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Species Bioprofile for the Hicatee (*Dermatemys mawii*)

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Abstract - *Dermatemys mawii* (Central American River Turtle) is one of the 25 most endangered turtle species in the world and has been locally extirpated from much of its historical range in southern Mexico, lowland Belize, and northern Guatemala. As the sole living member of the primitive Dermatemydidae family, *D. mawii*, is unique and possesses some uncommon life-history traits, many of which are not fully understood. The cultural significance of this turtle, still important throughout its present-day range, dates back to pre-Classic Maya as a key ethno-herpetological icon in the culture and diet of Maya people in the Yucatan peninsula. Despite its protected status, the species continues to be exploited and has a dire future if current harvest rates continue. Relativley little is known of the biology of the species, but research and conservation efforts have increased in recent years. We provide a comprehensive summary of natural history findings on the species, including updated research and ongoing conservation efforts.

Introduction

Dermatemys mawii (Gray) (Central American River Turtle or Hicatee) is the only extant species of the Dermatemydidae family (Iverson and Mittermeier 1980) and is one of the 25 most endangered turtle species in the world (Rhodin et al. 2011). It is listed as critically endangered by the International Union for Conservation of Nature (IUCN 2016), listed as endangered under the provisions of the US Endangered Species Act (USFWS 1983), and listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2017). The historical range of *D. mawii* is from southern Mexico, throughout Belize, and into northern Guatemala (Alvarez del Toro 1982, Iverson 1992,Vogt et al. 2011). Because of continued harvesting for meat and egg consumption (Moll 1986; Polisar 1992, 1995), *D. mawii* has been virtually eliminated from wild populations in Mexico and Guatemala, and Belize has dwindling local populations (Campbell 1998, Rainwater et al. 2012). At the current rate of harvest and considering the slow generation time of ~10 years for this species, the IUCN (2016) has predicted that *D. mawii* will have a drastic population decline of 81.5% within 30 years, and the species may well be on the path to eventual extinction (Vogt et al. 2006).

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There has been a need for relevant scientific information on *D. mawii*, and thus in an earlier contribution to this special issue, we gathered and provided a comprehensive list of pertinent literature on the species in a working bibliography (Briggs-Gonzalez et al. 2018). Our purpose here in the species bioprofile is to summarize and update natural history findings, scientific research, and current species conservation. Our goal continues to be increasing scientific research in the region, encouraging regulatory law enforcement, promoting educational awareness and increasing attention on this species, and contributing toward conservation of *D. mawii*. This bioprofile is organized under a traditional template that provides relevant information on species classification, distribution, and ecology.

Classification

Taxonomy

Class Reptilia (reptiles)
Order Testudines (turtles)
Suborder Cryptodira
Superfamily Kinosternoidea
Family Dermatemydidae
Genus *Dermatemys*
Species *Dermatemys mawii*

Dermatemys mawii, commonly called the Central American River Turtle but also known colloquially as the Hicatee (Hickatee) or Tortuga Blanca, is a critically endangered species on the IUCN Red List (IUCN 2016) that is also listed as endangered by US Fish and Wildlife Service (USFWS 1983) and whose biology is not understood in its entirety. The Dermatemydidae is one of the oldest extant families of the Cryptodira suborder (Carr et al. 1981), and fossil remains date back 65 million years to the Cretaceous (Gaffney 1975). However, this family has been reduced to a single extant species, *Dermatemys mawii*, which occurs in southern México, throughout Belize, and eastern Guatemala (Iverson and Mittermeier 1980). *Dermatemys mawii* is closely related to mud and musk turtles of the Kinosternidae family (Carr et al. 1981, Frair 1964, Gaffney 1975, Zug 1966) and represents the most basal clade of the kinosternids (Carr et al. 1981, Zug 1971).

Dermatemys mawii was originally described by J.E. Gray in 1847 based on the holotype at the British Museum of Natural History that had been collected in 1833 by Lieutenant Maw of the British Royal Navy. However, the provenance of this specimen was unknown, and the holotype was later assigned to a specimen collected from Alvarado, Veracruz, México (Smith and Taylor 1950). The genus *Dermatemys* is derived from the unique shell of the turtle and is based on the Greek terms "Derma" for skin and "emys" for turtle. In the first description (Gray 1847), the name "Mawe" was used, although more recent communications with the British Museum of Natural History and Zoological Society of London suggest the spelling was "Maw" (Legler and Vogt 2013). This confusion has led to a variety of species epithets being used: *mawii, mawi, mawei*. Other, past synonyms have included

Dermatemys abnormis (Cope 1868), *Emys berardii* (Dumeril and Dumeril 1851), *Dermatemys mavei* (Cope 1865), and *Dermatemys salvinii* (Gray 1870). According to the IUCN and ITIS (Integrated Taxonomic Information System), *Dermatemys mawii* is the accepted and valid name.

Species description

Dermatemys mawii is a large-bodied freshwater turtle, with a maximum carapace length (CL) of 660 mm and maximum weight (mass) of 22 kg (Lee 1996). Typical CL from adult turtles measured in the field varies from 330 to 450 mm for males and 340 to 480 mm for females, and body mass for both sexes varies from 10 to15 kg (V. Briggs-Gonzalez et al., unpubl. data; Polisar 1995; Rainwater et al. 2012; Rangel-Mendoza et al. 2009). Average CL and body mass of hatchlings vary from 50 to 58 mm and of 18 to 35 g, respectively (Fig. 1; Platt et al. 2019).

Figure 1. Hatchling *Dermatemys mawii* inside adult shell in Northern Belize. Photograph © Sergio Gonzalez.

The name Tortuga Blanca ("white turtle") is derived from the strikingly white or cream plastron that is connected to a smooth, broad carapace uniformly dark brown, gray or olive in color. Overall skin and scute color vary depending on habitat (Polisar 1992, Vogt et al. 2011). The tip of the snout of hatchlings and young turtles is bright orange, fading to yellow by the time they are ~2 y old (Fig. 1). Similarly, hatchlings exhibit a more distinct yellow orbital stripe (Vogt et al. 2011). Mature males develop a typically yellow to yellow-orange head, depending on habitat, and this color can vary among populations (Polisar 1992). Females are usually uniform in color, but they may have a slight yellow tint to the dorsal surface of the head (Vogt et al. 2011).

The hind lobe of the plastral margin is invaginated. A total of 11–12 plastral scutes are separated from 24 marginals (12 on either side) by 3–6 inframarginals. The gular scute(s) may or may not be divided (Vogt et al. 2011). Juveniles possess a keeled carapace, and the plastrons of young turtles tend to be round and then elongate as the turtle grows, presumably to maintain hydrodynamic shape (Morales et al. 2009). Morphometric analysis of plastrons and plastron scutes of turtles in Guatemala provide evidence for morphological differentiation among populations in different river systems (Morales et al. 2009). Labial ridges are strongly serrated, and tooth-like ridges are present on alveolar surfaces of the maxilla (Vogt et al. 2011). Specialized vascular tissue in the pharyngeal lining allows *D. mawii* to extract oxygen from the water and remain submerged for long periods of time (Rhodin et al. 2011).

The toes are webbed with long claws, and the outer margin of each foot is fringed with a series of enlarged scales (Lee 1996). Tails are sexually dimorphic. Males have long, muscular tails that extend well past the hind margin of the carapace and have some prehensile ability (Mendyk and Eisele 2016), whereas females have much smaller tails with reduced musculature.

Genetics

The phylogenetic assignment of the Dermatemydidae family within the Kinosternoidea superfamily is generally accepted (Iverson et al. 2007). *Dermatemys mawii* has a diploid chromosomal number of 56. This arrangement is primitive among turtles, suggesting the species is of a lineage ancestral to most extant species (Carr et al. 1981). There have been 16 distinct mtDNA haplotypes identified across the range of *D. mawii*, falling into 3 major lineages, which appear to have diverged during the Pliocene–Pleistocene (3.73–3.277 MYA). Low fine-scale phylogeographic resolution among these haplotypes suggests demographic fluctuations both historically (since the Pleistocene) and in recent history. There is evidence for recent mixing of genetic populations, likely because of harvest and transplantation by humans (González-Porter et al. 2011, 2013).

Distribution

Native range

Dermatemys is found in lowland freshwater systems of the Yucatán peninsula, spanning México, Guatemala, and Belize (Fig. 2; Lee 1996). In México, the species

is found from Veracruz, eastward throughout Tabasco, northern and central Chiapas, southern and central Campeche and Quintana Roo (Calderón-Mandujano et al. 2017, Vogt et al. 2011). Surveys (Moll 1986, Rainwater et al. 2010a) suggest that *Dermatemys* is found throughout Belize, except for the Maya Mountains in south-central Belize. This range includes the Rio Hondo, Belize's northern border with México, southward to the Macal River. To the south of the Macal River are the Maya Mountains, and *D. mawii* occurs from Golden Stream to Sarstoon River, Belize's southern border with Guatemala (Méndez 2012). Coastally, there is a large gap from Southern Lagoon to Golden Stream with the exception of the Sittee River. An accurate assessment of its range in Guatemala requires more extensive surveys, but *D. mawii* is found throughout the Petén and eastward in northern Huehuetenango, Quiche, Alta Verapaz, and Izabal (García-Anleu et al. 2007, 2010). There is still an unconfirmed presence and no data on the species' status in Honduras (Rhodin et al. 2011, 2017). Within these countries, *D. mawii* is found in 3 main watersheds of Mesoamerica, the Coatzaloalcos, Papaloapan, and the Grijalva-Usumacinta basins (González-Porter et al. 2011).

Figure 2. Distribution of *Dermatemys mawii* in southern México, Belize, and Guatemala.

Range expansion/contraction

Dermatemys mawii is the only extant species of a historically (pre-Pleistocene) abundant family, Dermatemydidae. This remnant species originated from a North American radiation into Central America and is now restricted to parts of the Yucatán Peninsula (Carr et al. 1981). Genetic analysis indicates populations may have diverged along major hydrological basins during the Pliocene–Pleistocene and have undergone large demographic fluctuations since. Human activities related to harvest and translocation appear to have increased population mixing since bottlenecking (González-Porter et al. 2011).

Humans have been consuming *D. mawii* meat for at least 7000 years, and it is believed that the early Maya translocated turtles, contributing to the evidenced population mixing (Vogt et al. 2011). However, the role of humans in historical bottlenecks is unclear, beyond evidence of relatively recent overharvesting that has resulted in the extirpation of *D. mawii* from much of its range. Early accounts from the 20th century suggest the species was abundant throughout its current range (Moll 1986), and recent surveys in Quintana Roo slightly expand the species' distribution to the north (Calderón-Mandujano et al. 2017). Surveys in Belize indicate this country remains a stronghold for *D. mawii*, but with ongoing harvesting, populations continue to decline (Rainwater et al. 2012). It is estimated that over 4000 turtles exist in the Maya Biosphere Reserve in Guatemala, believed to be home to the country's largest remaining population (García-Anleu et al. 2007).

Relative abundance

Fair comparisons of abundance and densities between surveys must take into account time of year (particularly wet or dry season). Individual *D. mawii* disperse during periods of high water in the wet season when connectivity between bodies of water is maximized. Conversely, during the dry season populations are concentrated in deepwater refugia in large lagoons and major rivers. Recognized as a critically endangered species, *D. mawii* is almost extirpated in México (Vogt and Flores-Villela 1992a). Few data are available regarding the species' abundance relative to other turtle species in the Yucatán. Anecdotal reports from local fishermen and turtle harvesters in the state of Veracruz report that *D. mawii* is exceedingly rare and difficult to capture compared to other species (Morales and Suarez 2010). However, surveys in 2009 and 2010 in southern Quintana Roo report an average of 1.74 turtles/net for areas sampled in the Rio Hondo (Calderón-Mandujano et al. 2017).

El Peru Lagoon in La Selva Maya Reserve is identified as currently maintaining the densest population of *D. mawii* in Guatemala. In 2008, the density of *D. mawii* in El Peru was estimated at 8.42 turtles/ha (García-Anleu et al. 2007). The San Pedro and San Juan rivers, which connect to the lagoon in the wet season, are identified as important features supporting this population. Other densities reported for *D. mawii* in the Selva Maya include 0.10 turtles/ha in Sacnab Lagoon, 0.26 turtles/ha in the SalPetén Lagoon, and 0.02 turtles/ha in the San Pedro River (García-Anleu et al. 2007).

In Belize, the densities of *D. mawii* populations appear to be greater in northern parts of the country. The species occurs in very low abundance from Dangriga to Punta Gorda in southern Belize, possibly because most rivers in this part of the country are shallow and fast moving. Moll (1986) reported a mean density of 2 turtles/ha at 22 sites surveyed in Belize during the early 1980s, and the New River Lagoon in northern Belize exhibited the highest density of *Dermatemys* (8.7 turtles/ha). Records from the 1940s indicate the *D. mawii* population in Belize was much larger at that time, including in areas where later surveys detected few or no turtles (Moll 1986, Waight 1983). Population densities have also consistently been reported as negatively correlated with proximity to human populations (Collins 1999, Garel 1998, Moll 1986, Rainwater et al. 2012). A country-wide survey in 2010 suggested *D. mawii* populations have continued to decline since the 1980s despite legislative protections (Rainwater et al. 2012). In some localities, small populations of *D. mawii* are locally abundant, but these are in areas further removed from human activity (Rainwater et al. 2012).

Habitat

Dermatemys mawii is a completely aquatic, freshwater species that is known to inhabit deep rivers, oxbows lakes, and lagoons throughout the year, expanding into seasonal floodplains and forests when waters rise (Moll 1986, Vogt et al. 2011). Most rivers and lagoons that *D. mawii* inhabit are very slow moving and well oxygenated (Rhodin et al. 2011), although these turtles have been occasionally observed in faster-moving rivers as well as in tidally influenced areas (Moll 1986, Rainwater et al. 2012). *Dermatemys mawii* are capable of tolerating brackish water and have been collected from Corozal Bay in Belize; some animals have been found with barnacles attached to their carapace (Neill and Allen 1959). Water in these habitats is typically dark brown, likely from tannins and organic substrates, but the species is also known from a few clear-water locations in México and Belize (Polisar 1992, Rainwater et al. 2012, Vogt and Flores-Villela 1992a). Within the Maya Biosphere Reserve, *D. mawii* were found at higher densities in lagoons than in main river channels (García-Anleu et al. 2008). Associated terrestrial habitats along waterways can include pine savannahs, broadleaf forests, and mangrove swamps. *Dermatemys mawii* can be associated with waterways that have surface vegetation, vegetation beds, or open water with little to no vegetation. The species has been observed to use habitat dominated by *Terminalia buceras* (L.) C. Wright (Gregorywood) and *Pachira aquatica* Aubl. (Guiana-chestnut) (García-Anleu et al. 2010) as well as overhanging *Ficus* spp., including *F. glabrata* Kunth (= *F. insipida* Willd.; Méndez 2012). In many studies, *Paspalum paniculatum* L. (Arrocillo) is a large component of their diet, and many individuals have been observed feeding on patches of *Paspalum* at night (Moll 1989). Within the New River Lagoon in northern Belize, *D. mawii* are often found in areas with patches of *Nymphaea ampla* (Salisb.) DC. (White Water Lily or Dotleaf Waterlily), and visible bite marks from turtles are frequently observed in the floating leaves (V. Briggs-Gonzalez, pers. observ.).

Adult and sub-adult *D. mawii* spend much of their time during the day resting on the bottom of water bodies, under fallen branches in the deeper portions of these habitats, partially buried in the sand and leaf-littered substrate (Vogt et al. 2011). They occupy that habitat more commonly in the dry season, when turtles may be confined to deeper pools until the water levels rise. As juveniles, *D. mawii* commonly occur in water among vegetation along the banks of rivers and lagoons, while adults are found in deeper water (>2.5 m and often >6 m) (Vogt et al. 2011). In a study of *D. mawii* in 2 waterways in México, turtle body temperatures were 23.5–32.0 °C, which correlated with corresponding water temperatures (Legler and Vogt 2013). This finding illustrates adaptations by *Dermatemys* for maintaining metabolism at cooler temperatures relative to other tropical species (Vogt et al. 2011).

Ecology

Reproduction

In México, female *D. mawii* mature at 395–420 mm carapace length (CL) and males at 365–385 mm CL (Vogt et al. 2011). In Belize, 70% of females mature at a CL of 400 mm in rivers and at 410–420 mm in lagoons, while 70% of males mature at a CL of 370 mm in rivers and at 380–390 mm in lagoons (Polisar 1992, Rhodin et al. 2011, Vogt et al. 2011). The largest river female captured and measured was <460 mm CL (406–451 mm CL, n = 12) and the largest lagoon female captured measured >480 mm CL (399–483 mm CL, n = 8) (Polisar 1992, Vogt et al. 2011). Individuals that live in slow-moving creeks and lagoons attain sexual maturity at larger sizes and exhibit larger maximum sizes than those in faster-moving rivers. Factors influencing size differences in mature females between lagoon and river habitats are unclear but may be related to nutrition, temperature, or energetic constraints of living in fast- or slow-flowing waters (Polisar 1995, Vogt et al. 2011).

The mating season of *D. mawii* begins in March and April and primarily occurs from May to September (Polisar 1992, 1996), though very few observations of mating have been observed in the wild. It is likely that most mating occurs during the dry season, when water levels are at their lowest and individuals are congregated. At the Nacajuca facility in Mexico, mass copulation occurred on 7 July 2002, and copulating pairs were found floating on the surface of the water the following morning (Vogt et al. 2011).

Most data on the reproductive cycle of *D. mawii* is based on examination of harvested animals from markets in Belize (Polisar 1992, 1996). Nesting occurs between September and December at the height of the rainy season (Polisar 1995, Vogt et al. 2011), and during a secondary nesting period in the early dry season (January through February; Vogt et al. 2011). In captivity at the Hicatee Conservation and Research Center (HCRC), Belize, nesting occurs from November through February (BFREE 2018) and as late as April with a single clutch laid in September likely from a female that double-clutched that year (J. Marlin, HCRC, Punta Gorda, Belize, pers. comm.). There have also been accounts of nesting in the wild during March and April (Lee 1969, Moll 1986).

Female *D. mawii* deposit eggs in moist soil along the shoreline to within 3 m of water in riparian forests and savannas, and nests are often inundated during the rainy season (Vogt et al. 2011). Eggs are large, hard-shelled and laid in solitary nests (Polisar 1995), though a nesting beach containing multiple clutches has been located post-hatching (F.J. Mazzotti, pers. observ.). Eggs are resilient and can withstand submersion in water for more than 30 days (Polisar 1996, Polisar and Horwich 1994), suggesting a complex embryonic diapause (Vogt et al. 2011). Development resumes after water levels recede and the nest is no longer saturated. Hatching is stimulated as moisture in the nest increases, usually with the summer rains in June and July (Polisar 1992, 1995), and hatching has occurred in the first week of June in captivity in Belize (BFREE 2018).

Fecundity in *D. mawii* has been shown to vary by region. In Belize, clutch size varied from 2 to 20 eggs with a mean clutch size of 10.98 eggs (Polisar 1995). Average clutch frequency was 2.05 per year in Belize, but a single female laid 4 clutches in one year. Total reproductive output varied from 0 to 47 eggs per year by females in Belize (Polisar 1995) and reproductive output increased with body size in early breeding, and large, older females (Polisar 1992, 1996). Of 44 oviductal and freshly laid eggs in Belize, egg morphometrics were as follows: length = 54–72 mm, width = 36–50 mm, and mass = 34–70 g (Polisar 1992, 1996). In México, clutch size varied from 10 to 24 eggs (mean = 14.8), and females laid on average 2.6 clutches per year (Vogt et al. 2011). R.C. Vogt (Universidad Nacional Autónoma de México, Ciudad de México, México, unpubl. data) also found that up to 4 clutches were laid per year in Chiapas, México. Of 121 eggs measured in México, egg morphometrics were as follows: length = 56–67 mm, width = 32–41 mm, and mass = 37–72 g (Vogt et al. 2011).

Dermatemys mawii exhibits temperature-dependent sex-determination (Vogt and Flores-Villela 1992b), and published accounts of incubation vary from 115 to 300 days (Polisar 1992, Rhodin et al. 2011, Vogt and Flores-Villela 1992b), depending on temperature. In the laboratory, ambient incubation temperatures above 28 ºC produced females and temperatures 25–26 ºC produced males; when incubated at 28 ºC, both sexes were produced (Vogt and Flores-Villela 1992b). Over-wintering temperatures during November and December in Belize can drop to 20–22 ºC when most nests are underwater, but development is most favorable during dry months of March and May at >25 ºC (Polisar 1995, Vogt et al. 2011).

Mean hatchling size is 31 g and 54 mm carapace length (Polisar 1995), and in captivity (at HCRC) mean hatchling mass was 29.1 g and a carapace length of 50.2 mm (Platt et al. 2019). Hatchlings have a bright orange snout tip, which fades to yellow over the first 2 years of life (Fig. 1). Individuals less than 35 mm CL are considered juveniles (Moll 1989). Growth is dependent on food availability and habitat conditions; growth is most rapid during the wet season when food is abundant, (Moll 1989, Vogt et al. 2011). Subadults can gain significant mass in 1 year (BFREE 2015). Wild turtles in Guatemala showed a greater mass/length ratio and also exhibited a gain in mass that was twice that of turtles reared in captivity per 2 cm growth in length (Alvarez et al. 2009). With growth, scutes are shed in the dry

season (April to May). Scutes fuse in older animals, and sheds may resemble an intact shell (Vogt et al. 2011).

Diet

Dermatemys mawii is almost completely herbivorous, with the aquatic grass *Paspalum paniculatum* making up the majority of diets of both adults and juveniles (Alvarez del Toro 1972, 1982; Alvarez del Toro et al. 1979; Lee 1969; Moll 1989). Large numbers of adults and juveniles converge on mats of *P. paniculatum* to feed at night and appear to be absent from these feeding sites during the day (Moll 1989). However, these feeding groups are seldom observed now in Belize (T.R. Rainwater, pers. obervs.). In northern Belize, *Nymphaea ampla* mats are a staple food item, and bite marks can be seen on the floating leaves on mornings after feeding (V. Briggs-Gonzalez, pers. observ.). The remainder of the diet is composed of various other leaves and twigs, flowers, and fruits, such as mangoes and figs that fall into rivers; insects are also ingested incidentally when turtles feed on vegetation (Moll 1989). In estuarine environments, *Dermatemys* will eat mangrove leaves and floating vegetation (Moll 1989, Polisar 1992).

Digestion of plant material is aided by naturally occurring foregut flora and fauna. This gut microbiota is believed to contribute to the ability of *D. mawii* to digest material at lower temperatures than other turtles, thus eliminating the need for basking time (Vogt et al. 2011). Hatchlings inoculated by feeding on adult feces for the first few days immediately after hatching grew 30% faster than clutch-mates that were isolated from adults but fed the same diet (Vogt et al. 2011).

Captive adult *D. mawii* are reported to occasionally accept fish, and small captive turtles are reported to readily eat raw meat and fish (Alvarez del Toro 1972, Alvarez del Toro et al. 1979, Lee 1969, Murphy and Collins 1983). Captive facilities in Chiapas, Mexico, feed *D. mawii* on *Nasturtium officinale* W.T. Aiton (Berro or Watercress), *Curcubita* spp. (calabacita or pumpkin), *Psidium guajava* L. (Guayaba or guava), *Malus* spp. (manzana or apple), and wild plants such as *Brosimum alicastrum* Sw. (Breadfruit), *Guazuma ulmifolia* Lam. (Bay Cedar), and *Moringa oleifera* Lam. (Moringa) (L. Sigler, The Dallas World Aquarium, Dallas, TX, USA, pers. comm.; M. Alvarez del Toro, Miguel Alvarez del Toro Zoo, Chiapas, Mexico, pers. comm.). More recently, zoological facilities in the United States have fed *D. mawii* diets including *Morus* spp. (mulberry leaves), *Solanum lycopersicum* L. (Tomato) fruits, *Lactuca sativa* L. (Lettuce), fish (*Mallotus villosus* (Müller) [Capelin] and smelt [Osmeridae]),and turtle brittle pellets (Nasco, Fort Arkinson, WI), and turtles have been observed feeding on algae within exhibits (J. Bell, Philadelphia Zoo, Philadelphia, PA, USA, pers comm.; R. Mendyk, (Jacksonville Zoo and Gardens, Jacksonville, FL, USA, pers comm.).

Seasonal activity pattern

As the rainy season begins, *D. mawii* disperses into larger rivers and water bodies, as well as flooded forests (García-Anleu et al. 2010, Legler and Vogt 2013), most of which are dry or inaccessible during the dry season. Little is known about long-term movements of *D. mawii* because of this long-distance dispersal. During

the dry season, turtles congregate in the deepest portions of the remaining water bodies. This movement and subsequent congregation during the dry season contribute to the success of *D. mawii* harvest by humans. Hunters comment that large numbers of *D. mawii* are harvested each year, but that the turtles recolonize the same areas during the wet season (Rainwater et al. 2012). This observation appears consistent with wet-season dispersal patterns and the notion that continued harvests each year would not be possible without high levels of immigration from less-exploited waters during the wet season (Rainwater et al. 2012).

Behavior and habits

Daily activity is based largely upon seasonal water levels and food availability. *Dermatemys mawii* is nocturnal and infrequently observed at the water's surface during the day, primarily because the species takes refuge during this time and does not bask. Adults spend most of the day resting on the bottom of ponds, lagoons, rivers, and other waterways, partially buried in sand, leaf litter, or under fallen logs, whereas.jJuveniles have been observed seeking refuge under vegetation at the water's edge (Vogt et al. 2011). Higher activity at night was corroborated by sonar surveys (Davy and Fenton 2013) and through visual surveys along with net surveys (T.R. Rainwater, pers. observ.; V. Briggs-Gonzalez et al., unpubl. data).

Dermatemys mawii have various adaptations to being almost completely aquatic, including the use of buccopharyngeal mucosa to extract oxygen from the water (Winokur 1988). Turtles at the Jacksonville Zoo (USA) have been observed using their tails in a prehensile manner (Mendyk and Eisele 2016). This ability may be used for grasping onto limbs or other structures in bodies of water, in addition to reproductive purposes (Mendyk and Eisele 2016). The terrestrial movements of *D. mawii* are quite arduous, and it is unlikely that turtles can traverse long distances on land (Holman 1964). *Dermatemys mawii* likely leaves the water only for oviposition.

Few studies have been conducted on the daily movement patterns of *D. mawii*, especially throughout the dry and rainy seasons. In Guatemala, one study showed minimal movement during the dry season; turtles remained in the deepest areas of the drying pools, and many turtles were concentrated in the same areas (García-Anleu et al. 2010). When the rainy season begins, movements increase drastically, likely in response to food availability. There have been some documented movements based on tidal changes; in estuarine environments, *D. mawii* will feed on floating vegetation carried in at high tide, regardless of the time of day (Moll 1989). The presence of both *Paspalum* and mangrove leaves in the gut contents of coastal specimens suggests a potential daily migration of up to 4 km (Moll 1989). In México, most turtles that were tracked for 8 months moved a maximum of 1–2 km and preferred areas with higher food availability; turtles with less food availability moved >2 km and were lost from the study (Legler and Vogt 2013).

Predators, parasites, and disease

Dermatemys mawii have predators at all life stages, but predation occurs primarily early in life. Eggs are consumed by *Nasua nasua* (L.) (Coatimundi), *Procyon lotor* (L.) (Raccoon), *Aramides cajanea* (Statius Muller) (Gray-necked Wood Rail),

Rallus longirostris Boddaert (Clapper Rail), *Aramus guarauna* (L.) (Limpkin), *Butorides virescens* (L.) (Green Heron), *Nycticorax nycticorax* (L.) (Black-crowned Night Heron), and *Nyctanassa. violacea* (L.) (Yellow-crowned Night Heron) (Moll 1986). *Dermatemys mawii* are highly vulnerable after hatching, and young and intermediate-sized individuals are preyed upon by *Crocodylus moreletii* Duméril and Bibron (Morelet's Crocodile) and *C. acutus* Cuvier (American Crocodile) (Moll 1986, Smith and Smith 1980) and *Solenopsis invicta* Buren (Red Imported Fire Ant; F.J. Mazzotti, pers. observ.). Juveniles and subadults have been observed being consumed by *Lontra longicauda* (Olfers) (Neotropical Otter; García-Anleu et al. 2010, Platt and Rainwater 2011). Humans are the largest sources of predation of adult *D. mawii*, often harvesting gravid females in the spring months in large numbers (Moll 1986; Polisar 1990; Rainwater et al. 2010a, 2010b; Vogt et al. 2011).

Dermatemys is frequently parasitized by leeches (Hirudinea), sometimes in high numbers, without apparent significant health effects (Rangel-Mendoza et al. 2009). All wild turtles sampled in the Tabasquillo River, México, were parasitized by intracellular hemoparasites (*Haemogregarina* sp.), and parasite loads were higher in turtles sampled during the wet season than the dry season (Rangel-Mendoza et al. 2009). These are common hemoparasites in reptiles and are generally considered non-pathogenic, barring other concomitant infection. Rangel-Mendoza et al. (2009) found wild populations in better health than the captive population they examined, despite finding hemoparasites in 100% of wild samples and none in samples from captivity.

Threats

Dermatemys mawii continues to hold cultural significance throughout its range and played an iconic role in the ethno-herpetological depictions and diet of pre-Classic Maya populations in the Yucatan peninsula. Intact turtle shells and pottery with smooth-shelled turtle carvings thought to be representing Hicatee have been recovered from burial sites at Lamanai and Altun Ha Archaeological Reserves, Belize (M. Aguilar, Lamanai Archaeological Reserve, Indian Church, Belize, pers. comm).

Dermatemys mawii has been harvested for meat and eggs for human consumption throughout its range and has been over-hunted in México and Guatemala (Campbell 1998, Moll 1986, Polisar 1994; 1995, Rainwater et al. 2012). Additionally, older generations of fisherfolk and villagers in Belize speak of eating Hicatee much more often in the early 1900s (T. Garel, Belize Vivarium, Belmopan, Belize, pers. comm.). Harvest of *D. mawii* occurs primarily during the spring months coinciding with Lent and Easter, when the turtle is a prized dish and is served along the Belize River Valley during the La Ruta Maya canoe race, though recent enforcement in the past 3 years has prohibited the sale of live Hicatee or Hicatee meat (R. Quintanilla, Belize Fisheries Department, Belize City, Belize, pers. comm.). Harvest for sale in local and city markets, though now illegal, has been historically very high and lucrative (Holman 1964, Moll 1986, Polisar 1995).

Egg-laying females are targeted by hunters because eggs yield an additional high price as an added delicacy. In declining populations, gravid females are the greatest demographic loss. At a very conservative generation time of 10 years and

a below-average estimated annual harvest of 5%, *Dermatemys mawii* populations would decline by 81.5% in 30 years (IUCN 2016), but with continued high levels of exploitation, populations are expected to become extinct (Vogt et al. 2006). Even the earliest researchers on wild *D. mawii* appeared to recognize the need for protection from commercial harvest (Holman 1964). Three methods of take—harpooning, the use of nets, and free-diving—are common throughout the turtle's range. Harpooning is the primary method used for personal consumption, while free-diving is the most thorough and effective when visibility is good, usually in the dry season (Polisar 1995). Nets have become more widespread in use, particularly for commercial hunting when more than 30 individuals can be illegally harvested in 1 night at a given site (R. Quintana, Belize Forestry Department, Belize city, Belize, pers. comm.). Legislation is now in place in the tri-country region to address overhunting and conservation of *D. mawii* (see Conservation and Management section below).

Illegal logging and slash and burn practices are responsible for much of the habitat loss of *D. mawii* throughout Guatemala (García-Anleu et al. 2007, 2010), particularly in the loss of terrestrial habitat for nesting. In Belize, primary threats are related to sand excavation/mining in rivers, which when coupled with run-off from deforested areas result in siltation and sedimentation of river bottoms. In the Sibun River, Belize, Rainwater et al. (2010a; 2012) noted sand-covered river bottoms (which were previously productive areas for *D. mawii* with abundant leaf-litter and detritus circa 1998; T. Garel, pers. comm.), yielded no turtles during the survey. Since these turtles are almost completely aquatic, it is important to maintain connectivity among aquatic systems to ensure genetic diversity throughout the species range.

Pollution of waterways from agricultural run-off is a threat to the health of *D. mawii*. Harmful algal blooms and mass fish-die-offs have occurred in the northern Belize watershed and have the potential to negatively affect *Dermatemys* survival (R. Quintana, pers. comm.) as has been observed in *Chrysemys picta* (Schneider) (Painted Turtle) in freshwater habitats of the southeastern US (Mercurio et al. 2014), in *Pelodiscus sinensis* (Wiegmann) (Chinese Softshell Turtle) and other aquatic wildlife within Lake Taihu in China (Chen et al. 2009), and in both marine and freshwater environments affecting herbivorous *Chelonia mydas* (L.) (Green Sea Turtle) and *Trichechus manatus latirostris* (Harlan) (Florida Manatee) in Florida (Capper et al. 2013).

Conservation and Management

Dermatemys mawii is a high priority species in the IUCN Species Survival Commission Action Plan for the Conservation of Tortoises and Turtles (IUCN 2016) and garners interest based on its relatively low population numbers in the wild and continued overharvesting rates. In México, *D. mawii* has been legally protected since 1927 and was included in the Mexican Red Data List (NOM-059-ECOL 1994) as endangered, making all forms of harvest and exploitation illegal. However, enforcement is not strict, and few adhere to regulations (Vogt et al. 2006). The Rio Hondo area has recently been considered a priority site for the

conservation of *D. mawii* (Calderón-Mandujano 2008, Calderón-Mandujano et al. 2017). In Guatemala, *D. mawii* is on the Endangered Species List and has protected status (Campbell 1998), but similar to Mexico, law enforcement is difficult to non-existent and turtles continue to be harvested.

In Belize, protection of *D. mawii* was instituted in 1993 following recommendations of Polisar (1992). Legislation included year-round possession limits, a brief non-hunting season (1–31 May), protected zones in northern Belize, and a prohibition on buying and selling *D. mawii* (Vogt et al. 2006). In 2011, upon the recommendations of the National Hicatee Conservation and Monitoring Network (formed in 2010; Briggs-Gonzalez et al. 2018), legislation was revised and included a closed season from May 1st to 31st as well as a reduced harvest limit of 3 turtles per person or 5 per vehicle, catch size limits of females no greater than 43 cm and no less than 38 cm, and the prohibition to sell or purchase *D. mawii* (Government of Belize, Regulation 14:02, Fisheries Amendment No. 2, Chapter 210, July 2011). Nets were also prohibited for use in hunting, and *D. mawii* captures have been prohibited in a list of specified areas that include parts of the Belize River, New River, Sibun River, Rio Bravo, Cox and Mucklehany Lagoons, headwaters of Mussel Creek, and Northern and Southern Lagoons and tributaries (Government of Belize, Fifth Schedule Regulation 12:02[e]). Poaching and commercial exploitation are still major threats in Belize, but with increased enforcement and greater local involvement, conservation efforts have improved in the country relative to Mexico and Guatemala. However, despite these efforts, *D. mawii* harvest rates may remain unaffected (Rainwater et al. 2012).

Conservation efforts geared toward captive breeding have been ongoing since the 1980s in Nacajuca, Tabasco, México, and are supported by state and national wildlife resource funds. The facility houses a large breeding colony of *D. mawii* (up to 880 individuals; Vogt et al. 2006, 2011), but turtles appeared to be in poor physical condition compared to wild specimens, likely due to overcrowding, inadequate nutrition, and poor water quality (Rangel-Mendoza and Weber 2015, Rangel-Mendoza et al. 2014). Another breeding facility in La Florida, Veracruz, México, contains 45 individuals (Vogt et al. 2006). Across facilities in Mexico, colony size varies widely (10 females and 1 male in Las Lagunas; 450 females and 120 males in Nacajuca [reduced from 880], with 30 females, 8 males, 25 juveniles in Tabasquillo; 15 females, 7 males, 90 juveniles in Cicea; 67 females, 15 males in La Encantada; 14 females, 6 males, 95 juveniles in Guayacanes; 103 females, 50 males in Arca de Noe; and 20 females, 5 males, 35 juveniles in Hidalgo y Tamarindo) for a total of 1166 *D. mawii* housed across Mexico (2018 pers. comm. to R.C. Vogt from C. Zenteno Ruiz, Universidad Juárez Autónoma de Tabasco, Tabasco, Mexico).

In southern Belize, the Hicatee Conservation and Research Center houses 45 individuals (28 females and 17 males; BFREE 2016, 2018) and has had successful breeding in the last 2 years with 258 neonates hatched between June 2015 and July 2018 (BFREE 2018, Platt et al. 2019). Within zoological facilities in the United States, there are only 5 individual *D. mawii*, of which 3 are at Jacksonville Zoo and 2 at Oklahoma City Zoo. None of these turtles have produced offspring (Smith 2015, Mendyk and Smith 2016).

Over the past decade, *D. mawii* research has been underway throughout the tri-country region examining population structure (in Petén, Guatemala; Barahona and Lopez 2015) as well as population status and spatial ecology in Guatemala (García-Anleu et al. 2007, 2010; Juarez et al. 2009; Morales 2009) México (Calderón-Mandujano 2008; Calderón-Mandujano et al. 2017; Guichard Romero 2006; Ruiz et al. 2010; Solis et al. 2010; Zenteno 2007, 2011; Zenteno et al. 2010) and Belize (V. Briggs-Gonzalez et al., unpubl. data; Requeña et al. 2015; Rainwater et al. 2010a, 2012). Studies on population genetics have also provided information on the genetic diversity of *D. mawii* and illustrate patterns of movement or translocation via trade in the region (González-Porter et al. 2011, 2013; Syed et al. 2007).

Increased conservation efforts through action plans and management strategies for *D. mawii* in the tri-country region are at various stages of development and implementation in specific locales (CONABIO 2009, CONAP 2006, Government of Belize 2011). Public awareness campaigns in Belize, including billboards, radio and television advertisements, pamphlets, and school programs emphasizing the threatened status of *D. mawii* have met with some success (McLoughlin 2013). Current monitoring and population surveys in northern Belize (Lamanai Field Research Center), southern Belize (Toledo Institute for Development and the Environment), and in Chiapas, México (R.C. Vogt., unpubl. data) continue to provide estimates of wild populations. However, thorough and comprehensive population assessments across the range of *D. mawii* are still needed (Rainwater et al. 2012), as are basic demographic and reproductive data. *Dermatemys mawii* is the most critically endangered freshwater turtle in Central America and will likely become extinct if human consumption continues to deplete wild populations. A combination of legislation, enforcement, research, captive breeding, and public awareness are necessary for the survival of this unique species.

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