pers. comm.). These clutch sizes are close to the values reported for *M. macrocephala* (Dawson et al. 2018). In contrast, local people in Cambodia made unsubstantiated claims of clutches containing up to 20 eggs (Platt et al. 2008). This number is likely an overestimate and presumably was based on observations of yolked ova within females captured during the reproductive period. These ova are probably laid in multiple clutches throughout the nesting season. Captive females have deposited 4–6 clutches per year, with a mean time of 27 days (range = 21–38 days) between clutches (S. Szymanski, pers. comm.).

Platt et al. (2008) found no correlation between female SCL and clutch size. However, as wild females likely lay multiple clutches per nesting season, total annual fecundity could be related to body size in *M. subtrijuga*. Although larger females did not appear to lay more eggs per clutch, a significant positive correlation did exist between female SCL and both egg mass and clutch mass, indicating that egg size increased with increasing female body size. Yet, in contradiction to theoretical models of optimal clutch size, there was no evidence of a trade-off between clutch size and egg mass (Platt et al. 2008).

We are unaware of any research on temperature-dependent sex determination (TSD), incubation period, or hatching rate among wild populations. As TSD is exhibited in *M. macrocephala* (reviewed by Dawson et al. 2018), this phenomenon likely also occurs in *M. subtrijuga*. Without providing any additional data, Meynell et al. (2014) gave the incubation period as around 167 days at 28–30°C. Four eggs incubated in artificially constructed nests by Platt et al. (2008) in central Cambodia hatched after 99 days. The hatch rate during this study was extremely low (3.1%), due to issues with predation, egg quality, and perhaps incubation method (Platt et al. 2008). In Cambodia, hatchlings emerge at the start of the wet season, with most reports of emergence occurring from May to July (Platt et al. 2008; Meynell et al. 2014), although it can occur earlier (C. Held, pers. comm.) depending on the timing of the first rains. Information on the timing of hatching and emergence is unavailable for any other locations.

Studies on natural growth rates and sexual maturity have not yet been conducted. According to Meynell et al. (2014), males reach maturity at around three years of age, while females mature at about five years, but the basis for this statement is unknown. Captive males start breeding at 130–140 mm maximum SCL (S. Nickl, pers. comm.). In central Cambodia, the midline SCL of the smallest female to be successfully induced to deposit eggs was 162.2 mm (Platt et al. 2008). However, whether these body sizes represent typical sizes at which individuals become capable of reproduction in the wild is not known.

Malayemys subtrijuga is host to several ecto- and endoparasites. An adult female, encountered in dense bamboo near a small stream in Kulen Promtep Wildlife Sanctuary of northern Cambodia, had four leeches (*Hirudinaria javanica*) attached to the posterior marginals of the carapace and one leech at the rear of the plastron (Hartmann et al. 2013). Infestations by another leech species (*Placobdelloides siamensis*) have also been reported (Chiangkul et al. 2018). Intestinal nematodes are common in *Malayemys*. Blood flukes (*Platt sinuosus* and *P. snyderi*) were found in the kidneys and mesenteric blood vessels of *M. subtrijuga* from the Mekong Delta of Vietnam (Roberts et al. 2018).

The species is also subject to natural predation. In central Cambodia, Long-tailed Macaques (*Macaca fascicularis*) have been documented to rob nests, while local people reported that otters (*Lutra* spp.), Greater Coucals (*Centropus sinensis*), and Water Monitors (*Varanus salvator*) were also nest predators (Platt et al. 2008). Young turtles may be taken by large fish, snakes, wading birds, and crows (Meynell et al. 2014).

Population Status. — Early works on the herpetofauna of Java lack any details on the historical population size of *M. subtrijuga*. However, an array of specimens from a number of sites on the island were placed in natural history collections and documented in scientific reports during the nineteenth and early twentieth centuries (e.g., Schweigger 1812; Schlegel and Müller 1845; Bleeker 1857; Blyth 1863; Gray 1871; Ouwens 1914; Kopstein 1932; Reijst 1949). Although speculative, it seems reasonable to assume that the species was not uncommon, perhaps even locally abundant at some sites with suitable habitat, over that time period. In comparison, Samedi and Iskandar (2000) considered it to be rare in Indonesia by the late 1990s. However, evidence regarding the status of *M. subtrijuga* on Java remains limited, and despite ongoing trade of the species in Indonesia, we are unaware of any recent systematic surveys or attempts at assessing the possible persistence or size of any of the Javan populations.

Measurable historical population data on *M. subtrijuga* are also nonexistent for southeastern Indochina, but previous authors noted that the species was common in the region (Tirant 1884; Bourret 1939). In the mid-twentieth century, armed conflicts, civil unrest, and political instability in Southeast Asia precluded scientific fieldwork (Stuart and Platt 2004), and little is known about the status of *M. subtrijuga* in Cambodia, Laos, or Vietnam during that time. By the 1990s, security and stability in the region had increased, providing greater opportunity for research.

However, recent estimates for the sizes of *M. subtrijuga* populations in Indochina have generally relied upon indirect methods, such as interviews of local people or observations of trade, and many population status assessments include a large degree of subjectivity. As a result, the sizes and trends of Indochinese *M. subtrijuga* populations remain incompletely known, particularly in Laos and Vietnam. In southern Laos, some villagers viewed the species as being as abundant in 1998 as it had been 10 years earlier, but others reported that it was rarer than before (Stuart 1998). Stuart and Timmins (2000) stated that *M. subtrijuga* was probably one of the most common turtle species in Laos. However, they also noted that turtle populations in general had undergone serious declines within the country. Hence, although *M. subtrijuga* was apparently faring better than the majority of turtle species and continued to exist in appropriate habitat, Stuart and Timmins (2000) suggested that the Lao population was likely quite reduced from its past size. In 2018, collection of *M. subtrijuga* was reported by 55 out of 65 residents interviewed around Beung Kiat Ngong Wetlands in Champassak Province, southern Laos (Brakels 2018). The approximate number of turtles caught by each respondent ranged from 2–150 turtles per year, with a maximum estimate of 1500 turtles collected from the area per year. Similar to previous assessments, most residents perceived *M. subtrijuga* to be the most common turtle species in the wetland. Again, however, all turtles in the area appeared to have suffered declines, and market prices provided a strong incentive for locals to continue harvesting (Brakels 2018). In Vietnam, while the actual population status and trends of *M. subtrijuga* were unknown, Hendrie (2000b) contended that the population was unlikely to be able to sustain the level of collection. Touch et al. (2000) regarded the Vietnamese population to already be very low.

The most comprehensive information on the population status of *M. subtrijuga* originates from central Cambodia. Touch et al. (2000) described *M. subtrijuga* as likely to be the most abundant turtle species in Cambodia. Similarly, Emmett (2009) surmised that the Cambodian population of *M. subtrijuga* was slowly decreasing, but maintained that a large number still inhabited Tonle Sap Lake. Platt et al. (2008) provided a more rigorous assessment by investigating the exploitation of turtles in Tonle Sap Biosphere Reserve (TSBR) from 2000–2001. Although annual collection levels of turtles were difficult to quantify, an interview survey of local residents suggested that regional turtle populations were in decline. One collector stated that it had been possible to harvest as many as 150 turtles (an aggregate of all species in the area, including *M. subtrijuga*) in a single night in the early 1980s, whereas catch rates of 1–5 turtles per day were reported at the time of the survey (Platt et al. 2008). During the investigation, *M. subtrijuga* was the species of turtle most frequently harvested from TSBR (constituting 92% of all traded turtles). The sex ratio of *M. subtrijuga* in the trade was heavily skewed towards females (1:3.1), which Platt et al. (2008) suggested was due to the preferential collection and sale of large individuals and the female-biased sexual dimorphism of the species. Platt et al. (2008) concluded that commercial collection of turtles in TSBR was unsustainable and represented a serious threat to the continued viability of turtle populations in central Cambodia.

Subsequent work by Ihlow and Dawson (2016a,b) found credible signs of a further decline in the *M. subtrijuga* population within one portion of TSBR. During interviews, local residents viewed hunting specifically for turtles to be unprofitable and indicated that recent collection was mostly incidental to other fishing. A single fisherman would reportedly deploy around 60 traps each day but capture only 3 or 4 turtles per month, a catch per unit effort of 1 turtle/450 trap days (Ihlow and Dawson 2016a,b). As in the study by Platt et al. (2008), *M. subtrijuga* was the most frequently traded species. However, the sex ratio being traded was not significantly different from parity (1:1.06), and the size distributions of both sexes in trade were skewed towards small individuals (Ihlow and Dawson 2016a,b). Although not directly comparable due to differences in study design and timing, the considerable differences between the sex ratios and size distributions reported by Ihlow and Dawson (2016a,b) and Platt et al. (2008) suggest that large females, usually preferred by traders, had become scarce. Ihlow and Dawson (2016a) interpreted these findings as being indicators of both an altered population structure and a decrease in the local abundance of *M. subtrijuga* (sensu Schoppe 2009). Given the ubiquity of exploitation in Cambodia, it seems highly probable that *M. subtrijuga* has undergone similar demographic changes and population declines, not only at TSBR but throughout the country.

Figure 9. Adult female *Malayemys subtrijuga* at a local restaurant in Kampong Thom Province, Cambodia. The turtles were steam cooked with their plastra removed, and the developing eggs are visible as yellow yolks. These eggs likely would have been laid in multiple clutches over the nesting season. Photo by F. Ihlow.

Threats to Survival. — Humans have utilized *M. subtrijuga* for subsistence extending back to prehistory. *Malayemys subtrijuga* remains were discovered during archeological excavations of human occupation sites in Cambodia dating from the Protohistoric (Iron Age) Period at Angkor Borei (Ikehara-Quebral et al. 2017) and the Pre-Angkorian Period at Phum Snay (Voeun 2008). Turtles, including *M. subtrijuga*, also represented a rich food source for later civilizations of Indochina, such as the Khmer Empire of the Angkorian Period (Lehr and Holloway 2003). However, while subsistence use continues, this consumption was surpassed by collection for commercial purposes in recent

Figure 10. Forty-eight juvenile *Malayemys subtrijuga* at a trader's house in Prek Toal village, Battambang Province, Cambodia. These turtles were obtained from local fishermen and were reportedly intended for the production of traditional medicine. Photo by J.E. Dawson.

decades (Le and Broad 1995; Stuart 1998; Platt et al. 2008; Bezuijen et al. 2009; Brakels 2018).

While trade of turtles in Indonesia has been primarily for export (Samedi and Iskandar 2000), both domestic and international demand have driven the commercial trade of *M. subtrijuga* in Indochina. Large numbers have been documented in the food markets of towns and urban areas in Cambodia (Lehr and Holloway 2000; Platt et al. 2008), Laos (Stuart and Timmins 2000; Suzuki et al. 2015), and Vietnam (Jenkins 1995; Le and Broad 1995). In 1995, P.C.H. Pritchard (pers. comm.) saw several dozen freshly-killed, large, gravid females for sale in a market at Siem Reap, Cambodia. The plastra of the turtles had been removed, exposing the viscera and 8–10 unlaid eggs inside each individual. Cooked turtles are commonly presented in this manner to customers in Cambodian markets, restaurants, and roadside stalls (Lehr and Holloway 2000; Platt et al. 2008; Ihlow, pers. obs.). Khmer street vendors informed Lehr and Holloway (2000) that their patrons preferred to eat females. Likewise, Platt et al. (2008) stated that gravid females are considered a delicacy by people in Cambodia. In southern Vietnam, a specialty dish of the Ca Mau region is prepared by cooking *M. subtrijuga* with salt in earthen pots (ATP/IMC 2012). Outside of its range, *Malayemys* has been recorded in the live animal markets of southern China (Farkas and Sasvári 1992; Fong et al. 2002; Lee et al. 2004; Shi et al. 2004; Cheung and Dudgeon 2006; Chow et al. 2014).

Traditional medicine is another major use for *M. subtrijuga*, both within the species' range (Le and Broad 1995; Lehr and Holloway 2003; Balzer et al. 2005; Platt et al. 2008; Meynell et al. 2015; Ihlow and Dawson 2016a,b) and abroad (Chen et al. 2000; Chen et al. 2009; Lee et al. 2009). Lehr and Holloway (2003) reported that turtle shells were stocked by traditional Cambodian pharmacies. Plastra from *M. subtrijuga* were the most prevalent and the most expensive of these items, and they were alleged to promote healthy bones when consumed in powdered form (Lehr and Holloway 2003). In Cambodia, turtle shells are also used to create a tonic for postpartum women (Platt et al. 2008). Shells may be saved as by-products from the consumption of turtles for meat and then sold to traditional medicine dealers (Lehr and Holloway 2003; Chen et al. 2009). However, turtles may also be collected specifically for medicinal use. At a village on Tonle Sap Lake, small juveniles were being amassed from local fishermen, reportedly for sale to a trader who planned to produce traditional medicine (Ihlow and Dawson 2016a,b).

Individuals of *M. subtrijuga* are also sold near rivers, lakes, and temples for Buddhist release ceremonies (Lehr and Holloway 2003; Platt et al. 2008; Emmett 2009; Ihlow and Dawson 2016a). Practitioners purchase the captive turtles and then release them, believing this action to be a good deed that earns karmic merit towards higher incarnation in a future life (Lehr and Holloway 2003; Platt et al. 2008). Frequently, juveniles are sold for this purpose (Lehr and Holloway 2003; Platt et al. 2008; Emmett 2009), although larger individuals may also be used (Ihlow and Dawson 2016a). After release, turtles may be recaptured and returned to the trade. A vendor near a shrine in Siem Reap, Cambodia, offered a turtle bearing Khmer characters scratched into its carapace; these markings were likely the name of a person who had released it previously (Dawson and Ihlow, pers. obs.). Turtles that escape recapture are still likely to die from stress, disease, or release into unsuitable habitats. Furthermore, merit releases have the potential to spread diseases from captivity into wild populations, as well as introduce *M. subtrijuga* into areas outside of the species' native distribution.

Malayemys subtrijuga also appears in the pet trade, although this usage has not been as extensive as other forms of commerce. Observations of the species in the pet trade have been made in numerous countries, including Vietnam (Le and Broad 1995; Hendrie 2000b; Pham et al. 2019), China (Gong et al. 2009), Indonesia (Shepherd and Nijman 2007; Sinaga 2008; Stengel et al. 2011), the Philippines (Sy 2015), and the United States (Dawson, pers. obs.). *Malayemys subtrijuga* has been recorded in Chinese turtle farms, apparently to supply the national pet trade (Lam and Xu 2008). Albino specimens have been advertised as pets online in Vietnam and command a much higher price than normally pigmented individuals (Pham et al. 2019). The success of captive breeding operations for this species is unknown, but the potential exists for some small-scale production. However, the majority of the turtles that have been traded as pets undoubtedly originated from the wild. In general, *M. subtrijuga* has a reputation for being difficult to establish in captivity, and the demand for this species as pets is relatively low compared to other turtles.

Estimates of past and present trade volumes for *M. subtrijuga* are hampered by a number of factors, including difficulties in taxonomic identification, inadequate monitoring and incomplete records for legal trade, the clandestine nature of illegal trafficking, and the anonymity provided by the recent rise in online sales. While the available data provide only snapshots of the trade, they suggest that vast numbers were exploited during the 1990s and early 2000s. During this period, *M. subtrijuga* was reported to be one of the most heavily traded species in Cambodia, southern Laos, and Vietnam. During a four-week span in early 2000, Lehr and Holloway (2003) tallied 700 specimens in markets around Cambodia. During 2000–2001, Platt et al. (2008) examined 360 turtles in trade around central Cambodia but reported seeing many more in markets. In southern Laos, an informer stated that exports of *M. subtrijuga* shells to Thailand amounted to roughly a tonne (presumably dry weight) annually during the early 1990s. The shells were reportedly collected for months from around Pakse and then transported in bulk once a year through the border crossing at Chong Mek (Nash 1997).

Ho Chi Minh City, Vietnam, was a major transit point on the route to China for turtles originating from both southern Vietnam and Cambodia (Le and Broad 1995). In September 1993, vendors interviewed at Cau Mong Market in Ho Chi Minh City claimed to deal in 2,172 kg (fresh weight) of *M. subtrijuga* per day. About a quarter of the *M. subtrijuga* were said to originate from Cau Mau Province, at the southern tip of Vietnam. Based on figures provided by traders at Cau Mau, the weekly turnover of turtles there was estimated to be nearly 8 tonnes, and *M. subtrijuga* constituted 90% of the observed trade (Le and Broad 1995). According to official declarations, only 2,620 individuals of *M. subtrijuga* were exported legally from Vietnam during the period 1994–1999 (Hendrie 2000b). However, this figure is likely a gross underestimate of the actual trade volume. In 2000, permits were issued by three southern Vietnamese provinces (Ca Mau, Bac Lieu, and Soc Trang) to legally export 151,475 kg (presumably fresh weight) of *M. subtrijuga* (Nguyen 2003). According to Hendrie (1998, 2000a,b), *M. subtrijuga* was seen less frequently in northern Vietnam trade confiscations than other species in transit to China. Yet, when the species was present, there were typically hundreds of individuals, often comprising the entire shipment. Seizures of illegal wildlife shipments by Vietnamese officials in 1996, 1998, and 2000 contained large numbers of *M. subtrijuga* (Hendrie 1998, 2000a,b).

Lau et al. (2000) noted that *Malayemys* had already disappeared from the food markets of Hong Kong by 1999 and suggested that this could be the result of declining wild populations. However, *Malayemys* continued to be observed at markets in southern China, sometimes in considerable numbers, by other authors into the early 2000s (Lee et al. 2004; Shi et al. 2004; Cheung and Dudgeon 2006; Chow et al. 2014). According to Chen et al. (2009), *M. subtrijuga* was one of the three species most commonly traded in the traditional Chinese medicine markets of Taiwan between 1996 and 2002. Together, these species accounted for 75% of the shells in markets. Java was likely the origin for much of this material, as *M. subtrijuga* was the most common species in imports to Taiwan from Indonesia during this period (Chen et al. 2000).

Based on the above statistics, a conservative estimate for the volume of *M. subtrijuga* traded during the 1990s and early 2000s would be several hundred thousand individuals annually. As previously mentioned, however, the actual number involved is impossible to ascertain and conceivably reached well over a million each year. Trade has decreased since that time, particularly to international markets, but continues within range countries, although seemingly at a lower magnitude than before. These declines may be attributable to conservation efforts but also to reduced population sizes in the wild. In addition, a proportion of the current trade is now conducted online (Sinaga 2008; Tran et al. 2016; Pham et al. 2019), where the scale can be difficult to assess.

Local people employ a variety of methods, depending on the season, to capture *M. subtrijuga*. In the wet season, partially submerged bamboo funnel traps are commonly utilized (Stuart 1998; Platt et al. 2008; Ihlow and Dawson 2016a). Individuals may be caught in small funnel traps that are designed specifically for turtles or entrapped as bycatch in larger versions intended for fish; both types of traps are frequently used in combination with drift fences (Platt et al. 2008). *Malayemys subtrijuga* can also be taken from the water in lift nets (Stuart 2004). While planting or harvesting rice fields, farmers will opportunistically collect any turtles encountered (Platt et al. 2008). During the dry season, estivating turtles are found by using hunting dogs or through probing the mud with sharpened sticks (Stuart 1998; Platt et al. 2008). Concealed turtles may also be exposed by setting fires to remove dry vegetation (Balzer et al. 2005; Platt et al. 2008; Meynell et al. 2015). Platt et al. (2008) described several individuals with discolored carapacial scutes consistent with fire injuries. Turtles awaiting sale to traders may be temporarily tethered through holes in the marginal scutes (Stuart 1998) or kept in containers of water (Stuart 2004), but Emmett (2009) noted that villagers in Cambodia typically do not attempt to rear small animals to more valuable market sizes due to the high mortality rate of *M. subtrijuga* in captivity. Similarly, locals in Laos reported that *M. subtrijuga* was very difficult to keep (Brakels 2018).

In comparison with trade, other current threats to *M. subtrijuga* are regarded as minor. Eggs of the species are collected, occasionally using dogs, in Cambodia and southern Laos (Platt et al. 2008; Meynell et al. 2015) and are sold in local markets (Platt et al. 2008; P.C.H. Pritchard, pers. comm.). Considered delicacies, the eggs are consumed raw, sometimes in the belief that they are male aphrodisiacs (Holloway 2000, cited in Platt et al. 2008). Non-selective fishing practices may inadvertently impact *M. subtrijuga* through accidental drowning in gill nets (Stuart 1998) or the effects of illegal electrofishing (Le 2007). Given the specialized diet of *M. subtrijuga*, Le (2007) speculated that the collection of snails by humans could affect the food supply of the species. Recent declines in mollusc fisheries, partly due to overharvest, have been suggested at Tonle Sap Lake in central Cambodia (Ngor et al. 2016). Elevated levels of organochlorine pesticides (e.g., DDT) and other persistent, bioaccumulative, and toxic chemicals (e.g., PCBs) have been detected in the Mekong River (Nguyen et al. 2004) and Sai Gon-Dong Nai Rivers (Nguyen et al. 2007) of southern Vietnam. Due to the species' longevity and trophic position, *M. subtrijuga* is likely to be affected by biomagnification of these compounds.

Habitats within the distribution of *M. subtrijuga* have been degraded by many human activities, including agricultural conversion, fire, invasive species introductions, timber removal, wartime herbicide-spraying, and wetland drainage (e.g., Safford et al. 1998; Le 2007; Köhler et al. 2008; Platt et al. 2008; Duckworth and Timmins 2015). However, past habitat alteration is generally viewed as having had relatively little impact on *M. subtrijuga* populations since the species is capable of inhabiting anthropogenically-modified habitats. In the near future, changes in the hydrologic flow of the Mekong River as a result of dam construction (Platt et al. 2008) and irregular precipitation due to climate change (Meynell et al. 2014, 2015) are likely to be greater concerns. Anthropogenic climate change could also increase nest temperatures during incubation. Assuming that *M. subtrijuga* exhibits temperature-dependent sex determination (like *M. macrocephala*), higher nest temperatures might skew hatchling sex ratios (Meynell et al. 2014, 2015). However, the greatest threat posed by climate change is the projected rise in sea levels. Freshwater turtles in Southeast Asia are exceedingly vulnerable to habitat loss from sea-level rise (Agha et al. 2018), and a recent estimate suggested that 25% of the current area of the Mekong Delta could be below sea level by 2100 with even a moderate (~40 cm) projected rise (Minderhoud et al. 2019). This danger is further exacerbated by both extensive sediment extraction, via sand mining, and reduced sediment replenishment, a consequence of upstream dams, underway in the Lower Mekong Basin (Jordan et al. 2019).

Conservation Measures Taken. — The conservation status of *M. subtrijuga* has changed several times during the past few decades, but status assessments often included a great deal of uncertainty and seldom kept pace with taxonomic changes. In 1996, the status of *M. subtrijuga* (sensu lato, including *M. macrocephala* and *M. khoratensis*) was assessed by the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (TFTSG) as Least Concern, and the species was not included on the IUCN Red List of Threatened Species (TTWG 2017). However, the status of *M. subtrijuga* (sensu lato) was reassessed as Vulnerable for the IUCN Red List in 2000 (TTWG 2017; Rhodin et al. 2018). Reassessment of *M. subtrijuga* (sensu stricto, excluding *M. macrocephala* and *M. khoratensis*) by the TFTSG in 2018 resulted in a provisional Red List status of Near Threatened (Rhodin et al. 2018).

Restrictions were placed on the legal international trade of *M. subtrijuga* in 2005, when the species was listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). All of the range countries of *M. subtrijuga* are Parties to CITES. Indonesia continues to permit commercial trade of the species as pets under a harvest quota system (Shepherd and Nijman 2007; Stengel et al. 2011). The quota is determined yearly, and any unused portion does not rollover at the end of the year. Ninety percent of the annual quota is allocated for export, and the remainder is intended for domestic use (Shepherd and Nijman 2007; Stengel et al. 2011). The annual export quota for *M. subtrijuga* was lowered from 2,250 individuals in 2004 (Shepherd and Nijman 2007), to 500 individuals by 2006 (Schoppe 2009), and to 180 individuals by 2010 (Stengel et al. 2011). Annual quotas and exports remained relatively steady between 2008–2015 (UNEP-WCMC 2017). According to the CITES trade database, a total of slightly more than 2,000 wild-caught individuals were legally exported from Indonesia between 2005 and 2018 (UNEP-WCMC 2019). Trade is also reportedly limited to individuals below 150 mm in SCL, ostensibly to avoid collection of adults (UNEP-WCMC 2017).

Malayemys subtrijuga was included on a 2009 sub-decree of Cambodia's Law on Fisheries that banned the transport or trade of endangered aquatic species. However, exceptions to this ban are available for activities that comply with domestic laws and CITES regulations, such as aquaculture (Anonymous 2009). In Laos, *M. subtrijuga* is managed under the Wildlife and Aquatic Law (2007). While use is not prohibited, it is subject to controls (Brakels 2018). According to records labeled as *M. subtrijuga* in the CITES trade database, Laos was the origin of 5,000 live individuals shipped from Vietnam to China in 2008, while another 1,000 were exported alive from Laos to Vietnam in 2010. In both cases, ranching was listed as the source of the turtles (UNEP-WCMC 2019), although this source is suspect. In 2019, Vietnam approved a revised law on the management and protection of threatened species, Decree 06/2019/ND-

CP. While *M. subtrijuga* had not been specifically protected under previous decrees, it was listed within Group IIB of the new law, placing limits on commercial use in Vietnam (ATP/IMC 2019). Along with increased legal protection for *M. subtrijuga*, enforcement of wildlife laws has improved within many of the countries involved in trade of the species. Efforts made by authorities have included greater control of trans-boundary trade (Zhang et al. 2008) and the closure of wildlife markets (e.g., Cau Mong Market in Ho Chi Minh City; Hendrie 2000b). In some areas, educational programs have been successful in increasing public awareness of wildlife trade issues and laws (e.g., ENV 2010).

To our knowledge, *M. subtrijuga* has not yet been reported from any protected areas on Java. In Cambodia, the species has been documented from multiple protected areas, including Kulen Promtep Wildlife Sanctuary (Hartmann et al. 2013), Phnom Kulen National Park (Geissler et al. 2019), and the core areas of Tonle Sap Biosphere Reserve (Platt et al. 2008; Ihlow and Dawson 2016a,b). In Laos, *M. subtrijuga* has been recorded from wetlands within the borders of Xe Pian National Protected Area (Brakels 2018). Protected areas inhabited by *M. subtrijuga* in Vietnam include Bac Lieu Bird Sanctuary (Hoang and Le 2010), Cat Tien National Park (Le 2007), Tram Chin National Park (Krohn 2009), and U Minh Thuong National Park (Stuart 2004; Stuart and Platt 2004).

Conservation Measures Proposed. — Regulations on collection and trade are vital for the conservation of *M. subtrijuga*, but for these measures to be effective, robust education, monitoring, and enforcement are necessary. While these systems have strengthened substantially within the range countries of *M. subtrijuga* and their trading partners in recent decades, further improvements are still needed. Exploitation of *M. subtrijuga* for domestic trade continues in all range countries, at levels that arguably remain unsustainable. Educational programs should continue to dissuade consumers from using *M. subtrijuga* for food, traditional medicines, merit releases, and pets. Although raids and closures of markets have reduced the open trading of wildlife, underground trafficking networks continue to operate (Zhang et al. 2008; Brakels 2018). Combating black markets, including illicit online trade, represents a serious and growing challenge in Asia.

At present, international trade appears to be relatively well regulated, but some aspects remain open to doubt. Commercial trade of wild-caught *M. subtrijuga* as pets, primarily for export, is allowed in Indonesia through a harvest quota system. Under this scheme, non-detriment findings are required prior to quota-setting to ensure that the collection is sustainable and compliant with the provisions of CITES. However, gaps exist in the process and systematic assessments are not always conducted, resulting in relatively arbitrary quotas with little scientific basis (Shepherd and Nijman 2007; Stengel et al. 2011). For example, there is no evidence of any field surveys or population monitoring efforts (UNEP-WCMC 2017). Additionally, provinces outside of the known geographic distribution of *M. subtrijuga* have been included within past quotas for the species (Shepherd and Nijman 2007).

Ranching was listed in CITES records as the source of 6,000 individuals traded from Laos in 2008 and 2010 (UNEP-WCMC 2019). However, *M. subtrijuga* typically does poorly in captivity and the successful rearing of large numbers of small individuals to market sizes seems improbable. It appears more likely that these shipments represented the laundering of illegally wild-caught animals through turtle farms, a recognized problem in Southeast Asia (Malesky et al. 2019). Such regulatory loopholes need to be closed, and the penalties for violating wildlife laws must be applied consistently.

In 2014, following the sixteenth meeting of the Conference of the Parties, CITES initiated a Review of Significant Trade in *M. subtrijuga* from Indonesia and Laos (UNEP-WCMC 2017). At the time of writing this manuscript, reviews for both countries were still in progress. However, a provisional "action is needed" recommendation has been made regarding trade of *M. subtrijuga* from Indonesia, while trade from Laos has been provisionally categorized as "less concern." The proposed classification for Indonesia suggests that CITES provisions are not being met for international trade in *M. subtrijuga* from the country, with the primary concern being the apparent lack of robust data for non-detriment findings (UNEP-WCMC 2017). Rigorous research should be undertaken to determine the current size and trends of the population on Java, investigate whether populations definitively occur in any other areas of Indonesia, and further resolve the phylogeography of the species.

Because rises in sea levels could substantially reduce available habitat for *M. subtrijuga*, policies to limit the rate and magnitude of climate change should be implemented. Other threats, such as the hydrologic effects of dams, need to be thoroughly evaluated and monitored. As many aspects of the species' natural history remain poorly known, additional studies on biology and ecology at sites across the distribution of the species would greatly improve conservation and management capabilities.

In 2018, a provisional IUCN Red List assessment by the TFTSG recommended revising the status of *M. subtrijuga* from Vulnerable to Near Threatened (Rhodin et al. 2018). However, we disagree with this proposed change. Taxonomic changes (i.e., Brophy 2004; Ihlow et al. 2016) split *M. subtrijuga* (sensu lato) into multiple species since the previous assessment as Vulnerable in 2000. Accordingly, the sizes of the geographic range and population that remain assigned to *M. subtrijuga* (sensu stricto) have become more restricted. While growth and maturity in the wild are largely unknown, we conservatively estimate the generation time of *M. subtrijuga* to be at least 10 years, based on data from the closely related species *M. macrocephala* (reviewed by Dawson et al. 2018). Despite remaining relatively abundant compared to sympatric chelonians, extensive commercial exploitation of *M. subtrijuga* began around the early 1990s. The available data, although incomplete, are indicative of substantial demographic change and population decline in an area with extensive suitable habitat since that time (Platt et al. 2008; Ihlow and Dawson, 2016a,b). Elsewhere, declines may have been even more severe. While unregulated international trade has ceased for the most part, it seems plausible that the species' population size was halved over three generations (i.e., the last 30 years) based on the massive volume of past trade, potentially justifying a status of Vulnerable under current Red List criteria (A1d). Moreover, domestic consumption in range countries is an ongoing threat, hindering any potential recovery of the species and presenting an even more probable threshold for Vulnerable status – a 30% reduction in population over three generations (A2d). Therefore, at the present time, the current authors believe that it is prudent to retain a Vulnerable status for *M. subtrijuga* on the IUCN Red List.

Captive Husbandry. — The first mention of *M. subtrijuga* in captivity was by Tirant (1884), who described his amusement at the liveliness and gracefulness of juveniles swimming in an aquarium. Unfortunately, nothing was written regarding the care or survival of these turtles. Later accounts by Reijst (1949) and Wanke (1964) were more complete, providing details from their own experiences with keeping *M. subtrijuga*.

Most attempts at establishing and maintaining *Malayemys* have been unsuccessful long-term. In addition to having a specialized diet, wild-caught individuals are easily stressed, often carry heavy parasite loads, and can rapidly become ill when kept in inappropriate conditions (Gurley 2003; Auliya 2007). Individuals often succumb quickly once their health has been compromised. For example, seven *M. subtrijuga* were among a large shipment of Asian turtles confiscated from illegal trade in Hong Kong in 2001 and subsequently shipped to the United States; 86% of these individuals perished within six months, the highest mortality rate among the 16 species that were received during the rescue operation (Barzyk et al. 2002; Hudson and Buhlmann 2002). However, despite the overall low survival rate of *Malayemys* in captivity, some individuals of *M. subtrijuga* have been kept under human care for a number of years, and captive breeding has proven successful. The information that follows is specific to *M. subtrijuga*, but care appears to be similar for all *Malayemys* species. For further details on the husbandry of the genus, see Dawson et al. (2018).

Food is exclusively consumed in water (Reijst 1949; Wanke 1964). A wide variety of live and frozen-thawed snails are eagerly accepted, including members of the families Ampullariidae, Lymnaeidae, and Viviparidae. Long-term captives and captive-bred hatchlings will also readily consume freshwater prawns, shrimp, crayfish, krill, earthworms, non-biting midge larvae, commercial pellets (including turtle, koi, and flamingo breeder diets), and custom-prepared pudding (containing gelatin and a blend of seafood, meat, and vegetables), while some individuals will eat chopped whole fish (capelin and smelt), hard-boiled chicken egg, and freshwater mussels (Dawson, pers. obs.; B. Anders, T. Hartmann, S. Szymanski, pers. comm.). Terrestrial insects, such as crickets, are taken more reluctantly (S. Szymanski, pers. comm.).

Individuals are best housed separately or in large enclosures with numerous underwater hiding places and visual barriers. The species is intolerant of cold water (Reijst 1948), and Wanke (1964) recommended water temperatures between 20–25°C. Enclosures should feature a terrestrial section, as individuals often leave the water. Wanke (1964) reported that her turtles used a terrestrial area every night based on tracks found in the substrate, and S. Szymanski (pers. comm.) observed that most of the individuals under his care slept on land. While exposed cork bark or rocks might be sufficient for males and juveniles, the terrestrial area should ideally offer the opportunity for turtles to bury into a sandy substrate and hide beneath vegetation or leaf litter (Wanke 1964). Such behaviors have been seen in individuals kept under semi-natural conditions at the Angkor Centre for Conservation of Biodiversity in Cambodia (Ihlow, pers. obs.). In particular, adult females need a substrate-filled section of sufficient depth to facilitate nesting. If the substrate is not deep enough, females may not nest. A female of 180 mm SCL and 1260 g refused to nest in less than 200–250 mm of substrate; nests of this female were typically ca. 140 mm in depth (S. Szymanski, pers. comm.).

An egg laid on 31 December 2001 by a captive female in the United States hatched after 101 days, but the conditions during incubation were not reported (Hudson and Buhlmann 2002). In a private collection in Europe, the mean incubation period was 129 days (range = 98–169 days; S. Szymanski, pers. comm.). Eggs were successfully incubated using temperatures of 30 ± 1°C during the day (08:00-20:00) with a drop to 27 ± 1°C at night, but increasing the day-time temperatures to 32 ± 1°C improved the hatching rates to nearly 100%. In contrast to the challenges of keeping wild caught adults, rearing captive-bred hatchlings can be quite easy (S. Szymanski, pers. comm.).

Current Research. — We are unaware of any major research being conducted on *M. subtrijuga* at present. However, conservation and management efforts would greatly benefit from studies aimed at addressing current deficiencies in knowledge. In addition, the potential service that *Malayemys* could provide to humans in controlling aquatic snails deserves further exploration, particularly species that are harmful to agriculture (Carlsson et al. 2004) or vectors of disease (Hopkins 1973).

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